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FORAGING ECOLOGY OF MOUNTAIN LIONS IN THE

SIERRA NATIONAL FOREST, CALIFORNIA

by

Bradley C. Nichols

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Foraging Ecology of Mountain Lions in the Sierra National Forest, California

by

Bradley C. Nichols, Master of Science

Utah State University, 2017

Major Professor: Eric M. Gese
Department: Wildland Resources

Studies of predator-prey and predator-predator interactions are needed to provide information for decision-making processes in land management agencies. Mountain lions (*Puma concolor*) are opportunistic carnivores that prey on a wide variety of species. In the Sierra National Forest, CA, they have not been studied since 1987 and their current interactions with their prey and other predators are unknown. Forest managers in this region are concerned with declines of fishers (*Pekania pennanti*) and studies have shown intraguild predation to be a leading cause of fisher mortality in this area. Managers are interested in learning more about mountain lion predation patterns with regard to prey preference, but also how lions traverse and use the landscape and how anthropogenic activities may be increasing lion predation risk on fishers.

Using GPS radio-collar technology, we examined mountain lion kill rates and prey composition at 250 kill sites. We found mule deer (*Odocoileus hemionus*) to be their main source of prey (81%) with gray foxes (*Urocyon cinereoargenteus*) comprising 13.2% of prey composition. We did not detect any fisher predation during our 2-year

study; however, during our study, the Kings River Fisher Project experienced extremely low juvenile fisher survival.

To gain a better understanding of seasonal resource selection by mountain lions, we developed resource selection functions (RSF) while they were moving through the landscape and when killing prey. We developed RSF models for all data across the study area, as well as, for a subset of data encompassing an area where LiDAR (Light Detection and Ranging) data had been collected. Within the LiDAR study area, we digitized unmapped roads and skid trails using a Bare Earth data set. We found mountain lion 'moving' locations showed selection for close proximity to streams during summer months and selection for ruggedness and steeper slopes during both summer and winter. With 3 of the 4 RSF models at kill sites showing high risk of predation within close proximity to either digitized roads/skid trails or mapped roads, we recommend managers map all anthropogenically created linear landscape features and consider restoring these linear features to pre-treatment landscape conditions following timber harvest.

(125 pages)

PUBLIC ABSTRACT

Foraging Ecology of Mountain Lions in the Sierra National Forest, California

Bradley C. Nichols

We conducted this research to gain insight into mountain lion (*Puma concolor*) prey composition in the Sierra National Forest of California. Managers in the region are concerned with both causes of declines and inability to increase fisher (*Pekania pennanti*) populations. Research has shown that mountain lions are a threat to fishers due to direct predation of this forest specialist. We radio-collared 5 adult mountain lions in order to determine prey composition and kill rates. As expected, mountain lions selected primarily for mule deer (*Odocoileus hemionus*). However we did detect other prey such as gray foxes (*Urocyon cinereoargenteus*), coyotes (*Canis latrans*), one black bear (*Ursus americana*), one ringtail (*Bassariscus astutus*), and several squirrels.

Mountain lions are elusive, apex predators that rely on dense cover for stalking, ambushing, and caching prey. Our interest was to gain an understanding of landscape attributes selected for by mountain lions within the full study area and a subset of the study area where LiDAR (Light Detection and Ranging) data had been collected at both point clusters where we detected prey remains, as well as, non-cluster (moving) locations. We were interested in landscape attributes not only where lions successfully made a kill, but also where they were moving through the landscape. Based on kill sites where we detected evidence of a carcass drag (>95% were <50 m in length), we created zones of predation risk within the full study area and the LiDAR study area. We used the same

50m buffer around moving locations as well. We then developed resource selection function models for locations during two behavioral states: moving and killing, for winter and summer months. We found that zones of predation risk were mainly characterized by close proximity to mapped roads in the full study area and digitized roads and skid trails within the LiDAR study area. Moving locations were mainly associated with terrain variables such as ruggedness and slope along with close proximity to streams during summer months. Since we lack LiDAR data for most of the study area, we can assume that there is a high density of unmapped roads and skid trails. We recommend managers map any linear feature that has been anthropogenically created for future management actions. With respect to fisher populations, we recommend replanting skid trails and roads that increase habitat fragmentation which further puts fishers at risk of predation by mountain lions.

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Finally, I would like to thank my family and friends, especially my Dad, Mom, and my best friend 'Chaddog' who have always supported me through this wildlife journey that I set out on nearly 18 years ago when I began my journey putting wristbands on people at the Grizzly & Wolf Discovery Center in West Yellowstone, MT.

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CHAPTER 1

INTRODUCTION

Predators are essential components of ecosystems due to their ability to regulate

food webs (Terborgh and Estes 2010) and their capacity to shift amongst prey species in

response to prey abundance, an important mechanism in maintaining ecosystem stability

(McCann and Rooney 2005, Holt and Barfield 2009, Terborgh and Estes 2010). The loss

of apex predators can affect trophic cascades (Paine 1980) resulting in decreased levels of

biodiversity and can indirectly affect vegetation communities (Terborgh and Estes 2010).

Therefore, large carnivores are often considered indicators of ecosystem integrity

(Eisenberg 1980, Noss 1995, Noss et al. 1996).

Since many landscapes containing large carnivores have been modified by human

activities, the continued presence of large carnivores on the landscape may indicate a

relatively unbroken food web that has maintained a high potential for ecological integrity

(Noss et al. 1996). In North America, the distribution of apex predators like mountain

lions (*Puma concolor*) have been drastically reduced due to human exploitation (Young

and Goldman 1946, Nowak 1974, Sweanor et al. 2000). While the current worldwide

distribution of mountain lions remains one of the largest of any terrestrial mammal, its

overall geographic range has been reduced by >50% (Young and Goldman 1946, Nowak

1974, Logan and Sweanor 2000, Reith 2010). Since mammalian carnivores such as

mountain lions, occupy large home ranges, are low density, and are predisposed to

persecution by humans, they are thought to be particularly susceptible to local extinction

in fragmented landscapes (Noss et al. 1996, Woodroffe and Ginsberg 1998, Crooks 2002).

In the Sierra National Forest in central California, the mountain lion population has not been studied for several decades (Neal et al. 1987). Mountain lion habitat varies widely and is generally a function of prey abundance and ambush cover provided by various vegetation types and topography (Seidensticker et al. 1973, Reith 2010). Lions frequently use edges and ecotones (Belden et al. 1988, Laing 1988, Williams et al. 1995, Holmes and Laundre 2006) which provide stalking cover to approach prey at close range. Laundre and Hernandez (2003) found 72% of kills by lions in their study area were along edges compared to open patches or in forested areas. Mountain lion predation on ungulates is a function of landscape attributes (Husseman et al. 2003, Laundre and Hernandez 2003, Blake and Gese 2016) with dense vegetation providing low visibility for prey species and/or rugged topography providing increased ambush hunting opportunities (Blake and Gese 2016).

Within the Sierra National Forest, the Pacific fisher (*Pekania pennanti*) has become a species of increasing concern due to its isolation from other fisher populations. Ongoing research initiated in 2007 by the U.S. Forest Service Pacific Southwest Research Station prompted the U.S. Fish and Wildlife Service to propose listing the west coast population of fishers as threatened under the Endangered Species Act. The regional fisher population is highly fragmented and has been unable to expand despite decades of protection (Zielinski et al. 2006, Spencer et al. 2008). Zielinski et al. (2005) suggested that forest specialists (i.e., fishers and American martens, *Martes americana*)

distributions have changed more than forest generalists (e.g., mountain lions) due to the combination of loss of mature forest habitat, latent effects of commercial trapping, and increased residential development. Both mountain lions and fishers are native carnivores to the Sierra National Forest in California. Recent research has shown the fisher is often subject to predation by mountain lions (Sweitzer et al. 2015, 2016). Currently, intraguild predation upon fishers is poorly understood, but could have population-level effects, particularly within this sensitive western population of fishers (Wengert et al. 2014, Sweitzer et al. 2016).

During the 9 years of the Kings River Fisher Project (KRFP), researchers documented predation as the leading cause of fisher mortality (Gabriel et al. 2015). Moreover, in the southern portion of the research study near Shaver Lake, California, mountain lions have been the main predator of fishers accounting for 36% of all mortality causes and 50% of mortalities due to predation with bobcats (*Lynx rufus*) being the secondary predator (Craig Thompson, personal communication). Other documented causes of fisher mortality within the KRFP study area are rodenticide toxicosis from illegal marijuana grows, disease (mainly canine distemper), and vehicle strikes; however, the combination of all other mortality caused do not equal the amount of mortality caused by predation (Sweitzer et al. 2015). In California, mule deer (*Odocoileous hemionus*) comprise the largest percentage of mountain lion diets (Allen et al. 2015, Villepique et al. 2011, Smith et al. 2016). However, known lion depredation events of fishers in the study area, as well as research documenting mountain lions to be opportunistic hunters preying on a variety of species (Smith et al. 2016), prompted the need to gain insight into

the foraging patterns and resource selection of mountain lions in the Kings River study area. With regards to predation patterns, we were particularly interested in determining kill rate intervals, prey composition, and time spent at kills. Because black bears (*Ursus americanus*) are very numerous on the study area, we also examined the influence of kleptoparasitism (i.e., theft of a kill made by a mountain lion) by black bears (Elbroch et al. 2015) on kill rates of mountain lions. We also investigated patterns of resource selection among mountain lions to determine the influence of behavioral state (moving, killing), season (summer, winter), and sex (male, female) on landscape use in the Sierra National Forest.

In chapter 2, we examined lion kill rate intervals based on sex, season, and individual status (i.e., adult female, adult female with kitten, and adult male). We also examined the influence of kleptoparasitism by black bears in the summer months (April 15 – November 15 in our system) to determine if kill intervals changed following a lion being subplanted from its kill by a black bear. We also examined the time spent at kills, or handling time, based on the same variables used in the kill interval analysis.

In chapter 3, we investigated resource selection by mountain lions in the study area by determining the influence of landscape characteristics locations while they are moving through the landscape and while occupying kill sites. We examined the area around the cache site using 50-m buffers that would contain the cache and kill sites. We developed resource selection functions (RSF; Manly et al. 2002) to determine the relative probability of kill site selection based on certain landscape characteristics such as distance-to-roads, slope, elevation, ruggedness, aspect, and vegetation class (Blake and

Gese 2016). Although there was an extended drought in the area during the study, we did still consider the distance to streams as a variable mainly because prey of lions use riparian areas. Additionally, ravines may provide ambush cover for lions. Lastly, we analyzed a subset of locations with prey remains that fell within LiDAR coverage in the research area. The LiDAR data allowed us to digitize roads and skid trails that were previously unmapped allowing us to examine whether lions are using these anthropogenically introduced linear features not only for travel, but also for ambush sites.

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CHAPTER 2

KILL RATES AND PREDATION PATTERNS OF MOUNTAIN LIONS IN THE
SIERRA NATIONAL FOREST, CALIFORINIA

ABSTRACT

Mountain lions (*Puma concolor*) can affect prey populations and may play an important role in both regulation of trophic cascades and maintenance of biodiversity amongst flora and fauna. The fisher (*Pekania pennanti*) has been a species of special concern in the western United States due to decreasing numbers and isolated populations. Within the Sierra National Forest, California, researchers have documented interspecific killing of fishers by mountain lions prompting a need to understand the foraging patterns of mountain lions in this area. Therefore, we captured, GPS-collared, and monitored 5 adult mountain lions and documented prey composition, inter-kill intervals, and time spent at kills with respect to season and prey size in the Sierra National Forest, California, from April 2014 to August 2016. We determined prey composition of lion kills as the percent frequency of total prey selected with regard to season (winter, summer) and sex (female, male), as well as, categorized mule deer (*Odocoileus hemionus*) selection with respect to deer sex and age classes among different classes of lion status (adult female with kittens, adult female, and adult male). We found mule deer comprised the highest percentage of lion kills (81%), with gray foxes (*Urocyon cinereoargenteus*) being the next highest prey item (13%). We did not detect any fisher remains at lion kill sites during the 2-year study. While we were only able to radio-collar

one adult male, he exhibited shorter inter-kill intervals at fawn kills (deer <5-months-old) compared to adult females without kittens, yet he had similar kill intervals compared to adult females without kittens when killing adult deer (>10-months-old) during summer. We found no difference in kill rates between adult females with or without kittens when preying on fawns or adult deer. The adult male spent less time at carcasses compared to solitary adult females, and adult females with kittens demonstrated much shorter carcass handling times than adult females without kittens. We found an increase in mean carcass handling times for solitary adult females during winter. Lastly, we found no evidence to suggest that kleptoparasitism by black bears affected kill rates or handling times of mountain lions in the study area. Mountain lions of the study area mainly killed mule deer and gray foxes, while predation on fishers appeared to be a rare event. However, we acknowledge that acquiring locations every 2-hours may limit detection of fisher remains, but a mesocarnivore of equal body size (i.e., gray foxes) were readily detected at lion kill sites.

INTRODUCTION

Carnivores can significantly affect many prey populations and play an important role in the regulation of trophic cascades (Paine 1980) and maintaining biodiversity of both flora and fauna (Miller et al. 2001). In a system with top-down regulation with one or more apex predators, herbivore biomass intake is assumed to be regulated by carnivores (Hairston et al. 1960, Fretwell 1977, 1987; Oksanen et al. 1981, Oksanen and Oksanen 2000, Miller et al. 2001) implying strong interactions between the three trophic

levels: plants, herbivores, and carnivores (Miller et al. 2001). Although mid-sized

carnivores or mesocarnivores do not invoke the fear or respect of large apex predators,

they can play an important role in community structure and even fill ecological roles such

as dispersers of seeds (Roemer et al. 2009). Even in a 'natural' system that is undisturbed

from human-induced changes on the landscape, predators still must travel and hunt under

risk of detection and predation by other predators (Polis et al. 1989, Rosenheim 2004,

Thompson and Gese 2007). However, on a modified landscape, such as a national forest

that is highly fragmented and disturbed by logging, extensive road networks, and

silvicultural treatments, decreased habitat integrity due to habitat alterations and the

subsequent effects on predator-prey interactions and predator-predator interactions is not

fully understood.

Due to the cryptic nature of mountain lions (*Puma concolor*) and their mostly

nocturnal hunting strategy, actually observing predation and documenting prey

composition is virtually impossible (Blake and Gese 2016). However, with the advent of

global positioning system (GPS) radio-collar technology (Anderson and Lindzey 2003)

researchers have been able to develop a better understanding of lion predation patterns

and habitat utilization. Mountain lions generally prey on a variety of animals including

other predator species such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*), however,

native ungulates comprise the majority of prey biomass they consume and it is unlikely

that a lion population is sustainable in the absence of ungulates (CMGWG 2005).

The portion of the Sierra National Forest in California encompassing our study

area is a single-ungulate system made up of the North Kings Migratory Deer Herd

(*Odocoileus hemionus californicus*) herd (Evans et al. 1976, Neal et al. 1987). We assumed mule deer would comprise the largest percentage of mountain lion diets similar to other studies. Smith et al. (2016) found mule deer made up 79% of lion kills in the Santa Cruz Mountains, California. Similarly, Blake and Gese (2016) in the Pryor Mountains in Montana and Wyoming reported 71% of lion kills were mule deer. There is ample data to show that mountain lions make their living utilizing ungulates, but data is lacking in the Sierra National Forest in relation to cougar diets, kill rates, and handling time. Furthermore, interspecific killing and intraguild predation (IGP) (Polis et al. 1989) are common themes in predator communities. Data from the Kings River Fisher Project (KRFP) near Shaver Lake, California, showed that interspecific predation upon fishers (*Pekania pennanti*), mainly by mountain lions and bobcats (Wengert et al. 2014, Gabriel et al. 2015), could have population level effects on this sensitive forest specialist (Wengert et al. 2014, Sweitzer et al. 2016). We assumed if lions were killing fishers, there would be a high likelihood they would also depredate other mesocarnivores including coyotes, bobcats, gray foxes (*Urocyon cinereoargenteus*), ringtails (*Bassariscus astutus*), martens (*Martes americana*), black bears (*Ursus americanus*), and opossums (*Didelphis virginianus*).

Therefore, our objective was to determine predation patterns and prey composition for mountain lions in the Kings River study area, Sierra National Forest, California. Specifically we documented 1) kill rate intervals of lions in relation to sex and breeding status of the lions, season, and prey size; 2) prey composition of lion kills; 3) time spent at kills in relation to prey size; and 4) the influence of kleptoparasitism by

black bears on kill rates and handling times of mountain lions. We predicted mule deer would comprise the largest percentage of lion kills in our study area, with occasional predation on mesocarnivores (Allen et al. 2015). We predicted kill intervals would be shorter in the summer due to the availability of fawns (Knopff et al. 2010), black bear scavenging or kleptoparasitism of kills, and higher temperatures which would spoil meat faster and increase invertebrate decomposition (Bischoff-Mattson and Mattson 2009, Ruth and Murphy 2010, Krofel et al. 2012, Allen et al. 2014). We also predicted female lions with kittens would have shorter kill intervals and shorter handling times regardless of season than nonbreeding females or males. Since mule deer are the only ungulate present, we predicted male lions might kill more large bucks than lone females or females with kittens.

STUDY AREA

We focused our study on the current Kings River Fisher Project (KRFP) study area in the Sierra National Forest near Shaver Lake, California (Fig. 2.1). Based on our radio-collared lion locations, the minimum elevation of the study site was 289 m and the maximum elevation was 3,237 (which lions used during summer months). The total study area encompassed 1,336 km². The study site climate was Mediterranean with cool, wet winters and warm, dry summers (Sweitzer et al. 2015). Most precipitation occurred between late November and early March including rain and snow and, on average, persisted with snow accumulation into April, but can last into mid-May (Sweitzer et al. 2015). The study area was a mix of public and private lands and included public recreation, hunting, cattle grazing, sightseeing, prescription forest treatments and timber

harvest. The primary tree species were incense cedar (*Calocedrus decurrens),* white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), California black oak (*Quercus kelloggii*), mountain dogwood (*Cornus nuttallii*), and white alder (*Alnus rhombifolia*). Giant sequoia (*Sequoiadendron giganteum*) was present but restricted to remnant populations in a few areas. Shrubs in the area included willow (*Salix spp.),* whiteleaf manzanita (*Arctostaphylos viscida*), greenleaf manzanita *Arctostaphylos patula*), mountain misery (*Chamaebatia foliolosa*), blue elderberry (*Sambucus mexicana*), bush chinquapin (*Chrysolepis sempervirens*), mountain whitethorn (*Ceanothus cordulatus*), Sierra gooseberry (*Ribes roezlii*), and hoary coffeeberry (*Rhamnus tomentella cuspidata*) (Sweitzer et al. 2015). The topography ranged from large, open, flat meadows to steep, rugged canyons with a mixture of dense brush and granite.

METHODS

Mountain Lion Capture

Experienced researchers approved by California Department of Fish and Wildlife (CDFW) using an approved capture and handling protocol, captured mountain lions. Initial capture efforts of lions in the Kings River Study Area (KRSA) demonstrated higher success capturing lions with box traps (Shuler 1992) by using roadkill deer carcasses wired to a tree monitored with motion detection cameras, as opposed to using a houndsman to detect and tree lions, although we implemented both methods. We checked carcasses with cameras every morning for lion activity. If a lion had visited the carcass, we then wired the carcass inside a 2 x 3 m cage trap equipped with a trap transmitter that

would emit a signal when the trap door closed. Once a trap was set, a technician sat within range of the trap transmitter and monitored it until the lion returned. Captured lions were anesthetized with a mixture of tileamine hydrochloride and zolazepam hydrochloride, then affixed with a GPS collar (SirTrack Iridium, Havelock North, New Zealand), measured, weighed, sexed, aged and biological samples and measurements collected. We programmed the GPS-collars to collect a location every 2 hours. Collars had a built-in drop-off mechanism powered by a separate battery and were set to drop-off after 18 months.

GPS Locations and Cluster Site Investigation

The GPS-collars transmitted locations to the satellite whenever the collar had clear satellite coverage. We then downloaded our locations from the SirTrack website and we converted them into the Universal Transverse Mercator (UTM) grid system using ArcGIS 10.2. Not all locations transmitted successfully likely due to the rugged terrain over much of the study area. We did not use any cluster locations within 48 hours of a capture event.

Beier et al. (1995) found mountain lions typically fed on large mammal carcasses for several days and kills are often made <1 hour of arriving at a kill site. Therefore, with GPS collars collecting locations every 2 hours, we were able to determine when a lion localized at a site. We followed Anderson and Lindzey's (2003) protocol to define a cluster in which they designated a cluster as ≥2 locations <200-m apart during a consecutive 16-hour period. However, due to our low incidence of kills at clusters containing only 2-3 locations (7.7%), we redefined a cluster as having ≥4 locations

occurring sequentially within the centroid of a 100-m buffer (Blake and Gese 2016). Since we were still interested in locating remains of smaller prey items such as neonate mule deer during summer months and mesocarnivores, we did continue to search as many ≥2 and ≥3 point clusters as logistically possible. We visited these clusters and, if we did not find a kill immediately, searched a circle at least 100 m in diameter centered on the mean UTMs of the GPS locations of the cluster. We searched in concentric circles approximately 5–10 m apart depending upon visibility, with the goal of visually examining all of the ground within the search area. We note that on several occasions, dogs assisted in the cluster searches, which appeared to increase our ability to detect prey remains, or lion scat at kill sites. When we found prey remains, we recorded species, age, and sex. When sex or species could not be determined by physical characteristics, bones or hair samples were collected and sent to the National Wildlife Research Center (Fort Collins, CO) for analysis of DNA using a polymerase chain reaction (Yamamoto et al. 2002).

Based on age, we divided mule deer into 3 different age classes: <5-months-old, 5-10-months-old, and >10-months-old. We also divided prey items into 3 size classes: small prey (≤ 20 kg) which included mesocarnivores (i.e., gray fox, ringtail, coyote) and squirrels and mule deer fawns (0-5 months old); medium prey (20 – 40 kg) including 5 to 10-month-old mule deer, and large prey (≥40 kg) which included mule deer >10-months-old and one black bear. If black bear sign of similar age to the cluster was detected (i.e., bear scat), we classified that cluster as possibly kleptoparasitized by a black bear (Blake and Gese 2016).

Composition of Mountain Lion Kills

We determined prey composition of lion kills as the proportion of total prey selected with regard to season (winter versus summer months) and sex (Blake and Gese 2016). We also categorized selection of mule deer by lions with respect to deer sex and age classes with regard to lion status (i.e., adult female with kittens, adult female, and adult male).

Kill Rate Interval

For kill rate analysis, we designated a kill interval as the time between the first GPS location at a confirmed kill site cluster and the first GPS location at the next cluster containing prey remains. We used kill intervals where GPS-collars collected locations at a ≥45% acquisition rate of nocturnal locations (Knopff et al. 2009). If, for logistical reasons, we were unable to visit a cluster that was ≥4 points, we eliminated that kill interval from our analysis; there were instances where we were unable to visit a cluster due to treacherous terrain, private property, or illegal marijuana growers. Additionally, during the winter we delayed visiting some possible kill clusters to the spring due to heavy snowfall obscuring any prey remains. This may have reduced our ability of finding remains due to the number of scavengers in the study area. We did not include instances where lions scavenged on our bait carcasses. We used a Cox Proportional Hazard Analysis (CPH) to determine if there were any significant differences in average kill rates among individual lions with regard to sex and season and used the cox.zph tool in R Studio to test the data for proportionality (all *P*-values were >0.05). Merrill et al. 2010 used the CPH model as measure of the relative assessment of covariate effects on the kill

event with respect to time. For example, they found that more the likelihood of making the next kill increased as the amount of time increased after the previous kill. Whittington et al. (2011) and Decesare et al. (2014) also used the CPH model as a 'time to event' analysis as opposed to a survival analysis which CPH is most often applied. As we were also interested in the effects of kleptoparasitism by black bears at lion kills, we again used CPH to test for significant differences in the inter-kill interval at kill sites with and without signs of kleptoparasitism by black bears.

Time Spent at the Carcass

To determine the amount of time a lion spent at a kill site (i.e., handling time) "we subtracted the time of the last nocturnal location at a kill cluster from the first nocturnal location at the same cluster" (Blake and Gese 2016). We removed clusters when another lion was also at the cluster either scavenging, feeding simultaneously, or if it was a mating event as well as a kill. We used Cox Proportional Hazard (CPH) analysis to examine the influence of lion status, season, prey size, and signs of kleptoparasitism by black bears on the time a lion spent at the carcass. The CPH model incorporates time as a factor and allows us to assess covariate effects on the hazard (kill event) while assuming that the hazard ratio (time to event or kill in our case) is constant across all individuals (Merrill et al. 2010).

RESULTS

We captured and monitored 4 adult female mountain lions (≥2 years of age) and 1 adult male. We also radio-collared a sub-adult female, however her GPS-collar never

acquired locations and we never detected her in the study area after she left the bait station where she was captured. We also collared one of our adult female's ~8-month-old cub, but he slipped his collar after only one week. We monitored the GPS-collared lions for 130 to 731 days ($\bar{x} = 331.7 \pm 247.5$ SD) for a total of 1,659 lion-days. Our capture effort totaled 147 days. The majority of effort involved monitoring bait stations daily during December-early April while black bears were hibernating. Of these 147 days, houndsmen assisted us in attempting to locate and capture lions on 35 days. Due to the rough terrain and extremely dense shrub cover, bait stations combined with cage traps proved most effective. We focused our capture efforts to a 185-km² area overlapping the KRFP study area, which covered 14% of the eventual study area as determined by the home ranges of the 5 GPS-collared lions. We note that based on photos from the remote cameras, we did not capture all adult, resident individuals in the study area.

We acquired between 1,259 and 6,729 locations per lion ($\bar{x} = 3,136.8 \pm 2,260.6$ SD) for a total of 15,684 locations. The overall GPS-collar acquisition rate was 73.9% and the individual acquisition rate ranged from 63.9% to 80.0% (Table 2.1). We identified a total of 665 clusters containing ≥4 locations of which we visited 631 (95%) and documented 250 kills. We found mule deer remains at 202 (81%) of the 250 kill sites with 56 (22%) kill sites indicating signs of kleptoparasitism by black bears. We did not consider kleptoparasitism at sites containing a deer fawn (≤5-months-old) as Allen et al. (2014) reported kleptoparasitism by black bears only affected handling times of lions when deer were ≥1 year old. We only found signs of bear scavenging at kills containing deer remains. We also identified 457 clusters consisting of 2-3 locations; we visited and

searched 362 (79.4%) clusters, but found prey remains at only 28 (7.7%) of the 362

clusters.

Composition of Lion Kills

Of the 250 clusters where we found prey remains (this includes the 2-3 point

locations with remains), mule deer made up the majority of prey killed (81%) (Table 2.2).

Gray foxes were the only other species comprising a large portion of lion kills (13.2%).

Other prey species we documented were coyotes, one black bear estimated at 1.5 years

old and killed by the adult male, ringtail (*Bassariscus astutus*), gray squirrels (*Sciurus*

griseus), and Douglas squirrels (*Tamiasciurus douglasii*) (Table 2.2). Male lions

generally killed more large prey than females (Table 2.3). We documented radio-collared

fishers being killed by lions in our study area (Sweitzer et al. 2015), which prompted this

study; however, we did not detect any fisher remains at any of the lion kill sites

investigated. While the 2-hour acquisition interval for the GPS-collars could be

considered biased against finding remains of smaller prey, such as fishers, we did find

many gray fox remains at lion kill sites which are similar in body size (fishers: 2 to 6 kg,

gray foxes: 3.5 to 7 kg). Again, using GPS cluster-site investigation allows for inter-kill

interval and prey handling time analysis; however, we cannot say whether other smaller

animals make up a larger percentage of lion diets without an intensive scat collection

analysis.

We attempted to search clusters soon after downloading the data, but if we were

unable to determine sex from the remains, we collected hair or bone samples and tested

for sex identification via genetic methods. Of 200 samples, only 75 samples amplified

providing sex ID; low success was likely due to DNA degradation. Sex and age of mule

deer killed by lions varied among female and male lions (Table 2.4). Among known

female mule deer (n = 26) killed by adult female lions, 10 (38.5%) were fawns (<5-

months-old), none were between 5-10-months-old, 8 (30.8%) were >10 months old, and

8 (30.8%) were of unknown age. Of 28 known male mule deer, female lions killed 12

(42.9%) male deer <5-months-old, 2 (7.1%) between 5-10-months-old, 9 (32.1%) >10-

months-old, and 5 (17.6%) of unknown age. Again, since we only radio-collared one

adult male during the study, he accounted for killing no female mule deer between 0-10-

months-old, 1 doe >10-months-old, and 1 doe of unknown age. Of the three male mule

deer he killed, 1 was 0-5-months-old, none were between 5-10-months-old, and 2 were

>10-months-old. Of the 8 does and 9 bucks >10-months-old killed by female lions, 6

does and 6 bucks were ≥4-years-old, respectively. Of the 3 deer >10-months-old that the

male lion killed, all were ≥4-years-old.

Mountain Lion Kill Rates

Upon removing lion kill sites where we were unable to determine age of the deer

and, in turn, unable to assign to a size class, we retained 188 inter-kill intervals for

analysis (Table 2.5). The inter-kill interval among all lion statuses (adult male, adult

female, adult female with kitten) for all prey species averaged 1 kill every 5.52 ± 0.30

days (SE) (Table 2.6). As expected, kill intervals were shorter and there was a difference

in kill intervals following predation on coyotes ($P = 0.013$) and gray foxes ($P = 0.02$) in

contrast to adult deer (>10-months-old). We did not find any evidence that

kleptoparasitism by black bears affected kill intervals. The inter-kill interval when a kill

site cluster showed evidence of bear scavenging averaged 5.33 ± 0.28 days, while intervals among kill sites with no evidence of bear scavenging averaged 5.85 ± 0.40 days. At fawn kills, we found the adult male exhibited shorter inter-kill intervals (2.06 ± 0.38 days; $P < 0.001$) when compared to adult females without kittens (6.45 ± 1.16 days). When killing adult deer in the summer, the one male exhibited longer kill intervals (5.12 ± 0.81 days; $P = 0.043$) compared to adult females without kittens (4.68 ± 0.51 days). Lastly, we found no significant difference in kill rates on fawns or adult deer between adult females with or without kittens.

Time Spent at the Carcass

We analyzed a total of 223 lion kills in which we had a measure of time the lion spent at the carcass (Table 2.7). We found a significant difference ($P < 0.0001$) among seasons and lion statuses for the amount of time a lion spent at a carcass. Relative to solitary adult females, there were significant differences in overall handling times for both adult males ($P < 0.001$) and adult females with kittens ($P = 0.0005$). We found adult females spent more time (41.09 ± 4.21 hours) at kills than both adult males (28.53 ± 3.81 hours) and adult females with kittens (24.21 ± 2.62 hours). As expected, adult females (15.61 ± 3.54 hours), adult males (11.17 ± 1.77 hours), and adult females with kittens (10.78 ± 1.46 hours) all spent less time at small and medium-sized prey items as compared to large prey items. We found adult males displayed shorter handling times of adult deer and juvenile deer during summer months relative to adult females killing adult deer and juvenile deer in the summer (Table 2.9). Adult females mean handling time at kills containing large prey items (adult deer >10-months-old) during summer months was

54.94 ± 8.19 hours and 14.45 ± 2.63 hours at small and medium prey items. The adult

male and adult females with kittens mean handling times of large prey (adult deer >10-

months-old and 1 black bear) during the summer were 32.80 ± 3.75 hours and 31.57 ±

3.55 hours, respectively (all P-values < 0.05). Handling times of the adult male for small

and medium prey during the summer was 11.17 ± 1.77 hours, and adult females with

kittens had handling times averaging 10.78 ± 1.46 hours (Table 2.10). We found

kleptoparasitism by black bears did not affect handling time ($P = 0.399$) even though

there was a weak correlation demonstrating shorter handling times (r = -0.158) when

bears scavenged the carcass (Table 2.8).

DISCUSSION

Studies show that mountain lions may prey on a variety of animals including

other predators, such as coyotes and bobcats. However, ungulates comprise the majority

of prey biomass they consume (Hornocker 1970, Atwood et al. 2007, Cooley et al. 2008,

Knopff et al. 2010) and it is unlikely that a mountain lion population would be

sustainable in the absence of ungulates (CMGWG 2005). Mountain lions on our study

area showed they mainly killed mule deer (81% of all kills) consistent with other studies

(Ackerman et al. 1984, Anderson and Lindzey 2003, Blake and Gese 2016), as well as

some predation on mesocarnivores (17% of all kills). While we did not find evidence at

any kill site of a radio-collared lion scavenging another lion kill, remote cameras did

photograph a non-collared lion scavenging on a kill made by a radio-collared lion.

Oftentimes, we only found deer hair, legs, or bone fragments at a kill site, therefore

determining whether the event was a kill as opposed to scavenging was not always

definitive. The literature also shows that lions will sometimes usurp other lion kills (Koehler and Hornocker 1991).

Combining all lion social classes, deer age classes, and seasons, we found an overall predation rate of one deer killed every 7.26 days per lion or lion family group. Inter-kill intervals were approximately 5.5 days for adult females with kittens and around 5.3 days for solitary adult females. The mean inter-kill interval for adult females killing all prey species during the summer was just under 5 days compared to >6 days during winter months. These inter-kill intervals were slightly lower than other studies reporting kill intervals ranging from 5.4 – 15.2 days (Anderson and Lindzey 2003, Knopff et al. 2010, Ruth et al. 2010, Blake and Gese 2016). Our results were consistent with the differential prey use hypothesis in which the sexual dimorphism of cougars leads to females usually preying on smaller prey than males presumably because males are more capable of subduing larger prey (Ross and Jalkotzy 1996, Anderson and Lindzey 2003, White et al. 2011). The male cougar on our study exhibited longer inter-kill intervals after killing an adult deer and shorter inter-kill intervals when killing fawns as compared to adult female lions. We found no difference in the inter-kill interval between adult females with or without kittens after killing an adult deer, which was not consistent with other studies that generally found the energetic requirements of family groups were higher (Laundre 2005, Blake and Gese 2016). However, we could not definitively determine how long kittens stayed with their mother or how long they may have survived.

We found 17% of mountain lion kills in our study area consisted of other smaller predators, the majority of which were gray foxes (n = 33). One adult female lion,

estimated to be >8 years old, accounted for 21 of the 33 gray foxes killed. During the last 48 days her GPS-collar was active, this older female lion switched to killing mesocarnivores, killing 9 gray foxes, 1 coyote, and only 1 deer during this 48-day period, suggesting her health may have been compromised. Blake and Gese (2016) noted an adult male mountain lion prey-switching from ungulates to smaller prey items such as beavers (*Castor canadensis*) due to eventually losing a front paw after being caught in a foot-hold trap.

As expected, the one radio-collared adult male in our study spent less time at carcasses compared to solitary adult females (Mattson et al. 2007, Blake and Gese 2016). Due to energetic requirements of adult females with kittens, the time spent at a carcass for a family group was much shorter compared to solitary adult females during summer months. We did not have data for females with kittens during winter months due to either radio-collar failure or kitten dispersal. While not tested statistically, we did find an increase in mean handling times for solitary adult females during winter. Shorter handling times in the summer was consistent with Knopff et al. (2010) suggestion that spoilage and scavenging played a role in decreased prey handling times for lions during the summer. As expected, we also found shorter handling times for smaller prey items, which was consistent with other studies documenting shorter handling times and increased kill rates when lions depredate small prey as compared to large prey (e.g., Blake and Gese 2016).

We found that kleptoparasitism by black bears did not significantly affect kill rates and handling times of mountain lions on our study area. Blake and Gese (2016)

similarly found no influence of kleptoparasitism of black bears on kill rates of lions in Montana. In contrast, Allen et al. (2014) found a significant relationship between lion handling times and black bear detection rates of lion kills. While we found seasonal variation in kill rates (higher rates during summer months), we did not detect significant effects of lion kill detection by black bears even though we did find that black bears detected many lion kills (n = 61). Without an estimate of lion density and deer abundance, we are unable to determine why bear kleptoparasitism did not affect lion kill rates on our study area; perhaps deer density is low causing mountain lions to attempt to continue feeding even after usurpation by black bears.

The original impetus for the study was the finding that mountain lions were killing radio-collared fishers (Wengert et al. 2014, Gabriel et al. 2015). Overall, 23 radio-collared fishers were the result of mountain lion predation; 3 more were listed as felid predation (could not distinguish between mountain lion and bobcat); and still many others are awaiting necropsy. During the 2-year predation study with 5 GPS-collared lions, we did not find any fisher remains at any of the 250 kill sites. There are many possible explanations for not finding any fisher as prey. The 2-hour interval between acquisition times for the GPS locations may have been too long to have fisher remains persist in the environment, or the remains were consumed within a 2-hour period. However, we did find the remains of 33 gray foxes at lion kill sites. Fishers (2 to 6 kg body mass) and gray foxes (3 to 7 kg body mass) are similar in body size. Therefore, it may be more plausible that while lion predation on fishers could have a large effect on the growth rate of a small population of fishers (Sweitzer et al. 2016), it may in fact be a very rare event in the life

of a mountain lion. Alternatively, the previous predation events may have been due to prey specialization by a certain lion (Knopff et al. 2010). During the 2-year lion study, only 1 radio-collared fisher was confirmed to have been depredated by a mountain lion (R. Green, unpublished data). Studies have found individual lions specializing on certain prey species (Ross et al. 1997, Logan and Sweanor 2001, Elbroch and Wittmer 2013, Blake and Gese 2016).

MANAGEMENT IMPLICATIONS

Studies show that mountain lion prey on a variety of animals including other predators, but mainly survive killing native ungulates. Our prey composition of lion kills was consistent with these other studies. In the absence of knowledge regarding the size and demography of the North Kings Migratory Deer Herd, we are unable to understand the effects of lion predation on this deer herd. However, as this is a single ungulate system and our results show that lions sustain themselves on mule deer (81% of kills were deer), future research examining vital rates and cause specific mortality within this mule deer population would help managers better understand this predator-prey system. We found the majority of mule deer killed by lions occurred when deer were either <5-months-old or >10-months-old, with few kills occurring when deer were 5-10-months-old. Whether this reflects actual herd composition is unknown. Our data also showed 27 of the 33 instances of gray fox predation by mountain lions occurring during the winter. Perhaps if recruitment of mule deer fawns is low in this system, lions are switching to other sources of prey, such as gray foxes and other mesocarnivores, to sustain themselves during the winter. Lastly, we note that while capture, deployment of radio-collars, and

GPS cluster searches can be effective in documenting predation patterns of mountain lions, there are limitations. The GPS-collars we affixed to lions were $4,000 per collar and battery life was at times questionable, which affected sample sizes of lions and kill sites clusters. Augmenting our searches of potential kill sites with dogs seemed, at least anecdotally, to increase our ability to find prey remains. Future predation studies may find detection dogs a useful tool for finding prey remains more efficiently.

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TABLES AND FIGURES

Table 2.1. Social class, capture date, monitoring duration, number of GPS locations and acquisition rates, number of kills and kill rates of GPS-collared mountain lions, Sierra National Forest, California, 2014-2016.

Cougar ID	Social Class	Capture Date	Days Monitored	Number of GPS Locations	Acquisition Rate	Number of Kills	Number of kill Intervals Used	Kill Rates days ± SD
PF01	AFK/AF	4/16/2014	731	6729	69.85%	105	91	6.22 (±4.48)
PF02	AF	4/18/2014	130	1259	77.28%	8	3	8.03 (±5.17)
PF04	AFK/AF	4/6/2015	396	3915	78.62%	75	66	4.83 (±3.61)
PF05	AF	3/23/2016	143	1504	80.00%	20	12	5.21 (±5.44)
PM03	AM	5/13/2015	258	2277	64.00%	42	30	4.68 (±2.74)

Table 2.2. Number of prey items killed (% of kills) by individual mountain lions in the Sierra National Forest, California, 2014-2016.

Prey Species	PF01	PF02	PF04	PF05	PM03	Total
Mule deer >10-months-old	47 (44.8)	4 (50.0)	35 (46.7)	8 (40.0)	23 (54.8)	117 (47.0)
Mule deer 5-10-months-old	3 (3.8)	0	5 (6.7)	0	0	8 (3.2)
Mule deer 0-5-months-old	27 (25.7)	2 (25.0)	13 (17.3)	7 (35.0)	8 (19.0)	57 (22.9)
Deer of unknown age	5 (4.8)	2 (25.0)	8 (10.7)	2 (10.0)	3 (7.1)	20 (8.0)
Grey fox	21 (20.0)	0	9 (12.0)	1 (5.0)	2 (4.8)	33 (13.2)
Coyote	2 (1.9)	0	3 (4.0)	0	3 (7.1)	8 (3.2)
Black bear	0	0	0	0	1 (2.4)	1 (0.4)
Ringtail	0	0	0	1 (5.0)	0	1 (0.4)
Gray squirrel	0	0	2 (2.7)	1 (5.0)	0	3 (1.2)
Douglass squirrel	0	0	0	0	2 (4.8)	2 (0.8)
Totals	105	8	75	20	42	250

Table 2.3. Size class of prey killed by female and male mountain lions in the Sierra National Forest, California, 2014-2016. We did not include deer when we were unable to obtain an estimate of age (n = 21).

Prey size class	Female mountain lions		Male mountain lions	
	n	%	n	%
Large	102	53.7	24	61.5
Medium/small	88	46.3	15	38.6

Table 2.4. Sex and age class of mule deer killed by female and male mountain lions, Sierra National Forest, California, 2014-2016.

Sex-age class of mule deer	Female lions		Male lions	
	n	%	n	%
Female				
<5-months-old	10	38.5	0	0.0
5-10-months-old	0	0.0	0	0.0
>10-months-old	8	30.8	1	50.0
Unknown age	8	30.8	1	50.0
Total	26	100.1	2	100
Male				
<5-months-old	12	42.9	1	0.3
5-10-months-old	2	7.1	0	0.0
>10-months-old	9	32.1	2	0.7
Unknown age	5	17.9	0	0.0
Total	28	100.0	3	1.0

Table 2.5. Number of kill intervals used relative to lion status and season, Sierra National Forest, California, 2014-2016.

Lion status	Summer	Winter	Total
Adult female	52	40	92
Adult female with kittens	63	0	63
Adult male	29	4	33
Total	144	44	188

Table 2.6. Mean inter-kill intervals (days ± SD) for mountain lions among seasons and status, Sierra National Forest, California, 2014-2016.

	Adult females without kittens			Adult males			Adult females with kittens
	Summer	Winter	All seasons	Summer	Winter	All seasons	Summer
Mean ± SD	4.68 ± 3.64	6.09 ± 4.83	5.33 ± 4.27	5.12 ± 4.33	5.95 ± 4.91	5.25 ± 4.35	5.77 ± 3.78
# of kill intervals	52	45	97	29	5	34	69

Table 2.7. Number of handling time intervals used for 3 classes of mountain lion social status during summer and winter, Sierra National Forest, California, 2014-2016.

Lion status	Summer	Winter	Total
Adult female without kittens	63	52	115
Adult female with kitten	69	1	70
Adult male	32	6	38
Total	164	59	223

Table 2.8. Handling time differences and significance relative to adult females killing adult and juvenile deer during summer months, Sierra National Forest, California, 2014-2016.

Lion status and status of deer killed	coef	exp(coef)	Pr (> |z|)
Adult female with kittens	-0.244	0.783	0.333
Adult male	-0.318	0.728	0.043
Juvenile deer	0.006	1.006	0.934
Adult female with kittens and juvenile deer	0.066	1.068	0.824
Adult male and juvenile deer	0.063	1.877	<0.001

Table 2.9. Average time spent at a carcass (hours ± SD) by mountains lions relative to prey, season, and kleptoparasitism by black bears, Sierra National Forest, California, 2014-2016.

	PF01	PF02	PF04	PF05	PM03
Grey fox, coyote, deer <6-months-old	13.4 ± 12.7	11.0 ± 4.2	12.8 ± 9.2	7.0 ± 3.7	16.8 ± 14.7
Deer >6 months old (summer)	42.0 ± 36.6	57.0 ± 18.1	35.31 ± 19.3	38.0 ± 17.9	32.2 ± 16.1
Deer >6 months old (winter)	102.9 ± 62.3	N/A	54.63 ± 41.50	N/A	67.6 ± 44.5
Bear scavenged	29.4 ± 20.5	37.3 ± 45.7	36.88 ± 27.0	33.5 ± 14.3	42.4 ± 14.4
Not bear scavenged	75.3 ± 58.9	49.9 ± 24.6	50.05 ± 37.0	42.5 ± 22.3	36.6 ± 32.0

Table 2.10. Mean handling time (hours ± SD) relative to mountain lion status and prey size during the summer and winter, Sierra National Forest, California, 2014-2016.

Prey size	Summer		Winter	
Lion status	N	Mean ± SD	N	Mean ± SD
Small and medium prey				
Adult female	31	14.5 ± 14.7	28	16.8 ± 23.5
Adult female with kittens	27	10.8 ± 7.6	0	N/A
Adult male	12	11.2 ± 6.1	2	18.0
Large prey				
Adult female	32	54.9 ± 46.4	18	96.4 ± 49.3
Adult female with kittens	42	31.6 ± 23.0	0	N/A
Adult male	20	32.8 ± 16.8	3	32.7 ± 25.4
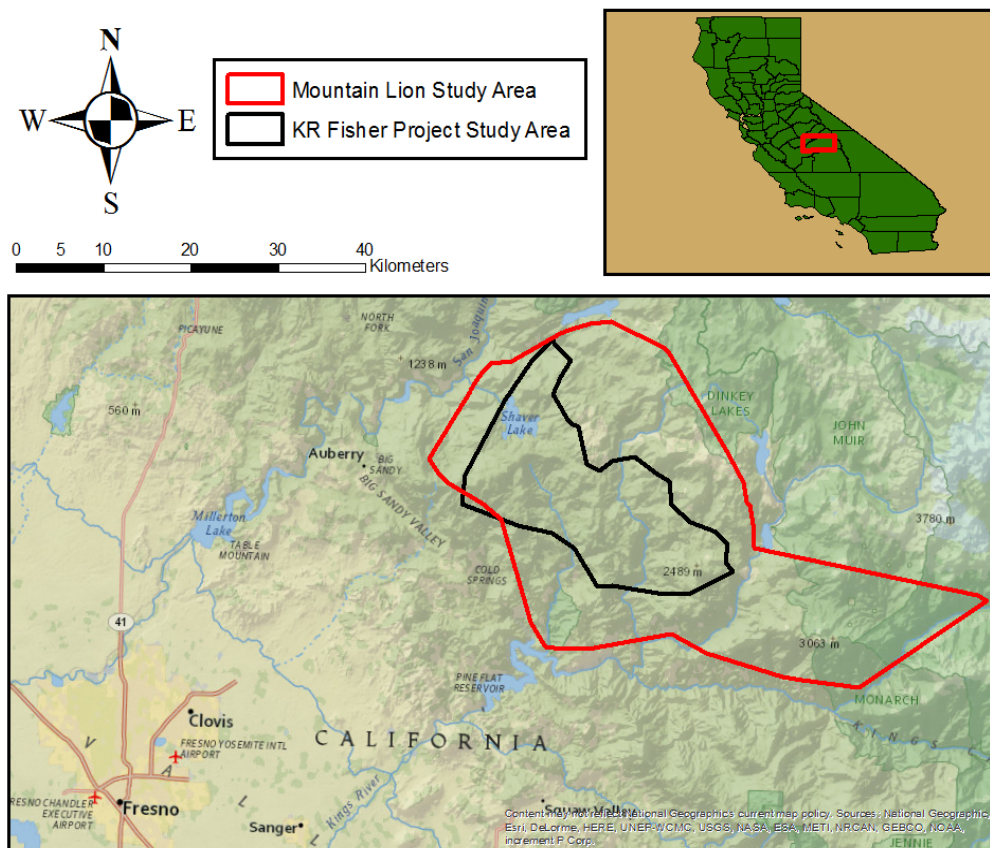
Figure 2.1. The 338-km² Kings River Fisher Project study area and the 1336-km² mountain lion study area encompassing all home ranges of radio-collared mountain lions, Sierra National Forest, California, 2014-2016.

CHAPTER 3

RESOURCE SELECTION BY MOUNTAIN LIONS IN THE SIERRA NATIONAL

FOREST, CALIFORNIA: INFLUENCE OF BEHAVIORAL STATE AND SEASON

ABSTRACT

Decreasing fisher (*Pekania pennanti*) populations in the southern Sierra Nevada in California have been of increasing concern to land managers. In the Sierra National Forest of California, research has shown mountain lions (*Puma concolor*) to be a main predator of fishers. In order to document landscape characteristics selected by mountain lions, we affixed GPS radio-collars to 5 adult, resident lions between April 2014 - August 2016. We examined resource selection at two behavioral states: locations where predation occurred (killing) versus non-cluster locations (moving). We examined resource selection using a broad-scale analysis covering the entire study area, and a subset of the study area where LiDAR data had been collected allowing for a more detailed map of roads and skid trails within the area. In both the full and LiDAR study areas, we buffered each used location (moving, killing) with a 50-m buffer which was based on >95% of carcass drags documented being ≤ 50 m. We generated 25 available points for every kill and moving location with the available location constrained to the mean distances between locations; we similarly buffered all available locations. We documented prey remains at 250 kill sites within the full study area, and a subset of 104 kill sites within the LiDAR study area. We developed resource selection functions (RSFs) for summer and winter seasons for the kill sites and moving locations in both study areas for a total of 8 RSF models. Our top

models during summer and winter within the full study area for moving locations showed selection for ruggedness and slope variables in a quadratic form, with a threshold at which lions began to select against these variables. In addition, top models included selection for higher elevation in comparison to available points; and selection for east aspects. Our top predation model for summer months within the full study area showed selection against steeper slopes. During winter, mountain lions selected for close proximity to roads. With respect to the moving locations within the LiDAR study area, lions showed selection for close proximity to streams, selection for north and south aspects, and selection against higher elevations. Our top model for moving locations during winter months within the LiDAR study area showed selection for north, south, and west aspects and selection for lower elevations. With respect to moving locations during both winter and summer months within the LiDAR study area, the quadratic slope and ruggedness variables were both in the top model which was the same top model for moving locations within the full study area. However, due to terrain variable data limitations, the regression plots displayed a U-shaped parabola suggesting that lions selected for flatter slopes and vertical slopes which does not make biological sense. After plotting this data, we found a limitation within the dataset due to the LiDAR data being collected in flatter regions of the study area slated for forest treatments. The top predation models within the LiDAR study area showed strong selection for close proximity to roads and skid trails, as well as, selection for close proximity to streams during both winter and summer. Lions selected against higher elevations during winter months, while selecting for higher elevations during the summer. To reduce predation pressure upon fishers by

mountains lions, we recommend removing linear features post-timber harvest by replanting them to alleviate forest fragmentation, as well as, mapping all roads and skid trails.

INTRODUCTION

Apart from humans, mountain lions (*Puma concolor*) display one of the broadest geographic distributions of terrestrial mammals, utilize areas ranging from sea level to 4,500 m above sea level (Logan and Sweanor 2001, CMGWG 2005), and occupy a range of vegetation types from coniferous and deciduous forests to mountains and desert canyons (Hansen 1992, CMGWG 2005). However, while mountain lions are considered to be forest generalists and populations have demonstrated an ability to persist in a wide range of terrain types and climes, ever-expanding human populations have led to conversion of land to agriculture, rural residential development, and habitat fragmentation. These landscape changes have in turn, decreased mountain lion habitat quantity, as well as winter range for ungulates (Mansfield 1986, Beier 1995, UDWR 1999, Logan and Sweanor 2001, Maehr and Cox 1995, Pearlstine et al. 1995, Pierce and Bleich 2003, CMGWG 2005, Reith 2010). Moreover, these anthropogenic landscape alterations and fragmentation have reduced overall mountain lion geographic range by at least 50% in the western hemisphere (Young and Goldman 1946, Nowak 1974, Logan and Sweanor 2000, Reith 2010). Due to ongoing increases in human populations, activities, and the potential effects on mountain lions, it is essential to understand

important habitat characteristics to manage and conserve the species (CMGWG 2005, Reith 2010).

Along with a reduction in mountain lion distribution in the western hemisphere, other carnivores such as fishers (*Pekania pennanti*) in California, Oregon, and Washington, which are more sensitive to habitat disturbance, have seen declines in their numbers as well (Lewis et al. 2012, Sweitzer et al. 2015, 2016). Fishers and mountain lions are both native carnivores to the Sierra National Forest in California and the fisher is often subject to intraguild predation by mountain lions (C. Thompson, personal communication). Currently, why lions exhibit intraguild predation upon fishers is poorly understood, this level of predation could have population-level effects, particularly on this sensitive western population of fishers (Wengert et al. 2014). As with lion predation on fishers in the Sierra National Forest, other studies in North America have also shown lions to kill a variety of prey species. While mountain lion diets can consist of a variety of small mammals and birds, as well as, livestock, mesocarnivores, and domestic pets (Villepique et al. 2011), the majority of their diet is native ungulates (CMGWG 2005). Additionally, research has shown that individual mountain lions can specialize on certain prey (Elbroch and Wittmer 2013, Allen et al. 2015) which could have significant implications on a rare species (Wittmer et al. 2014, Allen et al. 2015). Furthermore, the portion of the Sierra National Forest in California encompassing our study area is a single-ungulate system made up of the North Kings Migratory Deer Herd (*Odocoileus hemionus californicus*) herd (Evans et al. 1976, Neal et al. 1987). Previous research has shown mountain lions prey switched in systems consisting of multiple ungulate species

when the availability of one ungulate species increased (CMGWG 2005). However, in an ungulate system containing only mule deer, it is possible that predation upon fishers and other mesocarnivores and small mammals could increase due to seasonal changes in the distribution of mule deer.

Zielinski et al. (2005) suggested that forest specialists (i.e. fishers and American martens, *Martes americana*) distributions have changed more than forest generalists, such as mountain lions, due to the combination of loss of mature forest habitat, latent effects of commercial trapping, and increased residential development. Laundre and Hernandez (2003) found 72% of lion kills in their study occurred along edges compared to open patches or in forested areas. This combination of edge-utilization by mountain lions in contrast to contiguous, old-growth forest-utilization by fishers suggest that anthropogenic landscape activities might not only be directly affecting fisher habitat, but indirectly benefitting mountain lion hunting success through fragmentation which creates travel corridors and edge habitat/ambush habitat for mountain lions, combined with early successional browse for mule deer. Moreover, fishers are a cryptic species (Proulx and Aubry 2014) and the addition of extensive road and skid trail networks that fragment contiguous forest likely create 'gauntlet' areas for fishers due to patches of forest that have been opened by logging or other silvicultural practices.

Land managers have an interest in conserving existing fisher habitat as well as, learning what anthropogenic activities and treatments may have negative ramifications for fishers. The combination of the ongoing fisher research by KRFP and our overlapping research into resource selection and landscape use by mountain lions could provide

managers with the data they need to better understand and conserve fisher populations in the region. Thus, the first objective of our study was to examine resource selection of mountain lions in the Sierra National Forest. Due to shifts in elevation of their main prey, mule deer, during summer and winter, we determined seasonal resource selection. Because the behavioral state of the animal can also influence how mountain lions use the landscape, we examined resource selection for two behavioral states: killing versus moving. For winter and summer, we examined the influence of landscape variables including distance to streams, distance to mapped roads, ruggedness, slope, aspect, elevation, and majority vegetation type using the resource selection function (Manly et al. 2002) framework.

Our second objective was to examine a subset of the study area using LiDAR (Light Detection and Ranging) technology, which allowed mapping of roads and skid trails that conventional road mapping layers did not record. We used a subset of the data since the LiDAR coverage encompassed <50% of where prey remains were found in the study area. We ran an identical RSF as mentioned above, but in this analysis, we included distance to digitized roads and skid trails to determine if low use roads and skid trails may not only facilitate travel, but that it may also provide early successional browse and travel routes for mule deer, as well as, stalking and ambush cover for mountain lions. We hypothesized vegetation type would not be a significant influence on resource selection (Busch 1996, Woodruff 2006), but that mountain lions would select for dense vegetation cover. In addition, we expected lions to select for close proximity to low-use roads and skid trails, rugged terrain year-round, lower elevations during the winter to coincide with

a seasonally migratory deer herd, and close proximity to streams; not just for water, but for concealment due to topographic features, as well as, riparian browse and cover for mule deer.

STUDY AREA

We focused our study on the current Kings River Fisher Project (KRFP) study area in the Sierra National Forest near Shaver Lake, California (Fig. 3.1). Based on locations from the radio-collared mountain lions, the minimum elevation of the study site was 289 m and the maximum elevation was 3,237 m, which the lions used during summer months. The total study area encompassed 1,336 km². The study site climate was Mediterranean with cool, wet winters and warm, dry summers (Sweitzer et al. 2015). Most precipitation occurred between late November and early March including rain and snow and, on average, persisted with snow accumulation into April, but can last into mid-May (Sweitzer et al. 2015). The study area was a mix of public and private lands and included public recreation, hunting, cattle grazing, sightseeing, prescription forest treatments, and timber harvest.

The primary tree species were incense cedar (*Calocedrus decurrens),* white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), California black oak (*Quercus kelloggii*), mountain dogwood (*Cornus nuttallii*), and white alder (*Alnus rhombifolia*). Giant sequoia (*Sequoiadendron giganteum*) was present but restricted to remnant populations in a few areas. Shrubs in the area included willow (*Salix spp.),* whiteleaf manzanita (*Arctostaphylos viscida*), greenleaf manzanita

Arctostaphylos patula), mountain misery (*Chamaebatia foliolosa*), blue elderberry (*Sambucus mexicana*), bush chinquapin (*Chrysolepis sempervirens*), mountain whitethorn (*Ceanothus cordulatus*), Sierra gooseberry (*Ribes roezlii*), and hoary coffeeberry (*Rhamnus tomentella cuspidata*) (Sweitzer et al. 2015). The topography ranged from large, open, flat meadows to steep, rugged canyons with a mixture of dense brush and granite.

METHODS

Capture and GPS Locations

Experienced researchers approved by California Department of Fish and Wildlife (CDFW) using an approved capture and handling protocol, captured mountain lions. Initial capture efforts of lions in the Kings River Study Area (KRSA) demonstrated higher success capturing lions with box traps (Shuler 1992) by using roadkill deer carcasses wired to a tree monitored with motion detection cameras, as opposed to using a houndsman to detect and tree lions, although we implemented both methods. We checked carcasses with remote cameras every morning for lion activity. If a lion had visited the carcass, we then wired the carcass inside a 2 x 3 m cage trap equipped with a trap transmitter that would emit a signal when the trap door closed. Once a trap was set, a technician sat within range of the trap transmitter and monitored it until the lion returned. Captured lions were anesthetized with a mixture of tileamine hydrochloride and zolazepam hydrochloride, then affixed with a GPS collar (SirTrack Iridium, Havelock North, New Zealand), measured, weighed, sexed, aged and biological samples and

measurements collected. We programmed the GPS-collars to collect a location every 2 hours. Collars had a built-in drop-off mechanism powered by a separate battery and were set to drop-off after 18 months. The GPS-collars transmitted locations to the satellite whenever the collar had clear satellite coverage. We then downloaded our locations from the SirTrack website and converted them into the Universal Transverse Mercator (UTM) grid system using ArcGIS 10.2. Not all locations transmitted successfully likely due to the rugged terrain over much of the study area. We did not use any cluster locations within 48 hours of a capture event.

Beier et al. (1995) found mountain lions typically fed on large mammal carcasses for several days and kills are often made <1 hour of arriving at a kill site. Therefore, with GPS collars collecting locations every 2 hours, we were able to determine when a lion localized at a site. We followed Anderson and Lindzey's (2003) protocol to define a cluster in which they designated a cluster as ≥2 locations <200-m apart during a consecutive 16-hour period. However, due to our low incidence of kills at clusters containing only 2-3 locations (7.7%), we redefined a cluster as having ≥4 locations occurring sequentially within the centroid of a 100-m buffer (Blake and Gese 2016). Since we were still interested in locating remains of smaller prey items such as neonate mule deer during summer months and mesocarnivores, we did continue to search as many ≥2 and ≥3 point clusters as logistically possible. We visited these clusters and, if we did not find a kill immediately, searched a circle at least 100 m in diameter centered on the mean UTMs of the GPS locations of the cluster. We searched in concentric circles approximately 5–10 m apart depending upon visibility, with the goal of visually

examining all of the ground within the search area. We note that on several occasions, dogs assisted in the cluster searches, which appeared to increase our ability to detect prey remains, or lion scat at kill sites.

Resource Selection Functions for Two Behavioral States

To analyze the influence of behavioral state (kill site versus moving locations), we developed resource selection functions (RSF; Manly et al. 2002) for the entire study area and (Fig. 3.1), and within a subset of the research area where LiDAR data was available (Fig. 3.2). For clarity, the 'moving locations' were single points not involved with a cluster, as defined above, while 'killing locations' were points associated with a kill site. We generated a buffer around each kill site location based upon the distance a carcass was dragged from known kill sites (Blake and Gese 2016). Of the 250 kill sites with prey remains, we found evidence of a carcass being dragged at 57 kill sites; the average drag distance was 14.6 m with 54 (95%) of 57 drag distances being <50 m. Therefore, we chose 50-m as our buffer radius for all used and available kill site locations. We also applied this buffer to all used and available moving locations.

To determine the 'available' locations for comparison to the 'used' locations in the RSF framework, we first created minimum convex polygons (MCP's) to estimate the home ranges of the radio-collared mountain lions using ArcMap 10.3.1. We chose MCP's over kernel density estimators to alleviate 'islands' in the home ranges that appeared when creating home ranges using either 95% or 98% kernel density home ranges. Next, we calculated the mean distance between sequential kill sites and used this distance to calculate the extent of the 'available' locations for comparison to the 'used' kill site

locations (Table 3.1). For the moving locations, the extent of the available locations were

constrained to the average distance traveled between consecutive moving locations (i.e.,

every 2-hours). Constrained within the range of these average distances traveled between

kill sites and moving locations, we then randomly determined 25 'available' locations for

each 'used' location (Northrup et al. 2013) with the further constraint that the available

locations were within the boundaries of each lion's home range. We did not use a case-

control study framework (Keating and Cherry 2004) due to the distances traveled were

large and the extent of available locations overlapped among all the used locations. The

available locations were then similarly buffered by 50-m for comparison to the used

locations.

Landscape Covariates for the Entire Study Area

We were interested in how landscape variables influence resource selection. The

variables we examined included distance to roads, distance to streams, elevation, slope,

aspect, vegetation type, and ruggedness. We used ArcMap 10.3.1 (Environmental

Systems Research Institute, Inc., Redlands, CA) to analyze all spatial data. We

downloaded road layers from the U.S. Forest Service Pacific Southwestern Region

website (https://www.fs.usda.gov/main/r5/ landmanagement/gis; downloaded 17 January

2017). We obtained stream data from

https://www.wildlife.ca.gov/Data/GIS/Clearinghouse; downloaded 17 January 2017. We

used 30-m resolution Digital Elevation Models (DEM;

https://viewer.nationalmap.gov/basic/) to derive terrain data including slope, aspect,

elevation, and ruggedness. To calculate a ruggedness index from the DEM, we used a

Relative Topographic Position index (RTP) (http://gis4geomorphology.com/roughness-topographic-position/).

$$(MeanDEM - minDEM) / (maxDEM - minDEM)$$

Using a loop in R Studio (RStudio Team [2015] RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/), we reclassified aspect from a continuous variable (degrees 0 – 360) to a categorical variable, then binned it to the four cardinal directions: north (≥315 to <45), east (≥45 to <135), south (≥135 to <225), and west (≥225 to <315). We calculated the Euclidean distances to the nearest streams and roads using Analyst > Proximity > Near Tool in ArcMap. We then standardized distance to roads, distance to digitized skid trails and roads, distance to streams, and elevation, slope, and ruggedness covariates due to Eigenvalue and convergence errors when running initial models in R Studio:

$$(covariate - mean(covariate))/standard\ deviation(covariate)$$

We created a layer of 'Vegetation Type' by downloading and rescaling vegetation type into 4 categories: 'Conifer', 'Hardwood', 'Other', 'Shrub' (See Appendix A) using Landfire data (https://landfire.cr.usgs.gov/; downloaded 17 January 2017 (Appendix A). We also determined the 'Majority Vegetation Type' as the vegetation class that had the highest proportion within the buffered location. We reprojected all layers in ArcMap into NAD83 Zone 11N, and clipped them to the study area boundary. For the covariates of slope, aspect, elevation, and ruggedness, we used the mean value of these terrain variables within each 50 m buffer.

Landscape Covariates for the LiDAR Subset Area

For the subset of data contained within the boundary of the LiDAR imaged area, we used all the landscape variables mentioned previously for the 'Entire Study Area' and added another layer containing low-use roads and skid trails. We digitized these roads and skid trails using the Bare Earth LiDAR data (Figs. 3.3, 3.4, 3.5). We generated 10 random points within the LiDAR area and using the analyst tool 'Near', we then ground-truthed 10 digitized roads to confirm the existence of these features: 9 of the 10 sites were skid trails and 1 site was an unmapped, low-use, dirt road.

For the LiDAR area analysis, we clipped the mountain lion home ranges by the LiDAR study area boundaries. We used the same methods for developing RSF models for the LiDAR data set as for the entire study area data; however, we generated new 'available' locations that fell within the boundaries of the LiDAR imaged area. We generated 25 available points within those clipped buffers, then created 50 m buffers around all used and available locations within the clipped home range/LiDAR boundary so as to not include terrain, road distance, or stream distance data that fell outside of those boundaries.

Model Development

We compared landscape covariates with respect to 'used' kill sites and moving locations to the randomly generated 'available' locations. Use of RSF's are ideal for exploring binary data (i.e., used versus available) as they operate within a logistic regression framework (Blake 2014). We used Generalized Linear Mixed Models (GLMM) with the individual animal (Puma_ID) as a random effect. GLMM's are useful

in that they allow for modeling of data, that does not have a normal distribution, and can still flexibly accommodating covariates of different distributions (McCulloch and Neuhaus 2005). Since the GPS collars were set to collect a location at 2-hour intervals, our assumption was that GPS points not associated with clusters indicated the mountain lion was either traveling or hunting (i.e., moving). While they could have been napping between the 2-hour locations, our assumption was that if a lion was not associated with a point cluster, then they were classed as moving. The goal of the non-cluster (moving) analysis was to develop an understanding of resource selection with respect to preferred landscape characteristics while lions were moving through their home range. In total, we constructed 8 different RSF models with respect to season (summer = Apr 15 – Nov 15; winter = Nov 16 – Apr 14), kill site versus moving locations, and the full study area and the smaller subset LiDAR study area (Fig. 3.2). The LiDAR data was flown to encompass areas within the study area where forest treatments were to be conducted. Again, the main objective of the LiDAR subset data was to digitize roads and skid trails that were unmapped with the assumption that mountain lions may be utilizing these low-use roads and skid trails that have since turned into wildlife trails for travel and ambush sites for prey. This was necessary to determine the distances to and possible use of anthropogenically created linear features by mountain lions.

We used a Pearson statistic (Gloyne and Clevenger 2001) to test for multi-collinearity among terrain variables (slope, aspect, elevation, and ruggedness) since terrain variables such as slope and ruggedness are often highly correlated. For other variables (distance to stream, distance to mapped roads), we used a Variance Inflation

Factor (VIF) to assess collinearity in the models. A VIF of >2.5 may indicate variable

collinearity (Allison 1999, Reith, 2010); therefore, we removed any variable that was

collinear and excluded it from model consideration (Reith 2010). While there is

disagreement and pros and cons about whether to use Akaike's Information Criterion

(AIC) or Bayesian Information Criterion (BIC) (e.g., Weakliem 1999, Burnham and

Anderson 2004), for our purposes, we ranked models using BIC because it was more

appropriate for our dataset due to small sample sizes. When sample size is small (n =

5_{Lions}) in comparison to the number of parameters (n = $7_{Full Study Area}$, n = $8_{Lidar Study Area}$),

AIC may not be accurate (Sugiura 1978, Abascal et al. 2005) and BIC is considered a

more appropriate approach (Schwarz 1978, Abascal et al. 2005).

RESULTS

Capture and GPS Locations

We captured and monitored 4 adult female mountain lions (≥2 years of age) and 1

adult male. We also radio-collared a sub-adult female, however her GPS-collar never

acquired locations and we never detected her in the study area after she was captured. We

also radio-collared an 8-month-old cub of one of our adult females, but he slipped his

collar after only one week. We monitored the GPS-collared lions for 130 to 731 days ($\bar{x}$ =

331.7 ± 247.5 SD) for a total of 1,659 lion-days. Our capture effort totaled 147 days. The

majority of effort involved monitoring bait stations daily during December-early April

while black bears were hibernating. Of these 147 days, houndsmen assisted us in

attempting to locate and capture lions on 35 days. Due to the rough terrain and extremely

dense shrub cover, bait stations combined with cage traps proved most effective. We

focused our capture efforts to a 185-km² area overlapping the KRFP study area (Fig. 3.1),

which covered 14% of the eventual study area as determined by the home ranges of the 5

GPS-collared lions. We note that based on photos from the remote cameras, we did not

capture all adult, resident individuals in the study area.

We documented 250 kill sites (see Chapter 2 for prey composition) of which we

found 57 known instances of carcasses being dragged from kill sites to cache sites. Of the

57, >95% of the drag distances were ≤50 m. The mean drag distance was 14.56 ± 14.11

m (SD). After buffering the moving and kill site locations, the number of 'used' and

'available' locations for the RSF models varied by season and study area (entire study

area versus LiDAR subset; Fig. 3.2).

Resource Selection by Mountain Lions while Moving

Using the dataset set from the entire study area, the top-performing model for

resource selection while mountain lions were moving through the landscape during the

summer included the variables of ruggedness, ruggedness^2, slope, slope^2, aspects of

north, south, and west, plus elevation (Table 3.3). The relationship of ruggedness and

slope indicated that the lions selected for increasing ruggedness and slope up to a

threshold, after which they selected against terrain that was too rugged and very steep

slopes. The model also showed significant selection against northern and western facing

aspects, and selection for eastern aspect, which was the intercept. Lions also selected for

higher elevations during the summer.

Using the dataset from the entire study area, the top-performing model for

resource selection while mountain lions were moving through the landscape during the

winter was similar to the summer model and included ruggedness, ruggedness^2, slope, slope^2, aspects of north, south, and west, plus elevation (Table 3.3). Again, same as during the summer, lions selected for increasing ruggedness and slope up to a threshold, then selected against slope and ruggedness. Lions during winter months also selected for higher elevations with respect to available locations, as well as, selected for eastern aspects.

Restricting our analysis to the subset of data within the LiDAR study area, we found the top-performing model for resource selection while lions moved through the landscape during the summer showed the same variables as the model using the entire study area, plus the addition of distance to a stream (Table 3.4). During the summer, lions preferred locations closer to a stream. The quadratic terms for slope and ruggedness were included in this model, similarly to the model for the entire study area. During winter, the top-performing model for resource selection included the same variables as the model using the entire study area, but lions now showed preference for northern, southern, and western aspects with respect to eastern aspects.

Resource Selection by Mountain Lions when Killing Prey

Using the dataset set from the entire study area, the top-performing model for resource selection while mountain lions were killing prey during the summer showed selection against steeper slopes (Table 3.3). The top-performing model during the winter showed selection for being within close proximity to the nearest road (Table 3.3).

Restricting our analysis to the subset of data within the LiDAR study area, we found two top-performing models for resource selection when lions killed prey during the

summer (Table 3.4); these two models accounted for 70.5% of the BIC model weight.

The top model contained the variables of distance to nearest road and distance to nearest

stream, and showed strong selection for lion kill sites to be in close proximity to roads

and skid trails, and in close proximity to streams. The second model contained the

variables of distance to nearest road and elevation, and showed strong selection for kill

sites being in close proximity to roads and skid trails, plus kill sites being at higher

elevations compared to available locations. Similar to the models for the summer, we

found two top-performing models for resource selection when lions killed prey during the

winter (Table 3.4); these two models accounted for 84.7% of the BIC model weight. The

first model contained the variables of distance to the nearest road and elevation, with lion

kill sites being within close proximity to roads and skid trails, and kill sites being at lower

elevations compared to available locations within the LiDAR study area. The second top

model contained the variables of distance to nearest road or skid trail, and distance to

nearest stream with strong selection again lion kill sites being within close proximity to

roads and skid trails, as well as, kill sites being closer to streams.

DISCUSSION

Our study on resource selection of mountain lions in the Sierra National Forest in

central California focused on a lion population that had not been studied for >25 years

(Neal et al. 1987) and was initiated due to the high amount of intraguild predation upon

fishers (Sweitzer et al. 2015, 2016). While we did have a small sample size of radio-

collared mountain lions (4 females, 1 male) in the study area, we do feel that we acquired

a representative perspective of landscape use by the collared mountain lions in the study area through examination of 250 kill sites and >8,300 moving locations. Examining resource selection with a subset of these kill sites and moving locations within the LiDAR imaged area also provided insight into lion space use in an area heavily bisected by old roads and skid trails that general GIS layers or 'road maps' did not provide. Within the full study area using only the currently mapped roads, we found that close proximity to roads was the top model for lion resource selection when killing prey during the winter months. Our results also indicated strong selection for close proximity to digitized roads and skid trails within the LiDAR subset study area when making kills during summer and winter. Due to the sensitivity of the fisher population in this region, this fragmented network of roads could subject fishers to increased predation risk.

Resource Selection by Mountain Lions while Moving

During both the summer and winter, the top-performing models of resource selection while mountain lions were moving through the entire study area showed selection for landscape variables including a quadratic function of ruggedness and slope indicating the lions selected for increasing slope and ruggedness up to a threshold, then selected against these variables. They also showed a preference for eastern aspects and higher elevations when compared to available locations. Using the subset of data in the LiDAR study area, our results for moving locations during the summer and winter were similar to the top models from the entire study area with two exceptions. The first exception demonstrated lions selecting against the threshold for ruggedness and slope

variables. After plotting the used locations, we found data limitations to be the cause. As previously mentioned, the LiDAR was done in a small section of the overall mountain lion study area and focused on flatter regions concentrated around forest treatments. This biased the data in a manner that did not coincide with the results from the full, unbiased study area. The second exception was that lions in the LiDAR study area showed selection against higher elevations in comparison to available locations. These results intuitively make sense if we assume that when a mountain lion is not either sleeping or at a kill site (i.e., at a cluster not associated with prey remains), then they are likely moving through the landscape selecting for rugged and steeper terrain that provides ambush terrain. As with other large felid species (e.g., Karanth and Sunquist 2000), mountain lions are ambush predators that select for landscape features such as dense brush and rugged terrain to facilitate stalking and increase predation success (Holmes and Laundre 2006, Atwood et al. 2009, Kunkel et al. 2013, Blake and Gese 2016). Moreover, mountain lions evolved for short bursts of speed and rely on remaining undetected until within a close distance while ambushing prey (Hornocker 1970). Young and Goldman (1946), Wilson (1984), and Holmes and Laundre (2006) reported the probability of a mountain lion making a successful kill was unlikely if the ambush attempt was initiated at a distance >25 m from their prey (Blake and Gese 2016).

Relative to elevation, our findings are congruent with Neal et al. (1987). During our study, we found that the mean elevation used by the radio-collared lions during the summer and winter was 1,799 m and 1,352 m, respectively, suggesting they shifted their home ranges from summer to winter to coincide with the elevation shift during migration

by the North Kings deer herd. Even the distribution of kill sites by lions showed shifts from higher elevations in the summer to lower elevations in winter (Fig. 3.6). While similar to our results, Neal et al. (1987) showed two distinct patterns of space use by mountain lions: some lions remained at lower elevations year round, while others shifted seasonally with respect to elevation (summer: 1600 – 2000 m, winter: 1000 – 1400 m); they concluded the lions were also matching the migration pattern of the North Kings deer herd. We did not capture and radio-collar any individuals that remained at lower elevations year-round; rather, they all demonstrated seasonal home range shifts from lower elevations in winter to higher elevations in summer.

Resource Selection by Mountain Lions while Killing Prey

Using the dataset covering the entire study area, we found the top-performing model for resource selection at kill sites during summer included slope and the quadratic for slope. Selecting against less steep slopes during the summer at kill sites indicated lions preferred a flat location (Fig. 3.7) that possibly provided forest debris and vegetative cover in which to safely feed and cache their kill. The top model for kill sites during the winter for the entire study area showed selection for being within close proximity to roads in the study area. It is important to mention that the main paved roads (Highway 168, Dinkey Creek Road, McKinley Grove Road, and Peterson Mill Road) received high traffic use during the summer. During winter, with exception of Highway 168 and Dinkey Creek road, the rest of the roads in the study area were usually covered with snow most of the winter and behind locked entrance gates, which decreased anthropogenic road use during the winter, with the exception of a few snowmobilers.

Thus, during the winter, lions used these main roads more frequently and kill sites were in close proximity to these roads.

We re-emphasize that the main objective for examining resource selection within the LiDAR imaged area was to determine whether mountain lion kill sites was influenced by the network of old roads and skid trails that were not mapped in the conventional 'road layers'. Using the subset of data contained within the LiDAR imaged area, the resource selection models showed that kill sites for mountain lions during the summer and winter contained the same three landscape variables: distance to the nearest road, distance to the nearest stream, and elevation. As we predicted, kill sites within the LiDAR study area showed strong selection for close proximity to roads and skid trails in the top models during summer and winter months. These anthropogenically created linear landscape features were characterized by early successional browse and these old roads and skid trails have turned into wildlife trails for mule deer and, in turn, high selection by mountain lions. Consistent with the idea of mountain lions being a forest generalist, studies have shown they tend to avoid major highways, but will tolerate dirt roads and trails in habitat that is less human-dominated (Van Dyke et al. 1986, Laing 1988, Jalktozy et al. 1999, Fecske et al. 2003). Beier (1995) and Dickson et al. (2005) demonstrated that unpaved roads and trails may facilitate lion movement through thick vegetation. Lions have also been known to cache prey and even daybed near campgrounds and heavily used trails (Ruth 1991, Beier 1995, Jalkotzy et al. 1999, Sweanor et al. 2008, Reith 2010). Wallmo et al. (1972) conducted a study where they created strips of forest which alternated between clear-cut strips and uncut strips. Fifteen years after these logging

events, they recorded mule deer obtained 63.3% of their forage from these cut strips and 9.3% along logging roads, while 27.4% of their forage was obtained from the uncut strips. On a study in northern Utah, Collins and Urness (1983) found mule deer preferred clear-cut lodgepole pine and aspen forest, and that clear-cutting greatly increased mule deer and elk grazing use. Reynolds (1966a, 1966b) found deer and elk in Arizona to utilize logged areas adjacent to uncut timber which is synonymous with the fragmentation caused by roads and skid trails and adjacent uncut forest in our study area (Scotter 1980). Since LiDAR was done in only a small section of the study area to monitor prescription forest treatments, we assume there is a high density of unmapped roads and skid trails within the entire study area and these anthropogenically-created linear landscape features influence the movement and resource selection of both predator and prey.

MANAGEMENT IMPLICATIONS

The primary impetus for our study on resource selection was the finding that mountain lions were killing radio-collared fishers (Wengert et al. 2014, Gabriel et al. 2015). During the 2-year predation study, we did not find any fisher remains at any of the 250 kill sites made by our radio-collared lions (Chapter 2). Another study (Blake and Gese 2016) found while most lions preferred mule deer, there can be individuals that specialize killing another species (e.g., bighorn sheep). It is possible that we did not radio-collar an individual lion that had learned to specialize on fishers. However, our study overlapped with the continuing KRFP research which involved an intensive fisher

trapping and monitoring effort, and they only documented one instance of lion predation on a radio-collared fisher during our study.

Our data showed that mountain lions in the Sierra National Forest preferred certain landscape characteristics such as ruggedness, slope and elevation while moving through the landscape (Figs. 3.8 and 3.9). From a management perspective, little can be done to modify these landscape attributes to reduce predation risk from mountain lions. However, 3 of the 4 models for resource selection by lions when killing prey demonstrated a high probability of kills being within close proximity to roads and skid trails (Figs. 3.10 and 3.11). Research has demonstrated that logging and other forest habitat practices that modify forest structure have led to the decrease in fisher populations and overall habitat extent (Lewis et al. 2012, Sweitzer et al. 2015, 2016). While a fisher is not much of a meal for a mountain lion, we believe that mountain lions are not actively targeting fishers as prey items (Chapter 2) but moreover, lions are opportunistic hunters and are likely killing fishers that wander across their path or attempt to scavenge from a lion kill. However, even this low level of intraguild predation could have population level effects on fishers (Wengert et al. 2014). The fisher population in the Sierra National Forest is facing many obstacles to population expansion including predation, habitat loss and fragmentation, vehicle strikes, and toxicants used by illegal marijuana farmers (Sweitzer et al. 2015). To reduce predation risk on fishers, we recommend that skid trails and roads that were cut through the forest for timber harvest and fire management could be replanted to reduce ambush cover for lions. These linear features add to 'edge' habitat for mule deer, which is subsequently attractive to lions, and may even serve as 'gauntlets'

for fishers to travel through exposing them to predation by mountain lions. Historically, it is possible that mountains lions depredated upon fishers only occasionally. However, they likely encountered each other very rarely and there were no 'gauntlet-type areas' created by roads and skid trails. Moreover, fire return intervals in California have changed dramatically since European settlement. Historically, fire return intervals were shorter resulting in less intensive and severe fires that burned over larger expanses (Sugihara et al. 2006). Furthermore, fire does not create linear features that would funnel wildlife in the manner that roads and skid trails seem to in our study area. Lastly, extensive skid trail networks directly affect vegetation communities and can result in a shift away from interior forest species, which are less light tolerant and lower in nutrients as compared to ruderal and oftentimes noxious or invasive species (Zenner and Berger 2008). This shift in forest composition could contribute to a loss of fisher habitat since current timber practices within the study area do not incorporate replanting of tree species.

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TABLES AND FIGURES

Table 3.1. Mean distances (m) traveled by mountain lions between kill sites and moving locations during the summer and winter, Sierra National Forest, California, 2014-2016.

Mountain Lion ID	Summer		Winter	
	Kill site	Moving	Kill site	Moving
PF01	5246	693	4800	612
PF02	6920	462	N/A	N/A
PF04	5038	607	4504	753
PF05	4568	736	N/A	523
PM03	10,530	1321	8,633	823

Table 3.2. Total used and available locations for kill sites and moving locations of mountain lions in the full study area and the subset LiDAR area during summer and winter, Sierra National Forest, California, 2014-2016.

	Used	Available
Kill sites		
Full Study Area		
Summer	187	4675
Winter	63	1575
Total	250	6250
Lidar Area		
Summer	62	1550
Winter	42	1050
Total	104	2600
Moving locations		
Full Study Area		
Summer	5719	142974
Winter	2583	64575
Total	8302	207550
Lidar Area		
Summer	1869	46725
Winter	1058	26450
Total	2927	73175

Table 3.3. Coefficients, standard errors (SE), and P-values for the top-performing resource selection models for mountain lions while moving and killing for the dataset covering the entire study area during the summer and winter, Sierra National Forest, California, 2014-2016.

Season					
Behavioral state	BIC model weight (%)	Landscape variable	Coefficients	SE	P
Summer					
Moving	97.6	Ruggedness	0.194	0.079	0.013
		Ruggedness^2	-0.154	0.032	<0.001
		Slope	0.233	0.017	<0.001
		Slope^2	-0.183	0.012	<0.001
		Aspect_North	-0.814	0.053	<0.001
		Aspect_South	-0.020	0.037	0.591
		Aspect_West	-0.128	0.038	<0.001
		Elevation	0.312	0.018	<0.001
Kill sites	85.9	Slope	-0.341	0.094	<0.001
		Slope^2	-0.177	0.086	0.039
Winter					
Moving	97.8	Ruggedness	0.389	0.124	<0.001
		Ruggedness^2	-0.005	0.068	0.002
		Slope	0.141	0.255	0.939
		Slope^2	-0.154	0.020	<0.001
		Aspect_North	-0.857	0.082	<0.001
		Aspect_South	-0.001	0.056	0.987
		Aspect_West	-0.168	0.059	0.004
		Elevation	0.142	0.025	<0.001
Kill sites	63.1	Distance to mapped road	-0.520	0.196	0.008

Table 3.4. Coefficients, standard errors (SE), and P-values for the top-performing resource selection models for mountain lions while moving and killing for the subset of data covering the LiDAR study area during the summer and winter, Sierra National Forest, California, 2014-2016.

Season					
Behavioral state	BIC model weight (%)	Landscape variable	Coefficients	SE	P
Summer					
Moving	72.8	Distance to stream	-0.053	0.026	0.042
		Ruggedness	0.144	0.152	0.034
		Ruggedness²	0.249	0.075	<0.001
		Slope	-0.363	0.025	<0.001
		Slope²	0.139	0.017	<0.001
		Aspect_North	2.412	0.095	<0.001
		Aspect_South	0.209	0.107	0.050
		Aspect_West	-0.136	0.113	0.229
		Elevation	-0.433	0.022	<0.001
Kill sites	39.9	Distance to digitized road	-2.769	0.585	<0.001
		Distance to stream	-0.311	0.157	0.048
	30.6	Distance to digitized road	-2.748	0.581	<0.001
		Elevation	0.299	0.149	0.045
Winter					
Moving	94.7	Ruggedness	0.372	0.186	0.046
		Ruggedness²	0.420	0.099	<0.001
		Slope	-0.349	0.032	<0.001
		Slope²	0.163	0.026	<0.001
		Aspect_North	1.439	0.128	<0.001
		Aspect_South	0.326	0.143	0.023
		Aspect_West	0.499	0.145	<0.001
		Elevation	-0.251	0.029	<0.001
Kill sites	56.9	Distance to digitized road	-4.373	1.044	<0.001
		Elevation	-0.447	0.206	0.029
	27.8	Distance to digitized road	-4.418	1.069	<0.001
		Distance to stream	-0.33	0.187	0.077
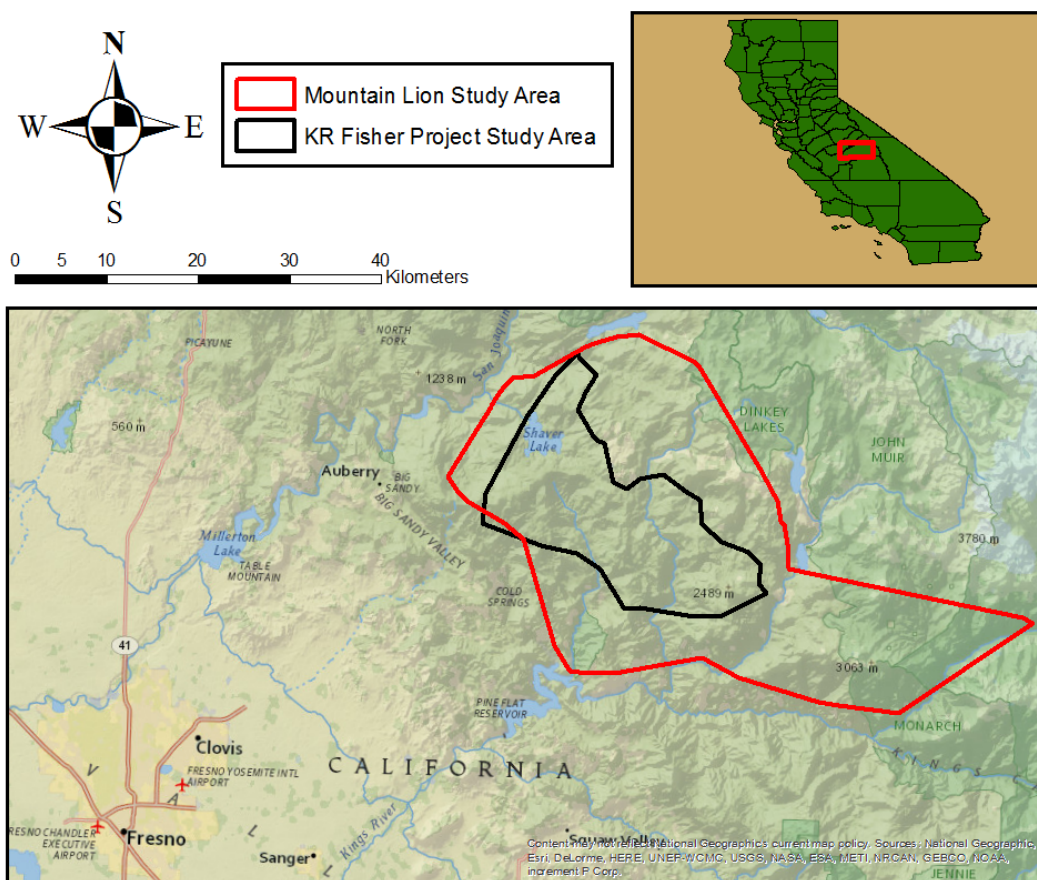
Figure 3.1. The 1336-km² study area encompassing all home ranges of radio-collared mountain lions, Sierra National Forest, California, 2014-2016.
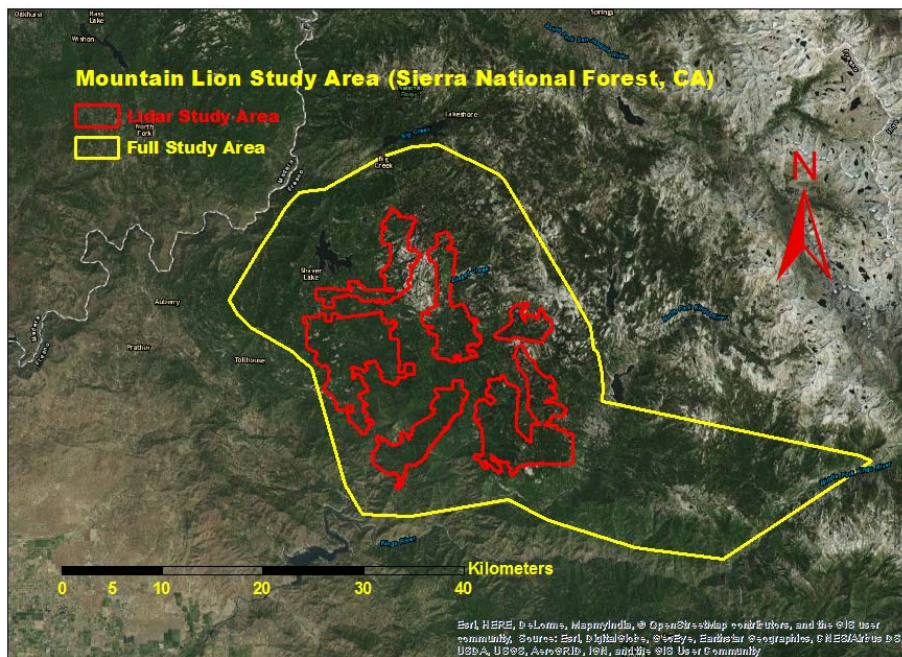
Figure 3.2. The 1336-km² full study area and the 238-km² LiDAR study area encompassing all home ranges of radio-collared mountain lions, Sierra National Forest, California, 2014-2016.
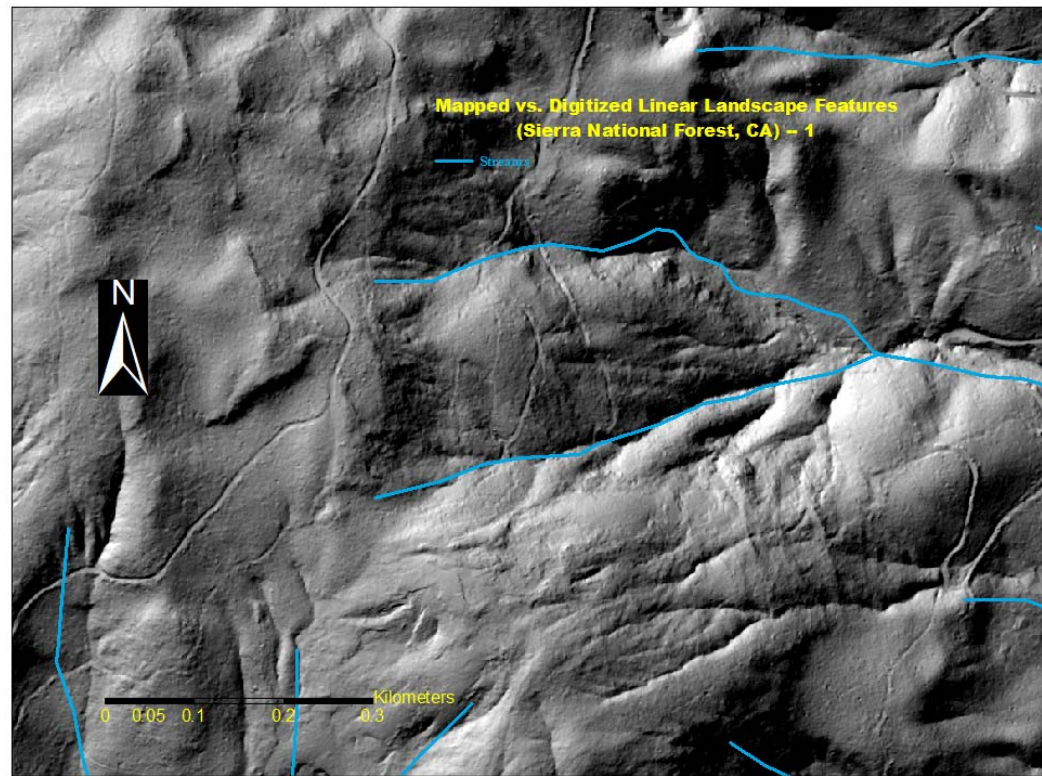
Figure 3.3. Map of study area with stream shapefile overlaying the LiDAR Bare Earth raster layer without mapped roads or digitized roads and skid trails, Sierra National Forest, California. The purpose is to illustrate the contrast between existing roads, skid trails, and roadless areas.
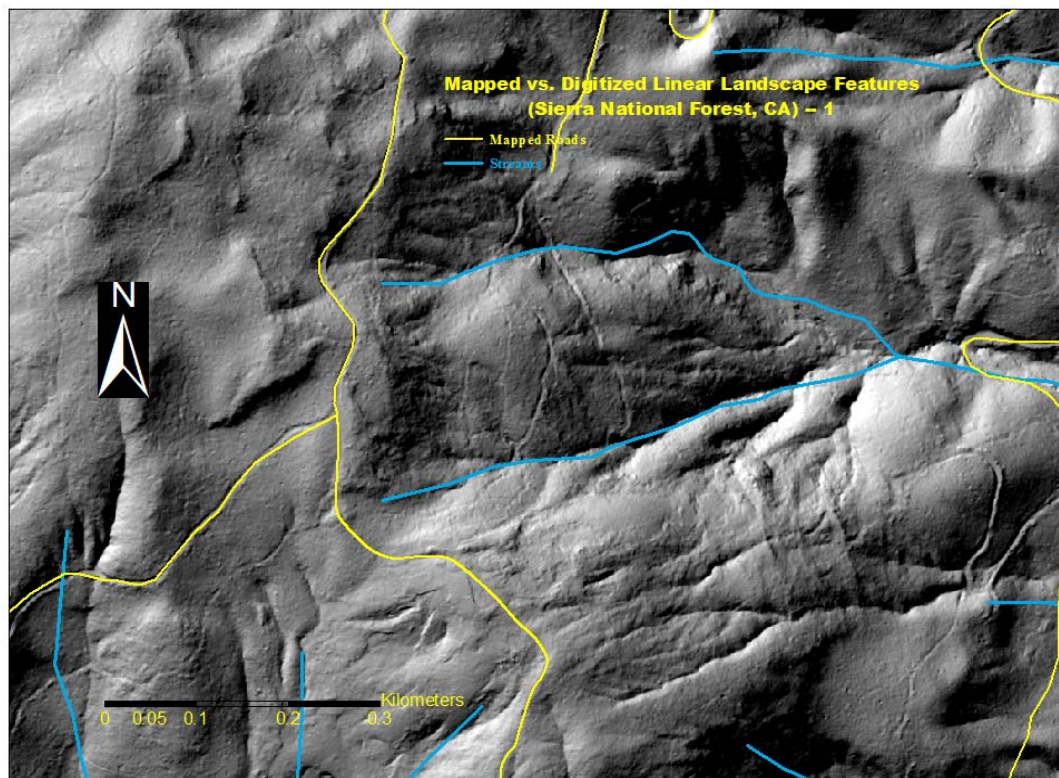
Figure 3.4. Map of study area with streams and mapped roads shapefiles overlaying the LiDAR Bare Earth raster layer illuminating existing unmapped roads and skid trails, Sierra National Forest, California.
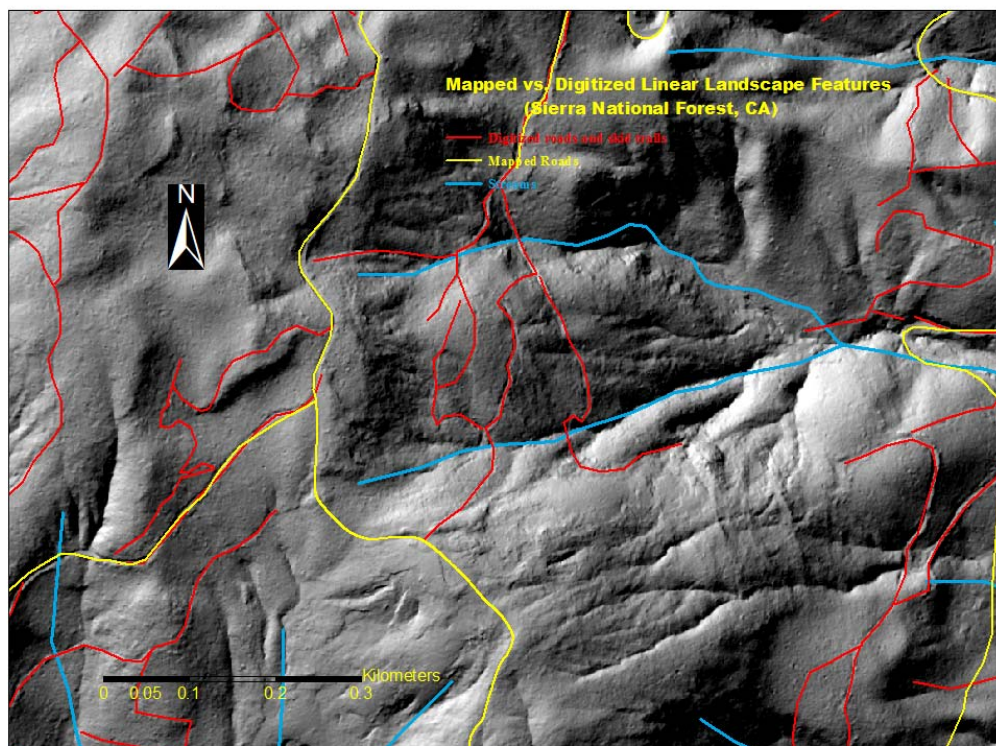
Figure 3.5. Map of study area showing streams, mapped roads, and digitized roads and skid trails shapefiles overlaying the LiDAR Bare Earth raster layer, Sierra National Forest, California.
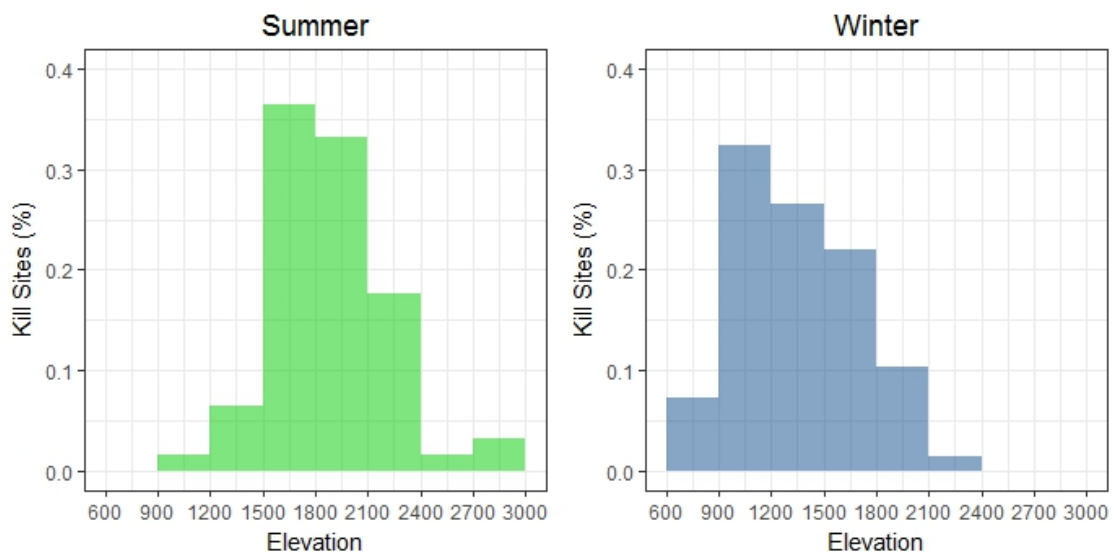
Figure 3.6. Influence of elevation on mountain lion kill sites during the summer and winter, Sierra National Forest, California, 2014-2016
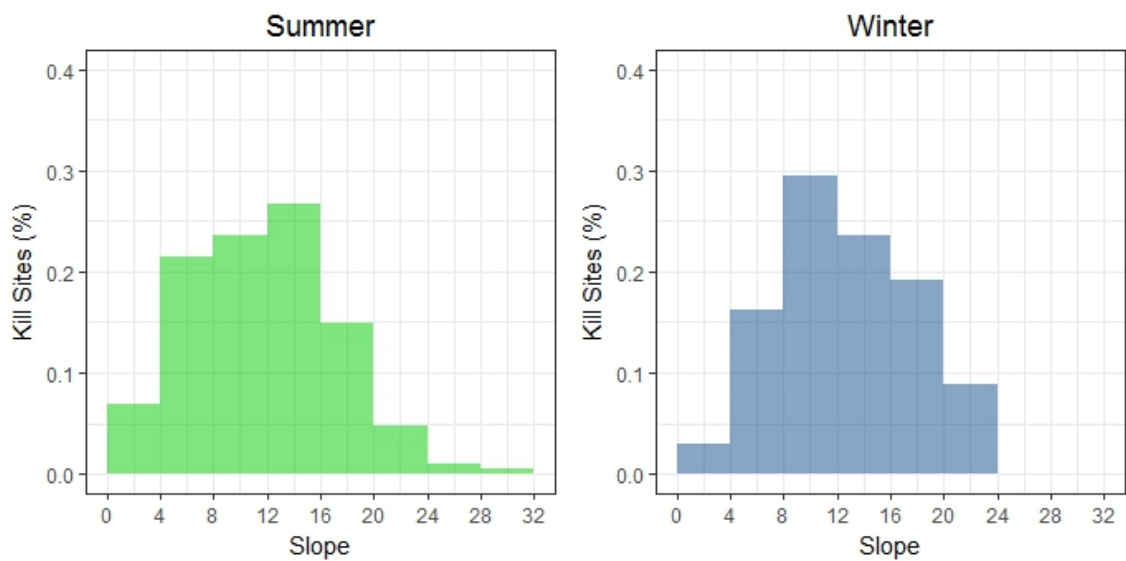
Figure 3.7. Influence of slope on mountain lion kill sites during the summer and winter, Sierra National Forest, California, 2014-2016.
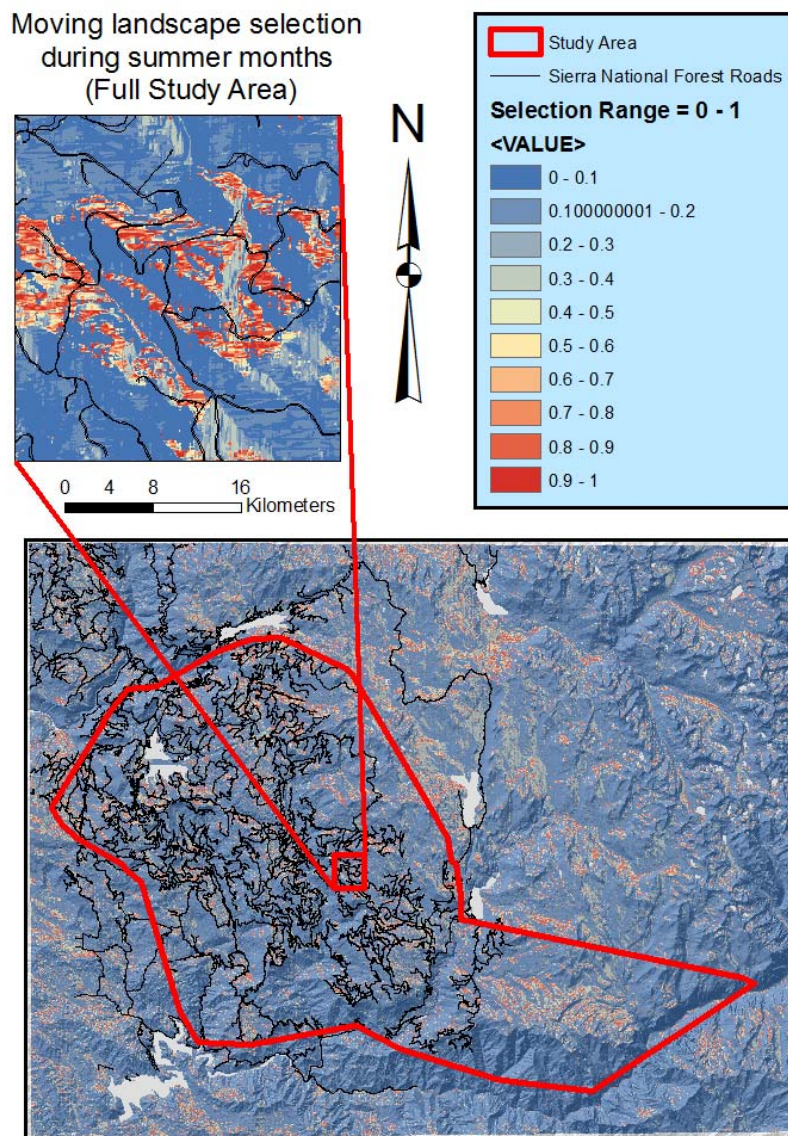
Figure 3.8. Map of resource selection by mountain lions while moving during the summer within the full study area, Sierra National Forest, California, 2014-2016. The top model showed selection a variety of terrain variables. The winter map consisted of the same top model.
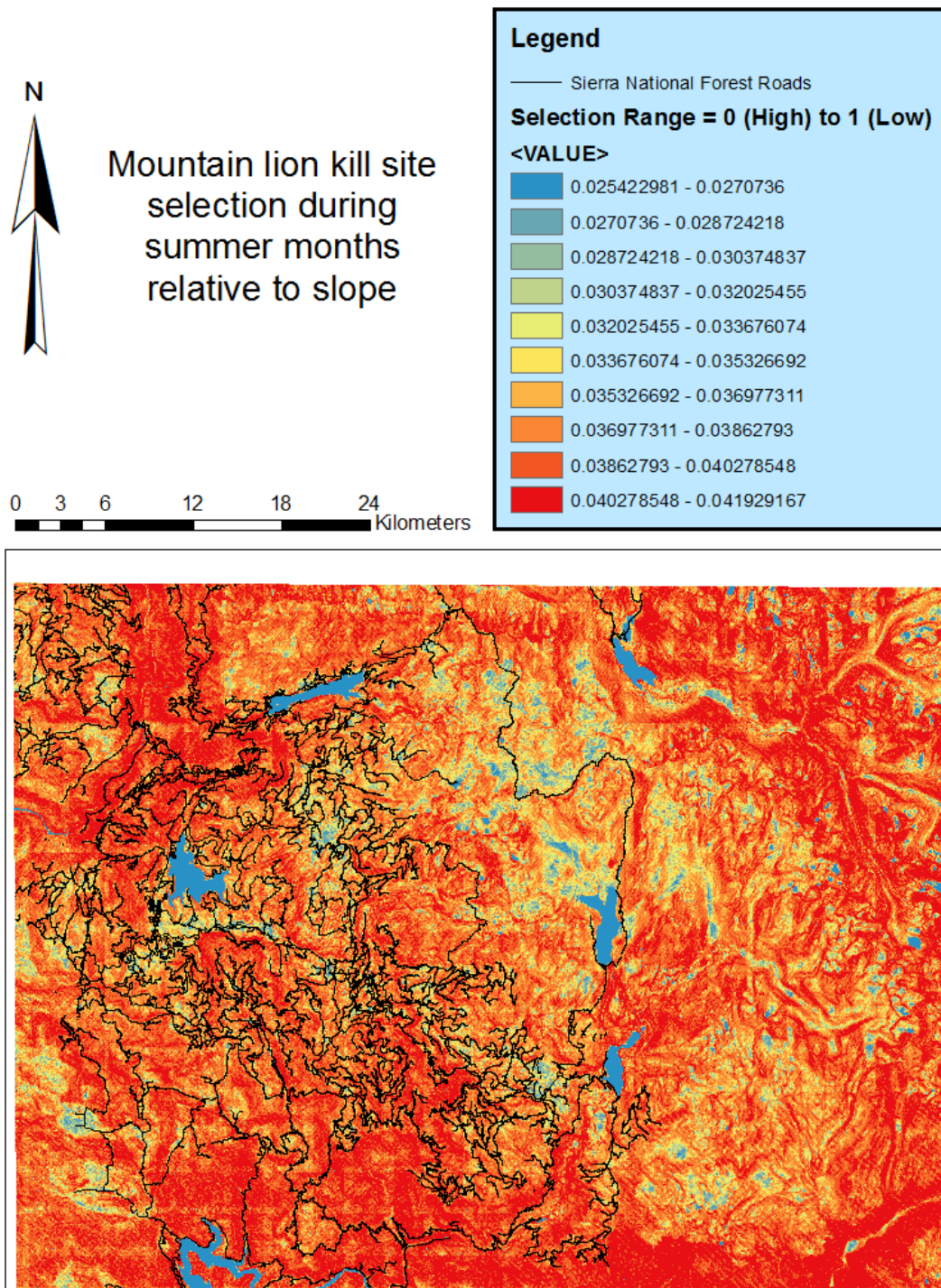
Figure 3.9. Map of resource selection for the quadratic of slope by mountain lions at kill sites during the summer within the full study area, Sierra National Forest, California, 2014-2016.

Figure 3.10. Map of resource selection for close proximity to roads by mountain lions at kill sites during the winter within the full study area, Sierra National Forest, California, 2014-2016.
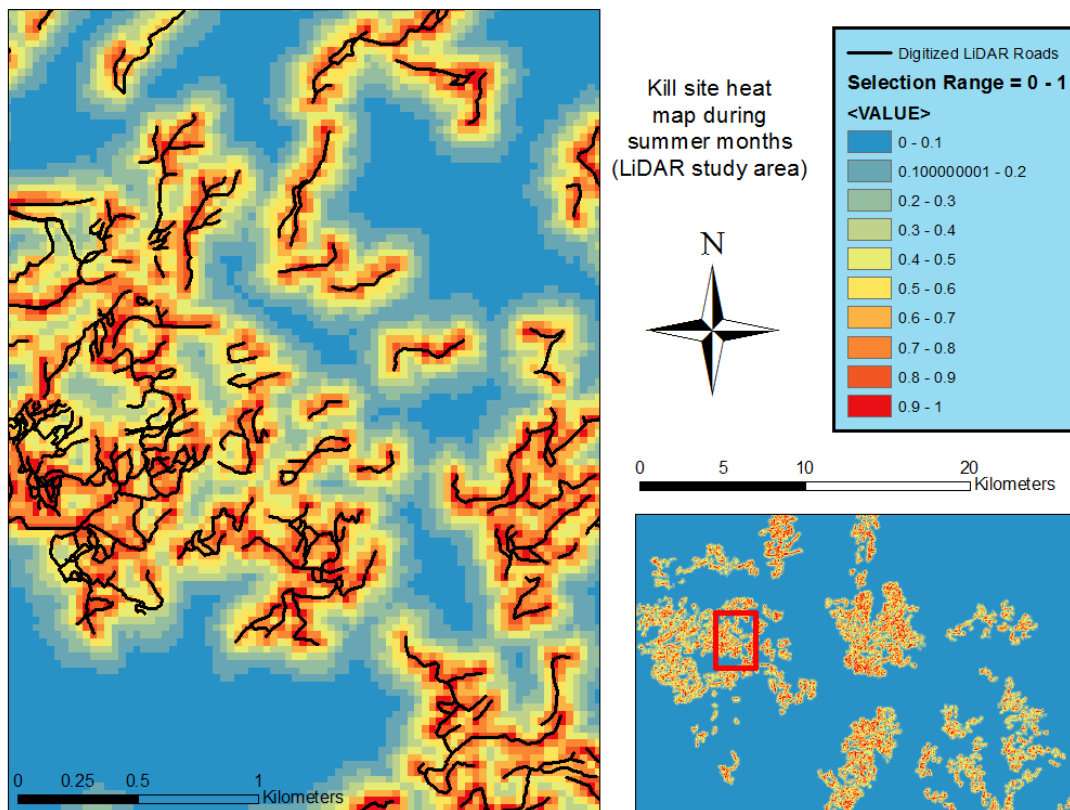
Figure 3.11. Map of resource selection for close proximity to digitized roads and skid trails by mountain lions at kill sites during the summer within the subset LiDAR study area, Sierra National Forest, California, 2014-2016. The top model for winter months showed selection for close proximity to digitized roads and skid trails as well.
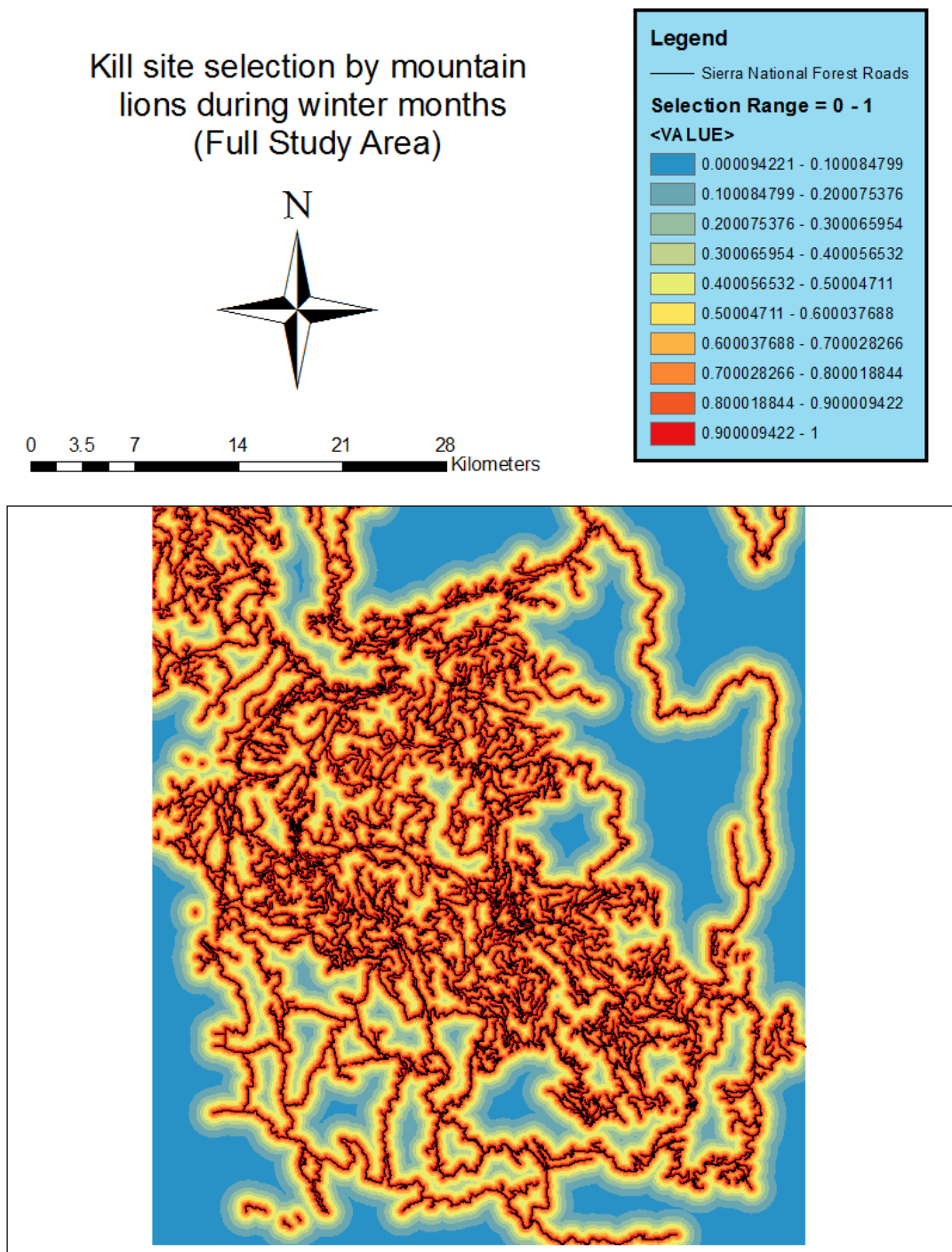
CHAPTER 4

CONCLUSIONS

Our research increased our understanding of the foraging ecology of mountain lions (*Puma concolor*) by examining prey composition, kill rates, and landscape use in the Sierra National Forest of California. Moreover, knowledge of resource selection by mountain lions may assist in ongoing efforts to mitigate intraguild predation upon fishers (*Pekania pennanti*) by lions. Based on the research conducted by the Kings River Fisher Project (KRFP), we were aware that mountain lions killed fishers (Sweitzer et al. 2015). We predicted that mule deer (*Odocoileus hemionus*) would comprise the largest percentage of lion kills, but we did not expect to document gray foxes (*Urocyon cinereoargenteus*) making up 13% of overall prey composition (Chapter 2). Though we did not detect any predation upon fishers at kill sites of our radio-collared lions, we point out that we did not have all lions in the research area radio-collared as evidenced by photos of non-collared lions from the remote camera surveys. Prior research has shown that certain individual mountain lions can become specialists on a particular prey species (Ross et al. 1997, Logan and Sweanor 2001, Blake and Gese 2016). Therefore, it is possible there was an individual lion that had specialized on killing fishers in the earlier years of the KRFP research. It is also important to mention that there was extremely low fisher juvenile (kit) survival in the study area during our study between 2014-2016, which could explain our not detecting fisher remains at mountain lion GPS clusters (R. Green, personal communication). Of equal importance is the knowledge that the ecosystem on the Sierra National Forest is a single-ungulate system comprised of mule deer, and

therefore, it is possible that during winter, fishers will be at a greater risk of predation by mountain lions due to a lack of fawns or another ungulate species to supplement lion diets. Knopff et al. (2010) found that subadult lions killed the highest percentage of non-ungulate prey which also suggests that fishers may be at a higher risk of predation when subadult lions are present.

Consistent with Laundre (2005), we found adult females spent more time at kills than both adult males and adult females with kittens. We found adult males displayed shorter handling times of adult deer and juvenile deer during summer months relative to adult females killing adult deer and juvenile deer in the summer. We found kleptoparasitism by black bears did not affect handling time even though there was a weak correlation demonstrating shorter handling times when bears scavenged the carcass. In contrast, Allen et al. (2014) found a significant relationship between lion handling times and black bear detection rates of lion kills. We did notice seasonal variation in kill rates (i.e., higher rates during summer months) but did not detect significant effects of lion kill detection by black bears even though we found that black bears detected many lion kills. Without an estimate of lion density and deer abundance, however, we are unable to determine why bear kleptoparasitism did not affect lion kill rates on our study area; perhaps deer density is low and mountain lions in our study area are more likely to attempt to continue feeding after black bear detection of their kill.

Similar to other studies, we found mountain lions in the study area selected for certain landscape attributes at kill sites and while moving. During the summer and winter, lions selected for rugged terrain and slope up to a threshold where they began selecting

against these variables, as well as, higher elevations as compared to random locations. Regarding kill sites, lions selected for less steep slopes during the summer. However, during winter months in the full study area, as well as during the summer and winter in the LiDAR area, lions showed strong selection for close proximity to roads (entire study area) and close proximity to the old roads and skid trails (LiDAR study area). From a management perspective, not much can be done with respect to landscape factors such as slope, elevation, aspect, and ruggedness to mitigate fisher predation by mountain lions. Attempts to replant temporary skid trails and old roads to alleviate habitat fragmentation and reduce ambush habitat for lions may be of benefit to fisher survival, but this effect remains untested.

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APPENDICES

Appendix A. Vegetation Landfire data reclassification for the Sierra National Forest, California.

Vegetation Reclassified	Landfire Vegetation Class Categories	Landfire Vegetation Classification
Other	Agricultural	Agricultural-Orchard
	Agricultural	Agricultural-Vineyard
	Agricultural	Agricultural-Bush fruit and berries
	Agricultural	Agricultural-Row Crop-Close Grown Crop
	Agricultural	Agricultural-Row Crop
	Agricultural	Agricultural-Close Grown Crop
	Agricultural	Agricultural-Fallow/Idle Cropland
	Agricultural	Agricultural-Pasture and Hayland
	Agricultural	Agricultural-Wheat
	Agricultural	Agricultual-Aquaculture
	Agricultural	Agriculture-Pasture and Hay
	Agricultural	Agriculture-Cultivated Crops and Irrigated Agriculture
	Barren	Barren
	Developed	Developed-Upland Deciduous Forest
	Developed	Developed-Upland Evergreen Forest
	Developed	Developed-Upland Mixed Forest
	Developed	Developed-Upland Herbaceous
	Developed	Developed-Upland Shrubland
	Developed	Developed-General

Figure continues

Developed	Developed-Open Space
Developed	Developed-Low Intensity
Developed	Developed-Medium Intensity
Developed	Developed-High Intensity
Developed-High Intensity	Developed-High Intensity
Developed-Low Intensity	Developed-Low Intensity
Developed-Medium Intensity	Developed-Medium Intensity
Developed-Roads	Developed-Roads
Exotic Herbaceous	Introduced Annual Grassland
Exotic Herbaceous	Introduced Perennial Grassland and Forbland
Exotic Herbaceous	Introduced Annual and Biennial Forbland
Exotic Herbaceous	Introduced Herbaceous Wetland Vegetation
Exotic Tree-Shrub	Introduced Riparian Vegetation
Exotic Tree-Shrub	Introduced Wetland Vegetation
Exotic Tree-Shrub	Introduced Upland Vegetation-Treed
Grassland	Alpine Dwarf-Shrubland, Fell-field and Meadow
Grassland	Dry Tundra
Grassland	Grassland
Grassland	Grassland and Steppe
Grassland	Mixedgrass Prairie
Grassland	Sand Prairie
Grassland	Shortgrass Prairie
Grassland	Tallgrass Prairie
Grassland	Atlantic Dunes and Grasslands

Figure continues

Grassland	Black Oak Woodland and Savanna
Grassland	Inland Marshes and Prairies
Grassland	Prairies and Barrens
Grassland	Introduced Perennial Grassland and Forbland
Grassland	Transitional Herbacous Vegetation
Grassland	Modified-Managed Prairie Grassland
Grassland	Beach Meadow
Grassland	Boreal Grassland
Grassland	Dune Grassland
Grassland	Herbaceous Meadow
Grassland	Hawai'i Dry Grassland
Grassland	Hawai'i Mesic Grassland
Non-vegetated	Open Water
Non-vegetated	Snow-Ice
Non-vegetated	Barren
Non-vegetated	Bedrock, Scree, and Talus
Open Water	Open Water
Quarries-Strip Mines-Gravel Pits	Quarries-Strip Mines-Gravel Pits
Riparian	Pacific Coastal Marsh
Riparian	Red Alder Forest and Woodland
Riparian	Western Riparian Woodland and Shrubland
Riparian	Western Herbaceous Wetland
Riparian	Spruce-Fir Forest and Woodland
Riparian	Western Red-cedar-Western Hemlock Forest
Riparian	Depressional Wetland

Figure continues

Riparian	Atlantic Coastal Marsh	
Riparian	Eastern Floodplain Forests	
Riparian	Eastern Small Stream Riparian Forests	
Riparian	Inland Marshes and Prairies	
Riparian	Jack Pine Forest	
Riparian	Mangrove	
Riparian	Peatland Forests	
Riparian	Atlantic Swamp Forests	
Riparian	Introduced Woody Wetland Vegetation	
Riparian	Introduced Herbaceous Wetland Vegetation	
Riparian	Freshwater Aquatic Bed	
Riparian	Freshwater Marsh	
Riparian	Riparian Stringer Forest and Shrubland	
Riparian	Shrub and Herbaceous Floodplain Wetland	
Riparian	Shrub and Herbaceous Peatlands	
Riparian	Tidal Flat	
Riparian	Tidal Marsh	
Riparian	Wet Meadow	
Riparian	Pacific Islands Scrub Forest/Shrub	
Riparian	Pacific Islands Swamp/Marsh	
Riparian	Caribbean Shrub/Herbaceous Wetland	
Riparian	Caribbean Mangrove Forest	
Riparian	Caribbean Forested Wetland	
Riparian	Caribbean Forested Wetland	
Snow-Ice	Snow-Ice	
Sparsely Vegetated	Sparse Vegetation	
Conifer	Conifer	Chaparral

Figure continues

Conifer	Conifer-Oak Forest and Woodland
Conifer	Douglas-fir Forest and Woodland
Conifer	Douglas-fir-Western Hemlock Forest and Woodland
Conifer	Juniper Woodland and Savanna
Conifer	Limber Pine Woodland
Conifer	Lodgepole Pine Forest and Woodland
Conifer	Douglas-fir-Ponderosa Pine-Lodgepole Pine Forest and Woodland
Conifer	California Mixed Evergreen Forest and Woodland
Conifer	Mountain Hemlock Forest and Woodland
Conifer	Mountain Mahogany Woodland and Shrubland
Conifer	Pinyon-Juniper Woodland
Conifer	Ponderosa Pine Forest, Woodland and Savanna
Conifer	Red Fir Forest and Woodland
Conifer	Redwood Forest and Woodland
Conifer	Sitka Spruce Forest
Conifer	Spruce-Fir Forest and Woodland
Conifer	Subalpine Woodland and Parkland
Conifer	Western Hemlock-Silver Fir Forest
Conifer	Douglas-fir-Grand Fir-White Fir Forest and Woodland
Conifer	Western Larch Forest and Woodland
Conifer	Western Red-cedar-Western Hemlock Forest
Conifer	Red Pine-White Pine Forest and Woodland
Conifer	Jack Pine Forest

Figure continues

	Longleaf Pine
Conifer	Woodland
Conifer	Peatland Forests
Conifer	Pine Flatwoods
	Pine-Hemlock-Hardwood
Conifer	Forest
	Pitch Pine
Conifer	Woodlands
	Shortleaf Pine
Conifer	Woodland
	Spruce-Fir-Hardwood
Conifer	Forest
	Virginia Pine
Conifer	Forest
	Loblolly Pine Forest and
Conifer	Woodland
	Loblolly Pine-Slash Pine Forest and
Conifer	Woodland
	Transitional Forest
Conifer	Vegetation
	Managed Tree
Conifer	Plantation
	Black Spruce Forest and
Conifer	Woodland
	Western Hemlock-Yellow-
Conifer	cedar Forest
	White Spruce Forest and
Conifer	Woodland
	White Spruce Forest and
Conifer	Woodland
	Aspen-Mixed Conifer Forest and
Conifer-Hardwood	Woodland
	Conifer-Oak Forest and
Conifer-Hardwood	Woodland
	Chestnut Oak-Virginia Pine Forest
Conifer-Hardwood	and Woodland
	Red Pine-White Pine Forest and
Conifer-Hardwood	Woodland
Conifer-Hardwood	Glades and Barrens
Conifer-Hardwood	Jack Pine Forest
Conifer-Hardwood	Pine Flatwoods
	Pine-Hemlock-Hardwood
Conifer-Hardwood	Forest

Figure continues

	Conifer-Hardwood	Shortleaf Pine-Oak Forest and Woodland
	Conifer-Hardwood	Spruce-Fir-Hardwood Forest
	Conifer-Hardwood	Juniper-Oak
	Conifer-Hardwood	Ruderal Forest
	Conifer-Hardwood	White Spruce-Hardwood Forest and Woodland
Hardwood	Hardwood	Aspen Forest, Woodland, and Parkland
	Hardwood	Bigtooth Maple Woodland
	Hardwood	Conifer-Oak Forest and Woodland
	Hardwood	Western Oak Woodland and Savanna
	Hardwood	Red Alder Forest and Woodland
	Hardwood	Aspen-Birch Forest
	Hardwood	Beech-Maple-Basswood Forest
	Hardwood	Texas Live Oak
	Hardwood	Cypress
	Hardwood	Coastal Plain Oak Forest
	Hardwood	Bur Oak Woodland and Savanna
	Hardwood	White Oak-Red Oak-Hickory Forest and Woodland
	Hardwood	Chestnut Oak Forest and Woodland
	Hardwood	Post Oak Woodland and Savanna
	Hardwood	Black Oak Woodland and Savanna
	Hardwood	Chestnut Oak-Virginia Pine Forest and Woodland
	Hardwood	Red Pine-White Pine Forest and Woodland
	Hardwood	White Oak-Beech Forest and Woodland
	Hardwood	Hammocks

Figure continues

	Hardwood
Hardwood	Flatwoods
Hardwood	Jack Pine Forest
Hardwood	Maritime Forest
Hardwood	Sweetgum-Water Oak Forest
Hardwood	Montane Oak Forest
Hardwood	Yellow Birch-Sugar Maple Forest
Hardwood	Pine-Hemlock-Hardwood Forest
Hardwood	Spruce-Fir-Hardwood Forest
Hardwood	Introduced Upland Vegetation-Treed
Hardwood	Managed Tree Plantation
Hardwood	Balsam Poplar-Aspen Woodland
Hardwood	Birch-Aspen Forest
Hardwood	Birch-Cottonwood-Poplar Forest
Hardwood	Dry Aspen-Steppe Bluff
Hardwood	Floodplain Forest and Shrubland
Hardwood	Hawai'i Rainforest
Hardwood	Hawai'i Dry Forest
Hardwood	Hawai'i Mesic Forest
Hardwood	Pacific Islands Limestone Forest
Hardwood	Pacific Islands Littoral/Strand Vegetation
Hardwood	Pacific Islands Lowland Forest
Hardwood	Pacific Islands Mangrove Forest
Hardwood	Pacific Islands Palm Forest
Hardwood	Pacific Islands Ravine Forest
Hardwood	Pacific Islands Savannah

Figure continues

	Hardwood	Pacific Islands Upland Forest
	Hardwood	Caribbean Deciduous Forest
	Hardwood	Caribbean Mixed Evergreen Deciduous Forest
	Hardwood	Caribbean Mixed Evergreen Deciduous Forest
	Hardwood	Caribbean Evergreen Forest
	Hardwood	Caribbean Evergreen Forest
	Hardwood	Caribbean Evergreen Forest
	Hardwood	Caribbean Evergreen Forest
	Hardwood-Conifer	Chestnut Oak-Virginia Pine Forest and Woodland
Shrubland	Shrubland	Aspen Forest, Woodland, and Parkland
	Shrubland	Big Sagebrush Shrubland and Steppe
	Shrubland	Blackbrush Shrubland
	Shrubland	Chaparral
	Shrubland	Pacific Coastal Scrub
	Shrubland	Creosotebush Desert Scrub
	Shrubland	Deciduous Shrubland
	Shrubland	Desert Scrub
	Shrubland	Grassland and Steppe
	Shrubland	Greasewood Shrubland
	Shrubland	Low Sagebrush Shrubland and Steppe
	Shrubland	Mesquite Woodland and Scrub
	Shrubland	Mountain Mahogany Woodland and Shrubland
	Shrubland	Salt Desert Scrub
	Shrubland	Sand Shrubland
	Shrubland	Succulent Desert Scrub
	Shrubland	Tallgrass Prairie

Figure continues

	Alpine-Subalpine
Shrubland	Barrens
Shrubland	Great Lakes Alvar
	Heathland and
Shrubland	Grassland
Shrubland	Jack Pine Forest
Shrubland	Pocosin
	Southern Scrub
Shrubland	Oak
	Introduced Upland
Shrubland	Vegetation-Shrub
	Transitional Shrub
Shrubland	Vegetation
Shrubland	Alder Shrubland
Shrubland	Avalanche Slope Shrubland
Shrubland	Dwarf Shrubland
	Periglacial Woodland and
Shrubland	Shrubland
Shrubland	Shrub Swamp
Shrubland	Shrub Tundra
Shrubland	Sparse Shrub and Fell-field
Shrubland	Sparse Tundra
	Spruce-Lichen
Shrubland	Woodland
Shrubland	Tussock Tundra
Shrubland	Willow Shrubland
	Hawai'i Dry
Shrubland	Shrubland
	Hawai'i Mesic
Shrubland	Shrubland