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Movement Behavior and Habitat Selection of Juvenile Mountain Lions (*Puma concolor*) During Three Behavioral States of Dispersal

John F. Randolph
Utah State University

MOVEMENT BEHAVIOR AND HABITAT SELECTION OF JUVENILE MOUNTAIN LIONS *(PUMA CONCOLOR)* DURING THREE BEHAVIORAL STATES OF DISPERSAL

by

John F. Randolph

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Approved:

Julie K. Young, Ph.D. Major Professor	David C. Stoner, Ph.D. Committee Member
Norah P. Saarman, Ph.D. Committee Member	D. Richard Cutler, Ph.D. Vice Provost of Graduate Studies

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ABSTRACT

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by

John F. Randolph, Master of Science

Utah State University, 2024

Major Professor: Dr. Julie K. Young
Department: Wildland Resources

Dispersal is dangerous. Animals must travel and forage in unfamiliar landscapes while finding a space to establish a home range. In addition to the ecological risks encountered during dispersal, novel anthropogenic risks exist such as crossing roads, avoiding harvest, and navigating urban landscapes. We explore the impacts of direct (i.e., hunter-harvest and livestock depredation) and indirect (human infrastructure) anthropogenic pressures on three states of dispersal by juvenile mountain lions (*Puma concolor*) from two geographically distinct populations in California and Nevada. These two sites are ecologically similar but have different management practices; hunting is permitted in Nevada, whereas mountain lions are protected in California. We used GPS-collar data and net-squared displacement analysis to identify three dispersal states: exploratory, departure, and transient home range. We then compared dispersal behavior of the two mountain lion populations using an integrated step selection analysis (iSSA) for each dispersal state. The model included explanatory variables hypothesized to influence one or more dispersal states, including distance to forest, shrub, water, hay and crop, developed lands, four-wheel drive roads, elevation, and terrain ruggedness. Results revealed surprisingly consistent habitat selection between sites across most landscape variables, with one notable exception: anthropogenic covariates, including distance to developed land, distance to hay and crop, and distance to four-wheeled drive roads, only had significant impact on modeled habitat selection during dispersal in the population subject to hunting. Results indicate avoidance of anthropogenic landscapes in the hunted population, suggesting that hunting and non-lethal pursuit increases avoidance of anthropogenic landscapes during dispersal for juvenile mountain lions. This thesis uses comparative populations to identify drivers of juvenile dispersal behavior and thereby provide valuable insights to managers to promote connectivity between populations. Additionally, this thesis suggests the use of non-lethal pursuit could be an underutilized tool to reduce human-mountain lion conflict.

(47 pages)

PUBLIC ABSTRACT

Movement Behavior and Habitat Selection of Juvenile Mountain Lions (*Puma Concolor*)

During Three Behavioral States of Dispersal

John F. Randolph

Juvenile dispersal, the act of moving from their natal range to the place where they eventually reproduce and establish an adult home range is hazardous. Juveniles must travel and find food across unfamiliar landscapes, where they must also cross roads, avoid harvest, and navigate developed landscapes. Despite the inherent dangers of dispersal, this demographic process is important for finding suitable mates and reducing inbreeding depression. Wildlife conservation concerns arise when individuals are unable to disperse due to a loss of connectivity, as this can negatively impact population demographics and genetic diversity. We explored the effects of hunting and human-developed landscapes on the dispersal behavior of juvenile mountain lions (*Puma concolor*) in two geographically separated populations subject to different management practices—one with hunting in Nevada and one protected from hunting in California. We used GPS-collar data from 12 and 13 individuals in Nevada and California, respectively, and divided juvenile dispersal into three distinct movement states: exploratory, departure, and transient home range. We then compared used and available locations to identify habitat selection and avoidance characteristics. Our study revealed consistencies between the two sites, including selection for habitat features such as forest, shrub, elevation, and terrain ruggedness. Notably, only the population subjected to hunting pressure exhibited avoidance of human-developed habitat types. Results suggest that hunting influences the

dispersal behavior of juvenile mountain lions. This thesis highlights the utility of research using comparative populations to further our understanding of dispersal behavior.

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CHAPTER I

INTRODUCTION

Dispersal is the movement of an animal from its natal range to the place where it reproduces if it survives (Howard 1960), and is a central component of an individual's fitness. Fitness impacts from dispersal include reduced competition for resources and improved reproductive success (e.g., finding suitable mates and reduced inbreeding depression; Oliveira et al. 2022). Dispersal also facilitates genetic and demographic connectivity within metapopulations, benefiting individuals and populations.

Despite the benefits of dispersal, it is also dangerous (Bonte et al. 2012). During dispersal, individuals navigate unfamiliar and lower-quality habitats in search of vacancies to establish home ranges (Anderson et al. 2004; Huck et al. 2010). Traveling through fragmented and unfamiliar terrain increases vulnerability to intraspecific strife, predation, human conflict, and human-related mortality, including vehicle collisions, depredation, and harvest pressure (Andrén et al. 2006; Soulsbury et al. 2008; Johnson et al. 2010; Riley et al. 2014). While navigating inferior or marginal habitat dispersing juveniles also face energetic strain from a lack of foraging opportunities or poor success rates (Smith 1993; Palomares et al. 2000; Benoit et al. 2020).

Dispersal can be facilitated or impeded by the degree of landscape connectivity (Taylor et al. 1993). Reductions in connectivity stemming from habitat loss and fragmentation, often caused by anthropogenic development and use, are problematic for juvenile dispersal. Large carnivores, for example, require large home ranges and can often travel long distances daily (Gittleman & Harvey 1982). Organisms with these traits suffer most from habitat loss and fragmentation, leading to an increase in overlap and interactions with humans. Encounters with anthropogenic landscapes may elevate the risk of human-related mortality for large carnivores (Woodroffe and Ginsberg 1998; Naude et al. 2020). Decreased connectivity can directly impact fitness by constraining juvenile dispersal and indirectly affect genetic diversity, potentially leading to inbreeding depression (Crooks 2002; Pelletier et al. 2012; Riley et al. 2014; Heim et al. 2019).

Mountain lions (*Puma concolor*) are large-bodied, obligate carnivores found throughout western North America. Mountain lions occur at low densities, require large home ranges, rely on immigration as a source of recruitment, and lack a distinct mating season. They can raise young year-round with a natal period that typically spans 13-17 months before juveniles disperse (Jansen & Jenks, 2012). During dispersal, females typically exhibit philopatry (establishment of an adult home range near or overlapping their natal range), while males tend to travel significantly farther from their natal home range (Sweanor et al. 2000; Thompson and Jenks 2010; Choate et al. 2018). This behavior is driven by the territorial intolerance of adult males already living in the natal range, and a reluctance of resident females to breed with their sons, prompting juvenile males to disperse (Sweanor et al. 2000). Newly independent juveniles possess poor hunting skills, which can lead them to seek easily accessible resources, such as livestock, roadkill, or prey in urban areas (Stoner et al. 2021). This period of exploratory, nomadic movements coupled with poor hunting skills, means dispersing juveniles are more likely to encounter human disturbance and anthropogenic barriers than residents (Dyke et al. 1986; Beier 1995; Riley et al. 2014). Yet, mountain lions are predominantly generalist species capable of surviving across a variety of landscapes, ranging from remote wilderness to more developed areas as long as they obtain food, avoid adult males, navigate the complex gradient of anthropogenic obstacles, and minimize human conflict risk.

Human-carnivore conflict is one of the primary causes of carnivore mortality (Woodroffe and Ginsberg 1998). Sources of conflict consist primarily of livestock or pet depredation (i.e., retaliatory killing of a mountain lion that killed livestock or a pet; Torres et al. 1996) and public safety (i.e., lethal removal of a mountain lion that causes risk to the public; Mattson et al. 2011). The typical management response to these conflicts is the lethal removal of the offending animal. In areas with increased urbanization, human-carnivore conflict is more likely to occur, simultaneously disrupting landscape connectivity and suitable habitat (Vickers et al. 2015, Stoner et al. 2023). Human-carnivore conflict is a common occurrence in rural areas where agricultural and hobby farms house small-hoofed stock (Mazzolli et al. 2002). Even in remote expanses of public lands where cattle and sheep grazing are permitted, conflict and depredation persist within otherwise suitable mountain lion habitat (Weaver 1978). Human-carnivore conflict poses a challenge with unpredictability in time, space, and magnitude across the landscape, and negatively impacts animal behavior, especially for dispersing juvenile mountain lions, who are more likely to be in proximity to human development and at a higher risk of depredation (Kertson et al. 2013; Thompson et al. 2014; Dellinger et al. 2021).

Mountain lions are legally hunted throughout most of their range in the western USA, except for California. To provide more opportunities for hunters, there are also non-lethal pursuit seasons that allow hunters with hounds to track and pursue mountain lions but harvesting mountain lions during this season is prohibited. Although hunting and harvest are terms used interchangeably, we define hunting as the pursuit or search for mountain lions, while harvest specifically refers to the lethal take of a mountain lion. There has been an overall increase in juvenile harvest reported across the western United States (Elbroch et al. 2022), which influences juvenile recruitment and impacts a population's age structure (Stoner et al. 2006, Robinson et al. 2008; Cooley et al. 2009; Newby et al. 2013; Logan and Runge 2021). Hunting pressure and habitat quality have also been shown to influence population dynamics (Lindzey et al. 1994, Andreasen et al. 2012). Harvest can influence post-dispersal habitat selection; mountain lions dispersing in protected populations establish in lower-quality habitat while mountain lions dispersing in a harvested population will move to equal-quality habitat (Stoner et al. 2013). This difference is likely reflecting density-dependent habitat selection in protected populations (Fretwell and Lucas 1969). However, other factors related to habitat availability and previous experience may also be important but have been largely unstudied for mountain lions.

Because dispersal behavior directly impacts individual survival, reproductive success, and recruitment, as well as indirect effects on population genetics and viability, it is crucial to understand how dispersal may differ in populations experiencing different management practices (Nisi et al. 2023). Yet, we rarely have fine-scale habitat selection data to understand how differing anthropogenic pressures influence landscape connectivity and dispersal behavior. Our goal was to assess fine-scale habitat selection during juvenile dispersal in two mountain lion populations subjected to different levels of hunting pressure and interactions with anthropogenic landscapes. While both populations are subject to lethal removal for depredation, only one is also subject to recreational hunting and harvest. We hypothesized that the hunted population would avoid human development features, but the protected population would neither select nor avoid these features because they would not associate them with mortality risk (Smith et al. 2015; Suraci et al. 2019). By comparing two populations subjected to differing management practices, we aim to understand the effects of anthropogenic pressure on juvenile dispersal and shed light on the non-lethal impacts of management practices (non-lethal pursuit seasons) on animal behavior, and consequently, landscape and population connectivity.

CHAPTER II

METHODS

Study Area

We conducted this study in two sites located within the Great Basin ecoregion of the western United States – one in northeastern California (hereafter, the protected site) and the second in southeastern Nevada (hereafter, the hunted site). The protected site was in Modoc County, California, on the Modoc Plateau and covered 10,890 km^2 (lat: 41.49450, long: -120.54262). The region experiences temperatures ranging from -11°C in the winter months to 32°C in the summer (Riegel et al. 2006). Elevations vary from 1,219m to 2,973m across the county. Annual precipitation can vary, with a range between 17.8 and 121.9 cm (Daly et al. 1994). The dominant vegetation in the area was sage steppe, juniper (*Juniperus occidentalis*) woodlands, conifer forest, and agriculture (Riegel et al. 2006). In higher-elevation habitats, the vegetation is predominantly Ponderosa pine (*Pinus ponderosa*) and Jeffery pine (*Pinus jeffreyi*), transitioning into Juniper and sagebrush steppe habitats within the plateaus. Located at the center of the county is Alturas, California, a small town with a population of 2,658. As you move away from town, the private land transitions to public land. Landownership across the plateau was primarily federal and state lands (US Forest Service Modoc National Forest, Bureau of Land Management, U.S. Fish and Wildlife), interspersed with private lands. Primary mountain lion prey consisted of mule deer (*Odocoileus hemionus*), feral horse (*Equus caballus*), pronghorn (*Antilocapra americana*), coyote (*Canis latrans*), and beaver (*Castor canadensis*). Mountain lions are the apex carnivore inhabiting the protected site, while also sharing the area with other large carnivorous mammals like black bears (*Ursus *americanus*), which are known to scavenge mountain lion kills. Mountain lion hunting was banned in California in 1972, later mountain lions became a protected species with the California Wildlife Protection Act in 1990. Nevertheless, mountain lions are still lethally removed through the issuance of depredation permits in response to verified cases of predation on livestock or public safety. In 2017, California implemented a three-strike process to reduce the number of lethal permits issued for depredations. Since 2018, 15 mountain lions have been removed from the protected site (0.01 mountain lion depredation/100 km^2/year; California Department of Fish and Wildlife, Unpublished data).

The hunted site was in the Delamar and Clover Mountain ranges within Lincoln County, Nevada, and covered ~4,995 km^2. Elevations vary from 1,371m to 2,449m in the Delamar and Clover ranges. The hunted site experiences annual mean precipitation ranging between 10.6 – 40.3 cm, with a mean annual temperature fluctuating from 11.7°C to 13.6°C (PRISM Climate Group 2023). The most common vegetation types were semi-arid pinyon-juniper (*Pinus monophylla*, *Juniperus osteosperma*) woodlands and sagebrush steppe. Near the center of this site lies Caliente, Nevada, a small town with a population of 1009. The Bureau of Land Management primarily managed these ranges with minimal private and local municipal land ownership. The mountain lion prey base was similar among sites, consisting of mule deer, feral horses, desert bighorn sheep (*Ovis canadensis*), and pronghorn. Mountain lions were the apex predator, and bears were not present. Mountain lions in this hunted site can be hunted year-round with no more than two lions harvested per person per year using hounds or opportunistically. Yet, due to environmental factors, the use of hounds is more frequent during winter months when persistent snow cover facilitates tracking. Harvesting mountain lions through trapping is illegal. From 2018 to 2022, a total of 27 mountain lions were harvested in four areas that encompass our study site (0.05 mountain lion harvest/100 km^2/year; Game Management Units 241, 242, 243, and 223), and one mountain lion was removed due to livestock depredation (0.0002 mountain lion depredation/100 km^2/year). A total of 28 individuals were removed from the hunted population (0.06 mountain lion removals/100 km^2/year; Nevada Department of Wildlife, Unpublished data).

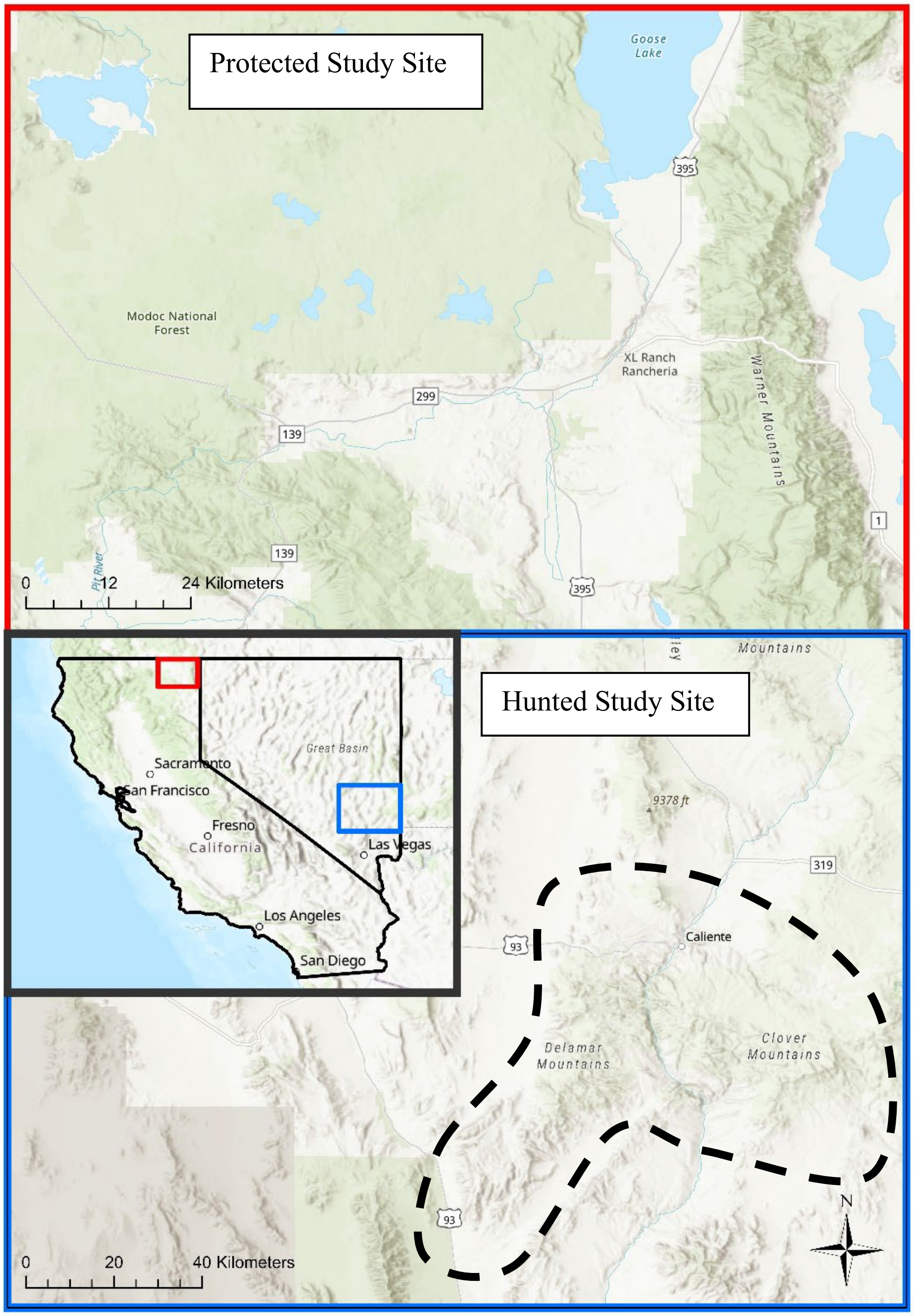

Figure 1: The top image (red) represents the Modoc County, California Protected site. The bottom image (depicted in blue) corresponds to a section of Lincoln County, Nevada, featuring the hunted site outlined by a black dashed polygon.

Capture and Collaring

From 2016 to 2022, mountain lions in the protected site were captured using cage traps and occasionally hounds (Ewanyk 2020). All animals were fitted with GPS collars (Vectronic Vertex Lite), programmed at a one- or two-hour fix rates that uploaded approximately every other day. GPS collars fitted on dispersal-age juveniles were equipped with a drop-off mechanism scheduled to release the collar eight months or two years from the collaring event. Animal handling was approved by two Institutional Animal Care and Use Committees (UC Davis protocol #22408, USU protocol #12972).

All data from the hunted site were collected between 2018-2021 and provided by the Nevada Department of Wildlife (NDOW) for this study. Mountain lion captures began in the Delamar Mountains as part of a desert bighorn sheep study in 2018, with capture efforts expanding into the Clover Mountains in 2020. Hounds and foot snares were used to opportunistically capture and collar mountain lions following methods by Jansen and Jenks (2012). Mountain lions were fitted with GPS collars (Vectronic Vertex Plus) programmed at a four-hour fix rate. Capture methods and handling followed guidelines from the American Society of Mammologists (Sikes and Gannon 2011), under approval from a NDOW veterinarian.

Data Analysis

Movement identification and characterization

To delineate differing movement states for dispersing juveniles, we used net square displacement (Bunnefeld 2011). By visually inspecting net-squared displacement plots we were able to identify three distinct movement states: exploratory, departure, and transient home range (defined in Table 1). Segmenting a dispersal event into these three movement states allows us to differentiate between failed dispersal attempts (exploratory and transient home range) and successful dispersal events (departure). Exploratory behavior occurs when the animal returns to its natal range, while transient home range behavior involves attempts to establish a new range that is ultimately abandoned, both of these events fail to establish an adult home range. Departure is the only successful behavioral state, representing instances where the animal leaves its natal range and does not return. We then estimated when individuals shifted between these states (Bunnefeld et al. 2011) using R package AMT (Signer et al. 2019; Table 1). Depending on the number of dispersal behaviors identified, we included one or more movement states for each individual in the subsequent analysis.

Table 1: Definitions of the three dispersal behavior states to categorize step data obtained from GPS-collars on juvenile mountain lions

Behavioral state	**Definition**	**NSD Segmenting using Bunnefeld 2011**
Exploratory	Departure from natal range or capture location but later returns	Nomadic movement from the original home range but returns to the natal home range
Departure	Departure from natal range or capture location without any return	Departure from the natal home range and later establishes an adult home range (> 6 months of home ranging behavior)
Transient Home Range	Home ranging behavior to explore the quality of habitat	Departure from natal home range but displays home ranging behavior before later abandoning that range. If the collar dropped when displaying home ranging behavior, we classified it as a transient home range if data were obtained for <6 months and as an established range if data were obtained for >6 months

Integrated Step Selection Analysis

We examined juvenile mountain lion dispersal and habitat selection by implementing an integrated step selection analysis (iSSA; Avgar et al. 2016). The iSSA uses straight line segments between two consecutive locations (start and end), hereafter referred to as steps, as the unit of observation. We used habitat features associated with the start location of a step to examine how the covariates influence the movement characteristics (step length and turn angle) of the subsequent movement. We used habitat features associated with the end location to examine habitat selection by the individual. To account for different sampling rates between sites, we resampled GPS locations of mountain lions in the protected site to four-hour fix rates to match the hunted site. We used a ±10-minute window from the fix rate to account for missed or delayed fixes. If two locations were not within the 10-minute window of the fix rate, they were not considered consecutive locations and therefore not considered a step. We then removed non-movement data such as kill-site GPS clusters using rASF in R (Mahoney and Young 2017). These data were removed to avoid selection bias during non-movement states. We kept the first and last point of each cluster to use as the end and then beginning of the next step. To generate random steps, we created a population-specific step length distribution and turn angle distribution for each behavior. We then generated 20 random steps based on these distributions for each GPS location to compare available and used steps (Nisi et al. 2022).

We considered the influence of several selection and movement covariates identified in previous mountain lion habitat studies (Nicholson et al. 2014; Robinson et al. 2015; Gigliotti et al. 2019; Dellinger et al. 2020; Benson et al. 2023). These included topography (terrain ruggedness index and elevation; elevatr; Hollister et al. 2017), distance to anthropogenic features (roads, agriculture, and structures; NLCD 2021 and USGS NTD, 2023), and distance to various land cover types (shrub, forest, and water; NLCD 2021 and USGS NHD, 2023) (Table 2). We also took the log of all distance-to variables to allow more sensitivity to distances closer to that land cover. We reformatted coordinate reference systems and resampled raster pixels to 30x30 meters using ArcGIS Pro V. 3.1.1 (ESRI 2023).

Table 2: Overview of variables, units, and source data for selected covariates in the integrated step selection analysis.

Variable	Notes	Unit	Resource
Distance to Developed landcover	Open space, low intensity, medium intensity, high intensity	Meters	NLCD 2021
Distance to Hay and Crop		Meters	NLCD 2021
Distance to Forest	Evergreen, mixed, deciduous	Meters	NLCD 2021
Distance to Shrub	Grassland, herbaceous	Meters	NLCD 2021
Distance to Water	Open water, emergent herbaceous wetlands, woody wetlands, linear streams and rivers	Meters	NLCD 2021 & USGS NHD, 2023
Four-wheeled Drive Roads		Meters	USGS NTD, 2023
Elevation		Meters	elevatr; Hollister et al. 2017
Terrain Ruggedness Index		Meters	elevatr; Hollister et al. 2017

We extracted habitat covariates at all used and available steps and fit a global step selection model for each of the three dispersal behavioral states with program R (R Core Team 2022, version 4.2.2) package AMT (Signer et al. 2019) to estimate selection of habitat variables for each individual (Table 3). The global model included all variables we hypothesized to influence mountain lion movements and habitat selection (Table 2). We considered interactions between step length (the distance between two GPS points) and turn angle (the degree that the GPS step trajectory changes from the second to third GPS point) with all anthropogenic covariates. To obtain population-level parameters, we used each individual's beta estimate to calculate an inverse-variance weighted mean for each study site. This provided us with a log-relative selection strength (log-RSS; Avgar et al. 2017) for each covariate by each population.

CHAPTER III

RESULTS

Capture and Collaring

We captured 13 juveniles (2 females and 11 males) in the protected site. There were two mortalities: one mountain lion died of starvation and one was lethally removed for depredation. Both individuals were included in the analysis until their mortality. GPS collars provided an average of 298 d (SE ± 46 d) of data per juvenile in the protected site. On the hunted site there were 12 juveniles (7 females and 5 males) fitted with GPS collars in the. Of these, we recorded eight mortalities; four mountain lions were harvested, one was removed for livestock depredation, and three died of unknown causes. All individuals were included in the analysis until the time of death. The average duration of data collected from GPS collars in our hunted site was 631 d (SE ± 154 d) per juvenile.

Net-squared Displacement

Three juveniles (3 males) in the protected site did not display any dispersal behavior and were consequently removed from the study, resulting in a reduced sample size of 10 individuals (2 females, 8 males; Table 1). Six mountain lions displayed exploratory behavior one or more times, resulting in a total of nine exploratory events for an average duration of 47 d (SE ± 14 d), with an average distance traveled during exploratory behavior of 154 km (SE ± 48 km). Nine juveniles exhibited departure behavior between February to June, averaging 50 d (SE ± 14 d) and traveling a mean distance of 188 km (SE ± 58 km). Eight juvenile mountain lions exhibited transient home range behavior nine times, with each juvenile spending an average of 38 d (SE ± 5 d) in this behavior. The average distance traveled from their natal ranges to a transient home range was 52 km (SE ± 9 km).

In our hunted site, one juvenile female did not display dispersal behavior and was removed from the analysis (Table 1); 11 juveniles (7 females and 4 males) were retained. There were seven exploratory events from six juveniles, averaging 66 d (SE ± 24 d) with an average distance traveled of 236 km (SE ± 64 km). Departure was observed for eight juveniles between February to December, lasting an average of 45 d (SE ± 8 d) and traveling a mean distance of 160 km (SE ± 32 km). Six juveniles displayed transient home ranges, averaging 164 d (SE ± 75 d) and traveling an average distance of 99 km (SE ± 11 km) from their natal range.

Behavioral Global Step Selection Models

Exploratory

We found nine covariates in the exploratory model that exhibited significance (Figure 2). Among them, six covariates are related to habitat selection, whereas the remaining three were associated with movement. In the exploratory state, mountain lions in both protected (P) and hunted (H) sites selected similarly for forest (P:β = -0.582 & H:β = -0.496) and terrain ruggedness index (P:β = 0.223 & H:β = 0.316; Figure 2). The protected mountain lions selected distances close to shrub land cover (P:β = -0.409), whereas those in the hunted site selected to be far away from developed landscapes (H:β = 0.169; Figure 2). Mountain lions in the hunted site selected for higher elevations (H:β = 0.308) while those from the protected site selected for elevations near and around the mean (1519 m, P:β = -0.380; Figure 2). In our hunted site, estimates of step lengths (H:β = -0.044) were longer and turn angles were more tortuous in developed landscapes (H:β = 0.186) and exhibited more direct movements when near or on four-wheel-drive roads

(H:β = -0.186; Figure 2).

Departure

The departure model contained six significant covariates (Figure 2). Of these, four were habitat covariates and one was a movement covariate. Mountain lions in both sites selected to be near or within forest (P:β = -0.618 & H:β = -0.725) and shrub land cover (P:β = -0.493 & H:β = -0.378; Figure 2). The protected mountain lions selected for higher terrain ruggedness (P:β = 0.221) and elevation near and around the mean (1746 m, P:β = -0.218; Figure 2). Hunted mountain lions selected for locations near or within hay and crop (H:β = -0.299) and turn angles were more tortuous within and near agricultural areas (H:β = 0.335; Figure 2).

Transient Home Range

In the transient home range model, we identified five significant covariates, which were categorized into four habitat and one movement covariate (Figure 2). Mountain lions in the transient home range state selected for more rugged terrain (P:β = 0.264 & H:β = 0.162), with elevations around 1619 m in the protected site (P:β = -0.815) and 1906 m in our hunted site (H:β = -0.141), and for forest land cover (P:β = -0.469 & H:β = -0.525; Figure 2). The mountain lions at the protected site selected for shrub habitat (P:β = -0.348) and at the hunted site selected for water features (H:β = -0.109; Figure 2). Hunted mountain lions had longer step lengths near and within developed landscapes (H:β = -0.045; Figure 2).

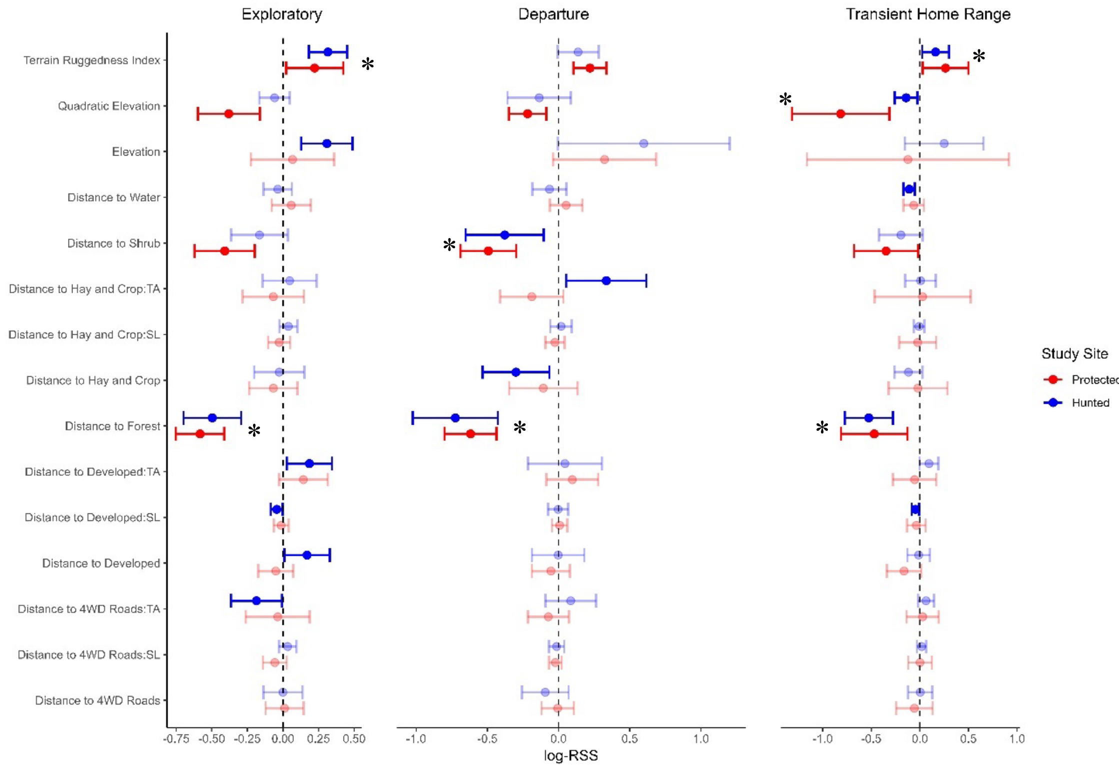

Figure 2: Global model of significant log Relative Selection Strength (log-RSS), i.e., beta coefficient, and 95% confidence intervals for a one-unit change in the covariate for each dispersal behavior between sites. If a covariate includes a colon, it indicates an interaction term with either TA (Turn Angle) or SL (Step Length). Covariates where both Study Sites are significant are marked with an asterisk (*).

CHAPTER IV

DISCUSSION

Mountain lions are widely distributed and exhibit broad habitat tolerance, but most studies on juvenile dispersal by mountain lions are confined to single or neighboring populations. This limitation introduces challenges in drawing meaningful comparisons across populations because of variations in environmental conditions and methodologies. By comparing juvenile dispersal behavior between two populations exposed to different wildlife management practices but inhabiting similar basin-and-range habitats, we were able to identify the impact of anthropogenic pressures that are present and growing across most of the species' range (Leu et al. 2008). We found minimal differences in habitat selection between our two study sites and across three dispersal states. Notably, however, the few differences in habitat selection between populations were associated with anthropogenic covariates. As predicted, the hunted population avoided developed landscapes, whereas the juveniles dispersing from the protected population did not select for or against developed landscapes.

We identified three distinct behavioral states of dispersal: exploratory, departure, and transient home range. Across these states, juveniles selected habitats similar to the habitat used by adult mountain lions, selecting for forest, shrub, increased terrain ruggedness, and higher elevation (Nicholson et al. 2014; Robinson et al. 2015; Gigliotti et al. 2019). These habitats are also important to herbivores that are the primary prey of mountain lions (Van Beest et al. 2014; Morano et al. 2019) and may facilitate hunting opportunities (Kunkel et al. 1999). As such, our data suggest that despite occasional forays into poor or unsuitable habitats, dispersing mountain lions predicate habitat selection on the general habitat associations of their primary prey.

The results of anthropogenic covariates differed between the two populations of juvenile mountain lions. While we acknowledge that these differences may be attributed to the varying sex ratios between sites, our observation of a range of dispersal characteristics within both sites leads us to conclude that this difference did not alter our findings. Models of mountain lions in the hunted site indicated habitat selection and avoidance related to anthropogenic factors. During failed dispersal states, exploratory and transient home range, there was evidence of avoidance of developed landcover, accompanied by varying movement behaviors. Conversely, during the successful dispersal state, departure, there was selection for hay and crop landcover. During the exploratory state, mountain lions in the hunted site exhibited increased step length and more torturous movements observed near or within developed landscapes, potentially driven by perceived risk or hindrance to movement (Dickie et al. 2020). Mountain lions have previously been shown to select areas in proximity to four-wheel drive and dirt roads for easier movement (Dellinger et al. 2020), suggesting that our observed increased step length could also relate to four-wheel drive and dirt roads facilitating movement of dispersing mountain lions (Dickie et al. 2020). During the transient home range state, juveniles in the hunted site exhibited straighter movement when near or within developed landscapes. Most studies show mountain lions typically avoid developed landscapes (Robinson et al. 2015; Riley et al. 2021), so it is likely that straight movement (i.e., increased step length) is a behavior exhibited by mountain lions trying to quickly move past developed areas.

Selection for hay and crop by juveniles in the hunted site during the departure state could relate to resource availability (Tucker et al. 2021). Our study sites experience dramatic seasonal shifts in environmental conditions throughout the year, whereas human-modified agricultural landscapes create more predictable environments with readily available resources for wildlife (Sih et al. 2011; Oro et al. 2013). Prey species are drawn to agricultural landscapes due to the increased availability and predictability of resources (Anderson et al. 2012). The combination of selecting hay and crop areas along with tortuous movements in these habitats suggests that mountain lions could be using these habitats for hunting or scavenging roadkill (Dickie et al. 2020). Hay and crop land cover may also serve as refugia from humans and adult mountain lions. Hay and crop fields are typically privately owned and not commonly accessible to hunters, meaning that carnivores may find refuge in hay and crops (Harden et al. 2005; Proffitt et al. 2013). Established adult mountain lions are also unlikely to regularly use agricultural areas (Dickson and Beier 2002), potentially offering refuge from intraspecific strife. Similarly, brown bears (*Ursus arctos*) use anthropogenic landscapes to reduce sexually selected infanticide, as adult males were less inclined to use these habitat types in their home range (Steyaert et al., 2016).

Interestingly, during the failed dispersal states, we observed avoidance of developed landscapes and altered movements within them. The avoidance observed during the exploratory event may be attributed to young juveniles navigating habitat most like their natal home range, with adult females likely avoiding home ranges with developed landscapes (Davis and Stamps, 2004, Stamps and Swaisgood, 2007, Robinson et al. 2015; Riley et al. 2021). They likely switch to using other habitat features as they learn to seek areas with increased resources like prey species. This is supported by our successful dispersal state, departure, wherein dispersing juvenile mountain lions actively select hay and crop areas. The differences in habitat section between movement states suggest that the entire juvenile dispersal event is a lengthy learning process.

Developed landscapes represent the most intense form of anthropogenic influence and are often avoided by large carnivores (Boydston et al. 2003; Dickson et al. 2005; Støen et al. 2015). Across developed landscapes, juvenile mountain lions are at risk of vehicle collision, human-wildlife conflict, and depredation (Kertson et al. 2013; Dellinger et al. 2021). In our study, only the hunted site showed avoidance of developed landscapes, while the protected population did not show selection for or avoidance of any anthropogenic covariates. Within our hunted site, the developed landscape is situated in and around the town of Caliente, within an otherwise suitable mountain lion habitat. The town was built in an area concentrated around water that is also used by ungulates that otherwise live in a dry, arid environment. The combination of suitable mountain lion habitat with increased resource availability should be attractive to dispersing mountain lions, suggesting the impact of hunting causes juvenile mountain lions to avoid this otherwise valuable habitat. This could suggest a learned avoidance of developed landscapes, potentially influenced by negative interactions with hounds and hunting. Unlike other carnivores that adjust their habitat selection and movement in response to increased perceived risk during specific hunting seasons (Basille et al. 2013; Stillfried et al. 2015; Lodberg-Holm et al. 2019), mountain lions in the hunted site consistently avoided developed landscapes during dispersal. The year-round avoidance could be due to the lengthiness of the combined pursuit and harvest seasons each year making it difficult to avoid seasonally or because pursuit season results in individual mountain lions experiencing hunters and hounds - possibly multiple times each year- without being harvested.

The use of dogs as a tool in wildlife management is an emerging field. Scat detection dogs, for example, are employed across the western regions for noninvasive genetic sampling (Wasser et al. 2004, McKeague et al. 2024). Livestock guardian dogs (LGD) are deployed to mitigate human-wildlife conflict by deterring carnivores from depredating livestock (Andelt and Hopper 2000, Young and Sarmento 2024). Additionally, dogs have been used for hazing nuisance black bears in urban settings (Beckmann et al., 2004). However, the use of dogs for hazing mountain lions is a relatively new area of exploration. Our findings suggest that our hunted population exhibits increased avoidance of developed landscapes compared to our protected population suggests the negative experiences during hunting may cause mountain lions to select against landscape features where they are less likely to encounter hunters and hounds. This implies the potential utility of dogs in deterring mountain lions and inducing negative experiences to reduce human-carnivore conflict.

In this study, we leveraged GPS-collar data from two study sites to compare juvenile dispersal between a hunted and protected population. Harvest of mountain lions is common in most of the western United States and serves multiple purposes, including managing mountain lion populations, mitigating human-wildlife conflicts, minimizing livestock depredation, reducing predation on ungulate populations, and providing hunting opportunities. However, harvest also influences the success of dispersal and modifies the spatial behavior of harvested species (Robinson et al., 2008; Newby 2013; Logan and Runge, 2021; Smith et al., 2022). Our findings expand our understanding of the influence of hunting by evaluating juvenile dispersal movements and habitat selection of mountain lions. We identified similarities in the selection and avoidance of most habitat covariates commonly correlated with mountain lions across their range (Nicholson et al. 2014; Robinson et al. 2015; Gigliotti et al. 2019; Riley et al. 2021), except that we found the two populations of mountain lions differed in their selection for and avoidance of anthropogenic landscapes. Despite similar environments, our hunted mountain lions avoided anthropogenic features, whereas the protected mountain lions did not. This suggests hunting affects fine-scale dispersal behavior. In most of the western United States, mountain lions may be exposed to hunting throughout the legal hunting season (legal to harvest) and pursuit season (illegal to harvest). The use of dogs to instill a negative interaction with humans has been hypothesized (Beckmann et al. 2004) but is only now being investigated in mountain lions. If true, pursuit with hounds could provide wildlife managers with a previously underutilized method for reducing human-mountain lion conflicts. More research on the direct response of mountain lions to anthropogenic activity and pressures is needed. Our findings contribute to the growing body of evidence that management practices can have behavioral effects on the movement and habitat selection of juvenile mountain lions during dispersal (Robinson et al. 2008; Cooley et al. 2009; Newby 2013; Logan and Runge 2021).

LITERATURE CITED

Andelt, W. F., and S. N. Hopper. 2000. Livestock guard dogs reduce predation on domestic sheep in Colorado. Journal of Range Management.

Anderson, C. R., F. G. Lindzey, and D. B. McDonald. 2004. Genetic structure of cougar populations across the Wyoming basin: Metapopulation or megapopulation. Journal of Mammalogy 85:1207–1214.

Anderson, E. D., R. A. Long, M. P. Atwood, J. G. Kie, T. R. Thomas, P. Zager, and R. T. Bowyer. 2012. Winter resource selection by female mule deer *Odocoileus hemionus:* functional response to spatio-temporal changes in habitat. Wildlife Biology 18:153–163.

Andreasen, A. M., K. M. Stewart, W. S. Longland, J. P. Beckmann, and M. L. Forister. 2012. Identification of source-sink dynamics in mountain lions of the Great Basin. Molecular Ecology 21:5689–5701.

Andrén, H., J. D. C. Linnell, O. Liberg, R. Andersen, A. Danell, J. Karlsson, J. Odden, P. F. Moa, P. Ahlqvist, T. Kvam, R. Franzén, and P. Segerström. 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation 131:23–32.

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Avgar, T., S. R. Lele, J. L. Keim, and M. S. Boyce. 2017. Relative Selection Strength: Quantifying effect size in habitat- and step-selection inference. Ecology and Evolution 7:5322–5330.

Basille, M., B. Van Moorter, I. Herfindal, J. Martin, J. D. C. Linnell, J. Odden, R. Andersen, and J.-M. Gaillard. 2013. Selecting habitat to survive: The impact of road density on survival in a large carnivore. PLoS ONE 8:e65493.

Beckmann, J. P., C. W. Lackey, and J. Berger. 2004. Evaluation of deterrent techniques and dogs to alter behavior of “nuisance” black bears. Wildlife Society Bulletin 32:1141–1146.

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. The Journal of Wildlife Management 59:228.

Benoit, L., A. J. M. Hewison, A. Coulon, L. Debeffe, D. Grémillet, D. Ducros, B. Cargnelutti, Y. Chaval, and N. Morellet. 2020. Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore. Journal of Animal

Ecology 89:173–185.

Benson, J. F., K. D. Dougherty, P. Beier, W. M. Boyce, B. Cristescu, D. J. Gammons, D. K. Garcelon, J. M. Higley, Q. E. Martins, A. C. Nisi, S. P. D. Riley, J. A. Sikich, T. R. Stephenson, T. W. Vickers, G. M. Wengert, C. C. Wilmers, H. U. Wittmer, and J. A. Dellinger. 2023. The ecology of human-caused mortality for a protected large carnivore. Proceedings of the National Academy of Sciences 120:e2220030120.

Boitani, L., and R. A. Powell, editors. 2012. Carnivore ecology and conservation: A handbook of techniques. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199558520.001.0001>. Accessed 1 Mar 2024.

Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E. Matthysen, K. Mustin, M. Saastamoinen, N. Schtickzelle, V. M. Stevens, S. Vandewoestijne, M. Baguette, K. Barton, T. G. Benton, A. Chaput-Bardy, J. Clobert, C. Dytham, T. Hovestadt, C. M. Meier, S. C. F. Palmer, C. Turlure, and J. M. J. Travis. 2012. Costs of dispersal. Biological Reviews 87:290–312.

Boydston, E. E., K. M. Kapheim, H. E. Watts, M. Szykman, and K. E. Holekamp. 2003. Altered behaviour in spotted hyenas associated with increased human activity. Animal Conservation 6:207–219.

Bunnefeld, N., L. Börger, B. Van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences: Quantifying migration patterns. Journal of Animal Ecology 80:466–476.

Choate, D. M., K. M. Longshore, and D. B. Thompson. 2018. Cougar dispersal and natal homing in a desert environment. Western North American Naturalist 78:221–235.

Cooley, H. S., R. B. Wielgus, G. Koehler, and B. Maletzke. 2009. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Animal Conservation 12:321–328.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33:140–158.

Davis, J., and J. A. Stamps. 2004. The effect of natal experience on habitat preferences. Trends in Ecology & Evolution 19:411–416.

Dellinger, J. A., B. Cristescu, J. Ewanyk, D. J. Gammons, D. Garcelon, P. Johnston, Q. Martins, C. Thompson, T. W. Vickers, C. C. Wilmers, H. U. Wittmer, and S. G. Torres. 2020. Using mountain lion habitat selection in management. The Journal of Wildlife Management 84:359–371.

Dellinger, J. A., R. Cordova, D. K. Macon, and J. L. Rudd. 2021. Temporal trends and drivers of mountain lion depredation in California, USA.

Dewitz, J., 2023, National Land Cover Database (NLCD) 2021 Products: U.S. Geological Survey data release, https://doi.org/10.5066/P9JZ7AO3.

Dickie, M., S. R. McNay, G. D. Sutherland, M. Cody, and T. Avgar. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. Journal of Animal Ecology 89:623–634.

Dickson, B. G., and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. The Journal of Wildlife Management 66:1235.

Dickson, B. G., J. S. Jenness, and P. Beier. 2005. Influence of vegetation, topography, and roads on cougar movement in southern California. Journal of Wildlife Management 69:264–276.

Dyke, F. G. V., R. H. Brocke, H. G. Shaw, B. B. Ackerman, T. P. Hemker, and F. G. Lindzey. 1986. Reactions of mountain lions to logging and human activity. The Journal of Wildlife Management 50:95.

Elbroch, L. M., L. S. Petracca, C. O'Malley, and H. Robinson. 2022. Analyses of national mountain lion harvest indices yield ambiguous interpretations. Ecological Solutions and Evidence 3.

ESRI 2023. ArcGIS Pro 3.1.1. Redlands, CA: Environmental Systems Research Institute.

Ewanyk, Jonathan, Habitat use and prey selection by mountain lions in an altered sagebrush steppe environment (2020). Cal Poly Humboldt theses and projects. 368. https://digitalcommons.humboldt.edu/etd/368

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Gigliotti, L. C., M. R. Matchett, and D. S. Jachowski. 2019. Mountain lions on the prairie: habitat selection by recolonizing mountain lions at the edge of their range. Restoration Ecology 27:1032–1040.

Gittleman, J. L., and P. H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. Behavioral Ecology and Sociobiology 10:57–63.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Harden, C. D., A. Woolf, and J. Roseberry. 2005. Influence of exurban development on hunting opportunity, hunter distribution, and harvest efficiency of white-tailed deer. Wildlife Society Bulletin 33:233–242.

Heim, N., J. T. Fisher, J. Volpe, A. P. Clevenger, and J. Paczkowski. 2019. Carnivore community response to anthropogenic landscape change: species-specificity foils generalizations. Landscape Ecology 34:2493–2507.

Hollister, J., Shah, T., Robitaille, A., Beck, M., & Johnson, M. (2017). elevatr: access elevation data from various APIs. R package version 0.1, 3.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist 63:152.

Huck, M., W. Jędrzejewski, T. Borowik, M. Miłosz-Cielma, K. Schmidt, B. Jędrzejewska, S. Nowak, and R. W. Mysłajek. 2010. Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. Acta Theriologica 55:177–192.

Jansen, B. D., and J. A. Jenks. 2012. Birth timing for mountain lions (*Puma concolor*); testing the prey availability hypothesis. PLoS ONE 7:e44625.

Johnson, S. A., H. D. Walker, and C. M. Hudson. 2010. Dispersal characteristics of juvenile bobcats in south-central Indiana. Journal of Wildlife Management 74:379–385.

Kertson, B. N., R. D. Spencer, and C. E. Grue. 2013. Demographic influences on cougar residential use and interactions with people in western Washington. Journal of Mammalogy 94:269–281.

Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park Montana. The Journal of Wildlife Management 63:901.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Lindzey, F. G., W. D. V. Sickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics in southern Utah. The Journal of Wildlife Management 58:619.

Lodberg-Holm, H. K., H. W. Gelink, A. G. Hertel, J. E. Swenson, M. Domevscik, and S. M. J. G. Steyaert. 2019. A human-induced landscape of fear influences foraging behavior of brown bears. Basic and Applied Ecology 35:18–27.

Logan, K. A., and J. P. Runge. 2021. Effects of hunting on a puma population in Colorado. Wildlife Monographs 209:1–35.

Mahoney, P. J., and J. K. Young. 2017. Uncovering behavioural states from animal activity and site fidelity patterns. Methods in Ecology and Evolution 8:174–183.

Mattson, D., K. Logan, and L. Sweanor. 2011. Factors governing risk of cougar attacks on humans. Human-Wildlife Interactions 5:135–158.

Mazzolli, M., M. E. Graipel, and N. Dunstone. 2002. Mountain lion depredation in southern Brazil. Biological Conservation 105:43–51.

McKeague, B., C. Finlay, and N. Rooney. 2024. Conservation detection dogs: A critical review of efficacy and methodology. Ecology and Evolution 14:e10866.

Morano, S., K. M. Stewart, T. Dilts, A. Ellsworth, and V. C. Bleich. 2019. Resource selection of mule deer in a shrub-steppe ecosystem: influence of woodland distribution and animal behavior. Ecosphere 10:e02811.

Naude, V. N., G. A. Balme, J. O'Riain, L. T. B. Hunter, J. Fattebert, T. Dickerson, and J. M. Bishop. 2020. Unsustainable anthropogenic mortality disrupts natal dispersal and promotes inbreeding in leopards. Ecology and Evolution 10:3605–3619.

Newby, J. R., L. Scott Mills, T. K. Ruth, D. H. Pletscher, M. S. Mitchell, H. B. Quigley, K. M. Murphy, and R. DeSimone. 2013. Human-caused mortality influences spatial population dynamics: Pumas in landscapes with varying mortality risks. Biological Conservation 159:230–239.

Nicholson, K. L., P. R. Krausman, T. Smith, W. B. Ballard, and T. McKinney. 2014. Mountain lion habitat selection in Arizona. The Southwestern Naturalist 59:372–380.

Nisi, A. C., J. P. Suraci, N. Ranc, L. G. Frank, A. Oriol-Cotterill, S. Ekwanga, T. M. Williams, and C. C. Wilmers. 2022. Temporal scale of habitat selection for large carnivores: Balancing energetics, risk and finding prey. Journal of Animal Ecology 91:182–195.

Nisi, A. C., J. F. Benson, R. King, and C. C. Wilmers. 2023. Habitat fragmentation reduces survival and drives source–sink dynamics for a large carnivore. Ecological Applications 33:e2822.

Oliveira, M. E., B. H. Saranholi, R. Dirzo, and P. M. Galetti. 2022. A review of philopatry and dispersal in felids living in an anthropised world. Mammal Review 52:208–220.

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501–1514.

Palomares, F., M. Delibes, P. Ferreras, J. M. Fedriani, J. Calzada, and E. Revilla. 2000. Iberian lynx in a fragmented landscape: predispersal, dispersal, and postdispersal habitats. Conservation Biology 14:809–818.

Pelletier, A., M. E. Obbard, K. Mills, E. J. Howe, F. G. Burrows, B. N. White, and C. J. Kyle. 2012. Delineating genetic groupings in continuously distributed species across largely homogeneous landscapes: a study of American black bears (*Ursus americanus*) in Ontario, Canada. Canadian Journal of Zoology 90:999–1014.

PRISM Climate Group. 2023. Time Series Values for Individual Locations. Oregon State University, Corvallis, OR. <https://www.prism.oregonstate.edu/>.

Proffitt, K. M., J. A. Gude, K. L. Hamlin, and M. A. Messer. 2013. Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. The Journal of Wildlife Management 77:514–524.

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Riegel, G. M., R. F. Miller, C. N. Skinner, and S. E. Smith. 2006. Northeastern Plateaus Bioregion. Pages 225–263. Fire in California's Ecosystems. University of California Press. <https://academic.oup.com/california-scholarship-online/book/20600/chapter/179900634>. Accessed 16 Apr 2023.

Riley, S. P. D., L. E. K. Serieys, J. P. Pollinger, J. A. Sikich, L. Dalbeck, R. K. Wayne, and H. B. Ernest. 2014. Individual behaviors dominate the dynamics of an urban mountain lion population isolated by roads. Current Biology 24:1989–1994.

Riley, S. P. D., J. A. Sikich, and J. F. Benson. 2021. Big cats in the big city: Spatial ecology of mountain lions in greater Los Angeles. The Journal of Wildlife Management 85:1527–1542.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Robinson, H. S., T. Ruth, J. A. Gude, D. Choate, R. DeSimone, M. Hebblewhite, K. Kunkel, M. R. Matchett, M. S. Mitchell, K. Murphy, and J. Williams. 2015. Linking resource selection and mortality modeling for population estimation of mountain lions in Montana. Ecological Modelling 312:11–25.

Signer, J., J. Fieberg, and T. Avgar. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 9:880–890.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367–387.

Sikes, R. S., and W. L. Gannon. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Smith, J. L. D. 1993. The role of dispersal in structuring the Chitwan tiger population. Behaviour 124:165–195.

Smith, J. A., Y. Wang, and C. C. Wilmers. 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. Proceedings of the Royal Society B: Biological Sciences 282:20142711.

Smith, J. B., D. B. Spitz, C. L. Brown, M. J. Wisdom, M. M. Rowland, T. D. Forrester, B. K. Johnson, and D. A. Clark. 2022. Behavioral responses of male elk to hunting risk. The Journal of Wildlife Management 86.

Soulsbury, C. D., P. J. Baker, G. Iossa, and S. Harris. 2008. Fitness costs of dispersal in red foxes (*Vulpes vulpes*). Behavioral Ecology and Sociobiology 62:1289–1298.

Stamps, J. A., and R. R. Swaisgood. 2007. Someplace like home: Experience, habitat selection and conservation biology. Applied Animal Behaviour Science 102:392–409.

Steyaert, S. M. J. G., M. Leclerc, F. Pelletier, J. Kindberg, S. Brunberg, J. E. Swenson, and A. Zedrosser. 2016. Human shields mediate sexual conflict in a top predator. Proceedings of the Royal Society B: Biological Sciences 283:20160906.

Stillfried, M., J. L. Belant, N. J. Svoboda, D. E. Beyer, and S. Kramer-Schadt. 2015. When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. Behavioural Processes 120:30–39.

Støen, O.-G., A. Ordiz, A. L. Evans, T. G. Laske, J. Kindberg, O. Fröbert, J. E. Swenson, and J. M. Arnemo. 2015. Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). Physiology & Behavior 152:244–248.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: Implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.

Stoner, D. C., M. L. Wolfe, C. Mecham, M. B. Mecham, S. L. Durham, and D. M. Choate. 2013. Dispersal behaviour of a polygynous carnivore: do cougars Puma concolor follow source-sink predictions? Wildlife Biology 19:289–301.

Stoner, D. C., M. A. Ditmer, D. L. Mitchell, J. K. Young, and M. L. Wolfe. 2021. Conflict, coexistence, or both? Cougar habitat selection, prey composition, and mortality in a multiple-use landscape. California Fish and Wildlife Journal 107:147–172.

Stoner, D. C., Z. McDonald, and C. A. C. Coon. 2023. Stepping stones to extirpation: Puma patch occupancy thresholds in an urban-wildland matrix. Ecology and Evolution 13:e10381.

Suraci, J. P., M. Clinchy, L. Y. Zanette, and C. C. Wilmers. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice.. Ecology Letters 22:1578–1586.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571.

Thompson, D. J., and J. A. Jenks. 2010. Dispersal movements of subadult cougars from the Black Hills: the notions of range expansion and recolonization. Ecosphere 1:1–11.

Thompson, D. J., J. A. Jenks, and D. M. Fecske. 2014. Prevalence of human-caused mortality in an unhunted cougar population and potential impacts to management. Wildlife Society Bulletin 38:341–347.

Torres, S., T. M. Mansfield, J. E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: Testing speculations. Wildlife Society Bulletin 24:451–460.

Tucker, M. A., L. Santini, C. Carbone, and T. Mueller. 2021. Mammal population densities at a global scale are higher in human-modified areas. Ecography 44:1–13.

Ullas Karanth, K., and J. D. Nichols. 2010. Non-invasive survey methods for assessing tiger populations. Pages 241–261 in. Tigers of the World. Elsevier. <https://linkinghub.elsevier.com/retrieve/pii/B9780815515708000189>. Accessed 1 Mar 2024.

U.S. Geological Survey, National Geospatial Technical Operations Center, 2023, USGS

National Transportation Dataset (NTD) downloadable data collection: U.S. Geological Survey.

U.S. Geological Survey, 2023, National Hydrography Dataset (NHD) - USGS national map downloadable data collection: USGS - National Geospatial Technical Operations Center (NGTOC).

Van Beest, F. M., P. D. McLoughlin, E. Vander Wal, and R. K. Brook. 2014. Density-dependent habitat selection and partitioning between two sympatric ungulates. Oecologia 175:1155–1165.

Vickers, T. W., J. N. Sanchez, C. K. Johnson, S. A. Morrison, R. Botta, T. Smith, B. S. Cohen, P. R. Huber, H. B. Ernest, and W. M. Boyce. 2015. Survival and mortality of pumas (*Puma concolor*) in a fragmented, urbanizing landscape. PLOS ONE 10:e0131490.

Wasser, S. K., B. Davenport, E. R. Ramage, K. E. Hunt, M. Parker, C. Clarke, and G. Stenhouse. 2004. Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. Canadian Journal of Zoology 82:475–492.

Weaver, R. A. 1978. Changing status of mountain lion in California and livestock depredation problems. Proceedings: Eighth Vertebrate Pest Conference.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126–2128.

Young, J. K., and W. Sarmento. 2024. Can an old dog learn a new trick? : Efficacy of livestock guardian dogs at keeping an apex predator away from people. Biological Conservation 292:110554.