PUMA (*PUMA CONCOLOR*) DIET AND HABITAT USE IN SOUTH-WEST NEW MEXICO

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CHAPTER ONE

A BRIEF INTRODUCTION TO THE PUMA (*PUMA CONCOLOR*)

Evolution and taxonomy

The puma (*Puma concolor*), otherwise commonly known as the cougar or mountain lion, is a member of the Family Felidae and Subfamily Felinae (Kitchener et al. 2017). The puma, jaguarundi (*Herpailurus yagouaroundi*), and African cheetah (*Acinonyx jubatus*) belong to the puma lineage, which dates back 5-8 million years with the divergence of the cheetah (Wayne et al. 1989, Janczewski et al. 1995, Johnson and O’Brien 1997, Slattery and O’Brien 1998), and within this lineage, puma and cheetah are most closely related (Johnson et al. 2006, Segura et al. 2013, Li et al. 2016).

Pumas have inhabited every biogeographic zone in the New World, apart from the arctic tundra (Culver 2009), and today, maintain the broadest latitudinal range of all native extant mammals in the Americas (Heilprin 1974, Walker and Paradiso 1975). Despite this broad distribution, modern-day puma populations occur in only one third of their historic range (Hansen 1992), and depending on the region, the International Union for the Conservation of Nature (IUCN) describes their conservation status as “unknown”, “extinct”, “endangered”, “decreasing”, or “stable” (Culver 2009).

In the 1970s, “*Puma*” was recognised as a separate genus (Ewer 1973). Between the 1700s and 1900s, 32 distinct subspecies of puma were described across the Americas (Young and Goldman 1946, Jackson 1955), however only two subspecies were retained in the latest taxonomic study (Kitchener et al. 2017), which are *Puma concolor cougar* distributed across North and Central America (Kerr 1792), and *Puma concolor concolor* in South America (Linnaeus 1771).

Morphology and predation

The puma is the fourth largest cat species in the world, and compares equally in average mass (61 kg) to the African leopard (*Panthera pardus*) and snow leopard (*P. uncia*) (Logan and Sweanor 2001). Puma feet are large, and have protractible sheathed, sharp claws to firmly hold prey, defend themselves, and climb trees (Eisenberg and Leyhausen 1972, Ewer 1973, Logan and Sweanor 2000). The hind limbs of puma are longer than the forelimbs to aid in jumping or bounding within varied terrain, and the shoulder and forelimb muscles are adapted for holding down and controlling large ungulate prey (Ewer 1973, Gonyea and Ashworth 1975, Gonyea 1976, Taylor 1989). The puma has a strong skull, jaw, and teeth to enable killing and eating prey (Biknevicius and Van Valkenburgh 1996), and additionally, the canine teeth are sturdy and do not bend, allowing the puma to safely and successfully handle prey as a solo predator (Van Valkenburgh and Ruff 1987). The puma has a small lung capacity, which hinders its ability to pursue prey and escape other apex predators (e.g., gray wolves, *Canis lupus*) at high speeds over long distances (Murphy and Ruth 2009). Pumas rely on their vision and hearing to detect prey in poor light during hours when they typically hunt, at night or dawn and dusk (Seidensticker et al. 1973, Sweanor 1990, Beier et al. 1995, Anderson and Lindzey 2003). Once prey is detected, the puma will stalk to within close distance of its quarry before bounding or galloping towards it (Young and Goldman 1946, Robinette et al. 1959). Pumas typically select their preferred ungulate prey species (Emmons 1987, Novaro et al. 2000), such as mule deer (*Odocoileus hemionus*) or elk (*Cervus elaphus*), but will display opportunism when hunting depending on the availability of prey (Ackerman 1982, Logan and Sweanor 2001, Clark et al. 2014, Stoner et al. 2021).

Like other large felids, puma habitat use occurs in a hierarchy, being, (1) geographic range, (2) home range, (3) time spent within the home range, and (4) kill site (Johnson 1980; Figure 1).

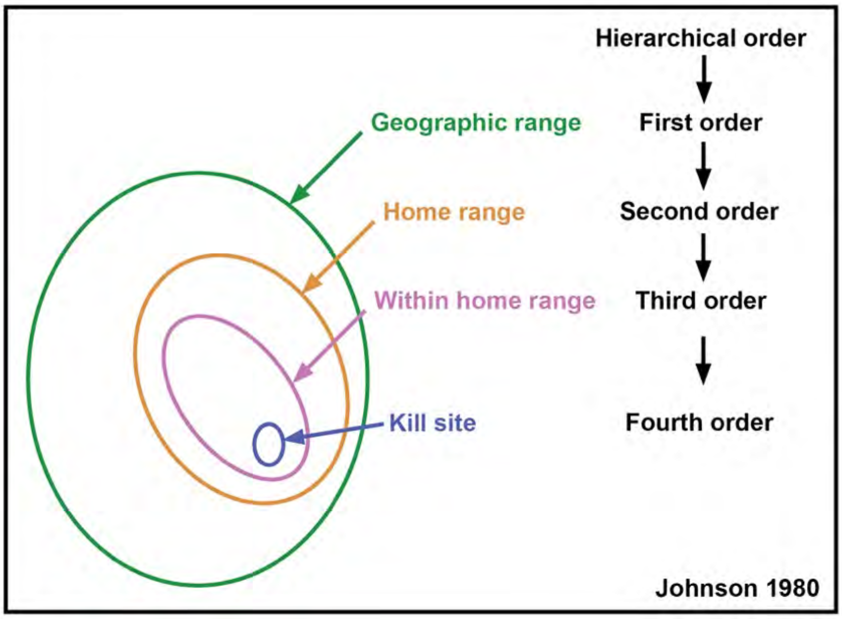

Figure 1. The hierarchy of habitat use by large felids like the puma.

Suitable habitat for pumas will include prey and water resources (Morrison et al. 2015, Gigliotti et al. 2019), and environmental features conducive to hunting, for example grassy shrubland and slightly rugged terrain (Smereka et al. 2020, Stoner et al. 2021).

Reproduction

In general, the only time adult male and female pumas come together is for mating, and males do not directly rear offspring, but indirectly protect them by defending a territory (Logan and Sweanor 2001, Elbroch et al. 2017). An adult male puma may mate with multiple females in his territory, and an adult female may mate with multiple males in one oestrous cycle, which lasts up to 16 days (Logan and Sweanor 2000, 2001, Elbroch et al. 2017). The female will give birth to an average litter of three cubs, in a protected nursery site amongst boulders or vegetation (Logan and Sweanor 2009). Puma cubs are born altricial and are dependent on instinct and the mother's ability to protect and feed them and herself (Logan and Sweanor 2009). Puma offspring become independent when they reach one to two years old and begin to disperse from their natal range to find their own home range or territory (Logan and Sweanor 2009, Jansen and Jenks 2012). At the onset of dispersal, the mother puma will recycle back into oestrus, and the subadult offspring will start to demonstrate divergent behaviour (Sweanor et al. 2000, Logan and Sweanor 2009). Female subadult pumas tend to be philopatric and establish their home ranges adjacent to their natal range, while male subadults disperse a greater distance away from their natal range to establish their own territories (Sweanor et al. 2000, Morrison et al. 2015, Elbroch et al. 2017). An adult male puma will spend most of his life defending his territory from other males and searching for mates (Logan and Sweanor 2000, 2001, Morrison et al. 2015), while an adult female will spend most of her life raising offspring (Trivers 1972).

Conservation and management

Population studies on the puma began in the 1970s, first by fitting numbered collars to obtain demographic data and enable re-identification (Hornocker 1970), and then by fitting Global Positioning System (GPS) radio telemetry collars, which accelerated research and knowledge acquisition on the species (Seidensticker et al. 1973). Since the 1990s, almost all western states in North America have developed periodic management plans in response to new scientific findings, that aim to balance stakeholder interests by maintaining healthy populations of pumas for ecological, social, and conservation goals (Anderson and Lindzey 2009, LaBarge et al. 2022). Critical information, necessary for the responsible development of management and conservation plans for the puma, includes prey preferences, habitat selection, and differences between the sexes with respect to these ecological requirements.

OUTLINE OF THESIS

The first data chapter of this thesis investigates puma diet, and the second is on the best environmental predictors of puma habitat use at the within home range and kill site scales. The two data chapters are written as scientific papers for publication, and thus there is some repetition in the methods and acknowledgements sections. The thesis is completed with a short conclusion chapter. The results from this study may contribute to the local understanding of puma ecology in south-west New Mexico, and enhance the regional conservation of pumas, and their preferred prey and habitat in this landscape.

DECLARATION

The data used in this thesis were collected over a 12-year period between February 2008 and July 2020 by Professor Travis Perry. I, Kelly Bernard, had no involvement in the collection of the data, nor in the construction of the raster files used in the data analysis for the second data chapter of this thesis. My part in this manuscript, with the advice from my two supervisors, Dr Nokubonga Mgqatsa and Professor Travis Perry, was creating the study questions; cleaning, manipulating, analysing, interpreting, and presenting the data; and writing and producing this thesis for my Master’s degree. Initially the intention was to spend six months on the Ladder Ranch learning field techniques for large carnivore research and to participate in data collection, however, the COVID-19 pandemic made this impossible.

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CHAPTER TWO

PUMA (*PUMA CONCOLOR*) SEX INFLUENCES DIET IN SOUTH-WEST NEW MEXICO

ABSTRACT

The puma (*Puma concolor*) is a wide-ranging large felid species occupying an extensive geographic range throughout North and South America, and site-specific research on their diet is important for local management. Like other large felids, puma diet may differ between sexes due to size dimorphism, and between seasons due to changes in prey vulnerability and availability. This study assessed the influence of sex and season on puma diet in south-west New Mexico in terms of prey species and prey size categories. Pumas specialised on mule deer and elk throughout the year, and killed a range of other species of different sizes. The diet of the smaller female puma was nested within the diet of males, supporting the size-nested strategy. The effect of puma sex on prey species and size categories was independent of season, and vice versa, and the probability of a female making a medium-sized kill such as mule deer was higher than for males, while the probability of an extra-large kill such as elk was substantially greater for males. The probability of pumas killing either mule deer or elk in each season was similar, and greater than other species categories. Additionally, individual puma strongly influenced all prey species and size categories killed. The results from this study concur with previous findings on the importance of mule deer and elk in puma diet, and suggest that puma predation may also impact a number of other species, particularly smaller herbivores like collared peccary, and mesocarnivores such as skunks.

Key words: carnivore, *Cervus elaphus,* conservation, cougar, elk, feeding ecology, mountain lion, mule deer, *Odocoileus hemionus,* ungulate

INTRODUCTION

Large felid species are wide-ranging and often occupy territories that extend past the boundaries of ranches, protected areas, and states (Forrest et al. 2012, Ripple et al. 2014). The need for great expanses of land renders these species susceptible to habitat loss, additional intra- and inter-specific competition, and changes in protection by different conservation practices between ranches and states (Loveridge et al. 2010, Elbroch and Kusler 2018, Elbroch 2020). However, the ability to cross boundaries and borders can also enable large felids to access suitable habitat, prey, and mates when natal ranges are saturated (Loveridge et al. 2010, Elbroch and Quigley 2019).

Large felid species will influence the ecosystems in which they occur by exerting top-down pressure on prey populations (Sergio et al. 2008, Cepeda-Duque 2021). To meet their energy requirements large felids may exhibit a generalist hunting strategy and kill a range of prey species of different sizes, or specialise on a narrow range of prey (Macdonald and Loveridge 2010, Elbroch and Quigley 2019, LaBarge et al. 2022). Additionally, predation may be influenced by the vulnerability and availability of prey between seasons, with more young, vulnerable prey being killed after birth in the warm-wet season and more old, weak prey being killed in the resource-scarce winter months (Knopff et al. 2010, Allen et al. 2014).

The effect of body size on diet has been widely reported (Radloff and du Toit 2004, Davidson et al. 2013, Clark et al. 2014, Elbroch and Quigley 2019) and larger felids preferentially kill larger prey than do smaller felids (Sinclair et al. 2003). However, both large and small felids kill prey that is outside their preferred size range and as a result, the diet of smaller felids is nested within the diet of larger felids (Sinclair et al. 2003). In this context, male and female felids displaying sexual size dimorphism may kill different species and sizes of prey (Laundré 2005, Elbroch and Wittmer 2013, Clark et al. 2014) and the diet of the smaller sex will be nested within that of the larger (Sinclair et al. 2003).

Populations of large ungulate species that display low recruitment rates may be negatively impacted by predation by large felids, especially if individuals killed are those that actively contribute to population persistence (e.g., adult females; Le Roux et al. 2019). Additionally, populations of small-sized species may be negatively impacted by large felids that also kill prey that is smaller than the preferred size although, the energetic benefit of including small prey in diet is often not great enough for these species to specialise on this size (Clements et al. 2014).

The puma (*Puma concolor*) is a wide-ranging large felid species that inhabits varied terrain throughout its extensive geographic distribution in the Western Hemisphere (Iriarte et al. 1990). The ecological plasticity displayed by pumas enables them to access prey and mates, but also renders them susceptible to varying degrees of protection by different conservation practices between states and countries (Jenks 2011, Wilckens et al. 2016, Gigliotti et al. 2019, Cepeda-Duque et al. 2021).

Pumas are solitary and sexually dimorphic (male body mass: 78 kg; females: 48 kg), with an average body mass comparable to the African leopard (*Panthera pardus*) and snow leopard (*Panthera uncia*) (Logan and Sweanor 2001, Elbroch and Wittmer 2013, Ripple et al. 2014). Pumas hunt at short-range and specialise on the most abundant large ungulates of a similar body mass to their own (e.g., mule deer *Odocoileus hemionus*), and will additionally prey upon a range of species of different sizes (Hornocker 1970, Logan and Sweanor 2001, Moss et al. 2016, LaBarge et al. 2022).

Seasonally, more new-born ungulates are killed by pumas when they are weak and vulnerable after birth in the warm-wet months (Knopff et al. 2010, Allen et al. 2014, Clark et al. 2014), and more juvenile and adult ungulates are preyed upon in the cold-dry season when their body condition is poor (Bischoff-Mattson and Mattson 2009, Clark et al. 2014). Body condition of ungulates may be poor in the cold-dry season due to limited resources and the negative impacts of rutting on adult males, making larger ungulates easier to hunt (Bischoff-Mattson and Mattson 2009, Clark et al. 2014). Moreover, carcasses may be better preserved in cold weather, allowing pumas to feed off a kill for longer (Hornocker 1970, Lima and Dill 1990, Bischoff-Mattson and Mattson 2009, Clark et al. 2014).

Recent studies have been published on puma diet in both North America (Clark et al. 2014, Elbroch and Quigley 2019, Prude and Cain 2021) and South America (Ávila–Nájera et al. 2018, Llanos et al. 2020, Cepeda-Duque et al. 2021), however there has been limited recent research published on puma diet in south-west New Mexico (but see Prude and Cain 2021 for recent research on pumas in south-central New Mexico, and Logan and Sweanor 2001 for a more dated but in-depth study of puma ecology in south-central New Mexico). Furthermore, few recent studies have focused on the effect of both sex and season on puma diet in this area (but see Elbroch and Wittmer 2013, Clark et al. 2014, and Elbroch and Quigley 2019 for similar research in other states).

This study investigated the diet of pumas on a private ranch in south-west New Mexico with the aim of aiding local conservation of both pumas and their prey in this state. The specific objective was to determine whether sex or season influenced puma diet in terms of prey species or prey size categories killed, and the prediction was that both predictor variables (puma sex and season) would influence prey killed (Elbroch and Wittmer 2013, Clark et al. 2014, Elbroch and Quigley 2019), and results would support the size-nested strategy with the diet of the female puma being nested within that of males (Sinclair et al. 2003, LaBarge et al. 2022).

METHODS

Study site

The Ladder Ranch study site (33°01’57.68”N, 107°30’39.11”W) is a privately owned 633 km^2 property in Sierra County, south-west New Mexico (Figure 1). The Ranch borders the Black Range mountains, and the Gila National Forest and Aldo Leopold Wilderness to the west (Figure 1). The property is multi-operational with bison (*Bison bison*) ranching, ecotourism, hunting, and research activities, and includes grazing leases on U.S. Forest Service, Bureau of Land Management, and New Mexico state properties (Pitman 2010). The Ranch has a limited human presence and the closest town is Caballo, which is 24 km east-south-east of the property.

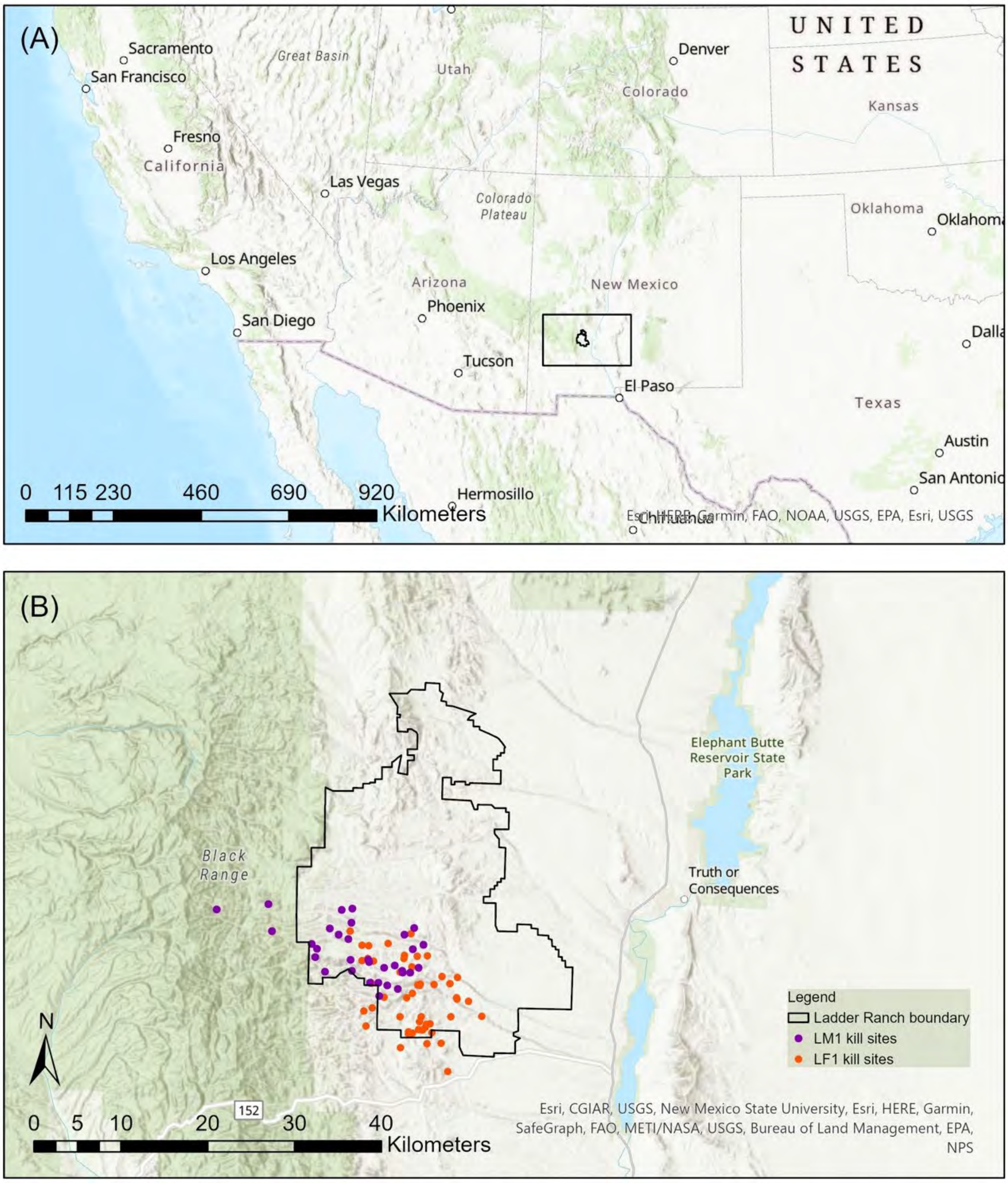

Figure 1. The Ladder Ranch study site in south-west New Mexico (A), depicting the kill sites (colored dots) for one male (LM1) and one female puma (LF1; B).

The most abundant apex predators on the Ranch are the puma and American black bear (*Ursus americanus*), and common prey species include mule deer, elk (*Cervus elaphus*), and collared peccary (*Tayassu tajacu*). Other carnivores present include the coyote (*Canis latrans*), bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*), Northern raccoon (*Procyon lotor*), ringtail (*Bassariscus astutus*), and several skunk species (*Spilogale gracilis*, *Mephitis mephitis, M. macroura,* and *Conepatus leuconotus*) (Rossettie 2019).

The warm-wet season during which the ungulate birth-pulse occurs is from April to September with an average temperature of 31 °C, while the temperature decreases to an average of 17 °C in the cold-dry winter months between October and March (Logan and Sweanor 2001). The mean yearly rainfall of 500 mm is indicative of a desert ecosystem, and occurs mainly at high elevation in the warm-wet season (Rossettie 2019).

The elevation varies between 1300 – 2400 meters above sea level from east to west, and is matched by the vegetation, being Chihuahua desert grassland at the foothills, pinyon-juniper woodland at mid-elevation, and mixed-conifer forest at high elevation (Pitman 2010). Four perennial streams run through the property and are surrounded by dense riparian woodland.

Data collection

Ethical clearance

This research was approved by the Rhodes University Animal Research Ethics Committee (reference: 5009), the Institutional Animal Care and Use Committee (IACUC) at Furman University, and the New Mexico Department of Game and Fish (permit number: 3456).

Collaring pumas

Sixteen pumas (10 males and six females) were fitted with Global Positioning System (GPS) collars between February 2008 and July 2020. Pumas were captured in foothold cables (Logan et al. 1999) that were continuously monitored by remote camera traps to alert the researchers to the capture of a puma. Upon alert, the researchers went to the site and darted the puma for immobilization with Ketamed (2 mg / kg ketamine + 0.075 mg / kg medetomidine; Kreeger et al. 2002). Immobilisation occurred approximately two and a half hours after the puma was captured in the foothold cable.

Once the puma was immobilized, lubricating eye gel was immediately applied to both eyes, and a dark cloth with an opening for breathing was placed over the head to protect the eyes and reduce visual stimulation. The immobilized puma was then transported to a level work area, the collar was fitted, and several biometrics were recorded, including total body length (mm) and weight (kg), and total length of each canine (mm). Additionally, basic observations were recorded, such as sex, reproductive status (e.g., not reproductive, lactating, pregnant, and post lactating), the presence of injuries, scars, possible identifying characteristics, and body condition (e.g., normal weight, underweight, and emaciated; based on the presence of stomach fat as estimated from external observation).

During collar fitting and data collection, the respiration of the anaesthetised puma was closely monitored, additional eye lubricant was applied every 15 minutes, and the temperature of the body was measured and recorded every two minutes. After the collar was fitted, biometrics were recorded, and a minimum time of 45 minutes per Ketamed dose had elapsed to allow for the metabolism of ketamine, the medetomidine component of the Ketamed drug was reversed with 0.3 mg / kg atipamezole (Kreeger et al. 2002).

Brands of collars used were Followit, Northstar, Telonics, and Lotek, and the average mass per collar was 900 g. All collars were programmed to record the location of a puma (i.e., one GPS fix) at either two- or three-hour intervals, depending on the brand of collar and battery life, every day of the week between 19:00 and 7:00 when pumas are most active (Beier 1995, Logan and Sweanor 2001).

Puma diet

Puma kill sites were identified by analysing clusters of GPS fixes (Anderson and Lindzey 2003) in RStudio (RStudio Team 2020). Potential kill sites were defined as clusters of GPS fixes within 100 m distance of each other and occurring within 100 hours of the first point in the cluster (Logan and Sweanor 2009). GPS fixes that showed at least two points indicating that the puma had spent a minimum of two-hours in the same location were visited by the researchers to confirm a kill site, and sites with more points per cluster were visited first (Anderson and Lindzey 2003, Davidson et al. 2012).

At each kill site, the remains of prey, and tracks and signs of the puma were identified within a 100 m radius of the first point in the cluster. Prey species were identified by bone, hair, pelage, and/or feather remains, and hair samples were collected for verification (Allen et al. 2014, Elbroch and Quigley 2019). The date of the kill was determined by the first GPS fix in the cluster (Clark et al. 2014), and assigned to the relative season (warm-wet or cold-dry).

When possible, kills were identified to sex and age class. Age class of ungulates was determined by size of prey, sutures in cranium, and tooth wear and eruption patterns. Sex was determined from antler pedicles, or the antlers themselves (Clark et al. 2014). Age classes were fawns and calves (< 6 months), juveniles (6 months – 2 years), and adults (> 2 years). For kills that could not be assigned to an age class, a record of “unidentifiable to age class” was given, and for kills unidentifiable to sex a record of “unidentifiable to sex” was given.

This method of collecting data on puma diet has the potential to confuse a scavenging event as a puma kill. In order to help confirm that the kill was made by the puma, the age of prey remains, signs of evisceration and caching, body parts consumed, and area of bite marks were assessed (Allen et al. 2014, Clark et al. 2014).

Data manipulation

Prey species categories

The prey dataset included 16 identifiable species (Appendix A), of which two were common (mule deer: n = 192; elk: n = 150). The remaining species were infrequently recorded. To permit statistical analysis, data from the rare species (where the number of kills was low) were grouped by prey type (Elbroch and Quigley 2019). Kills of collared peccary (n = 29), pronghorn (*Antilocapra americana*, n = 3), and North American porcupine (*Erethizon dorsatum*, n = 1) were categorised as ‘other herbivores’ (n = 33); kills of the order Carnivora were categorised as ‘carnivores’ (n = 21); and kills of the orders Galliformes (n = 4), Accipitriformes (n = 2), and Cuculiformes (n = 1) were grouped with one unidentifiable bird kill and categorised as ‘birds’ (n = 8). This resulted in five prey species categories (Appendix A).

Prey size categories

To further test the prediction that female puma diet is nested within that of males, and support the size-nested strategy (Sinclair et al. 2003) kills were categorised by body size according to mass. Kills > 183 kg (triple the average body mass of an adult puma, 61 kg) were considered extra-large (n = 87). Large kills were 92 – 183 kg (n = 72), medium sized kills were 41 – 91 kg (n = 142), and small kills were < 41 kg (n = 103). This resulted in four prey size categories which were assigned for both male and female pumas (Appendix B).

Body mass data for each age class category per prey species was obtained from published literature (e.g., Allen et al. 2014, Elbroch et al. 2017). For species unidentifiable to age (n = 100), ¾ of the adult female mass per species was used (Owen-Smith 1988, Hayward and Kerley 2005, Barnardo et al. 2020), and for adults unidentifiable to sex (n = 49) the average adult mass between the sexes of each species was used (Appendix B). For prey species classified as small (n = 59), the adult mass was used for all individuals killed (Radloff and du Toit 2004; Appendix B).

Statistical analyses

To investigate the effect of puma sex and season on the probability of different species and size categories being preyed upon, the data were analysed in Bayesian hierarchical multinomial logistic regression models (e.g., Koster and McElreath 2017, dos Anjos et al. 2022, Lancaster et al. 2022) in RStudio (RStudio 2022). The effect of puma sex and season were assessed on prey species and prey size categories separately. As such, prey species category (five levels: mule deer, elk, other herbivores, carnivores, and birds) and prey size category (four levels: extra-large, large, medium, and small) were entered as the multinomial response variables, and puma sex (two levels: male and female) and season (two levels: warm-wet and cold-dry) were entered as the predictor variables in each model. Per model, individual puma (16 levels: male = 10, female = six) was included as a group-level factor (random effect) to account for the potential preference that individuals may have for specific prey species or size categories.

Bayesian models were run through the program *RStan v 2.21.2* (Stan Development Team 2021) using the package *brms v 2.17.0* (Buerkner 2017, 2018) in R version 4.0.3 (RCore Team 2021). First, a set of five candidate models was created: (1) a null model containing only the intercept, (2) a full model containing both predictor variables with an interaction term, (3) a model containing both predictor variables with no interaction, (4) a model containing only puma sex, and (5) a model containing only season (Table 1). The interaction model (model 2) was included to test if the effect of puma sex on prey species and size category killed was independent of season, and vice versa.

Each model contained four chains, each with a minimum of 5000 iterations and 1500 burn-in samples. For each model, mixing was successful and converged to a minimum Rhat value of 1.0. Model validation was performed using approximate leave-one-out cross-validation, and model outputs were compared using the predictive expected accuracy (elpd_diff) of the Widely Applicable Information Criterion (WAIC; Watanabe 2010). To further define each model, model weights were obtained and assessed using the function loo_model_weights in the package *brms*. Probabilities with 95% confidence intervals for prey species and prey size categories were predicted from the model outputs for puma sex and season using the call conditional_effects in the package *brms* and were plotted using ggplot2 (Wickham 2016).

RESULTS

Prey species categories killed

The raw data indicated that pumas specialised on killing both mule deer and elk throughout the year, and that females preferred mule deer, while males killed more elk (Appendix A). The model without an interaction term (M3) ranked best (Table 1), indicating that the effect of puma sex on prey species category killed was independent of season, and vice versa.

Table 1. Bayesian hierarchical multinomial models evaluated probabilities of prey species categories killed by male and female pumas in the warm-wet and cold-dry seasons in south-west New Mexico. The Widely Applicable Information Criterion (WAIC), standard error (seWAIC), difference in the expected predictive accuracy (elpd_diff; ΔWAIC), and model weight (loo_model_weight; $WAIC_{(i)}$) are presented for each candidate model.

Models		WAIC	seWAIC	ΔWAIC	$WAIC_{(i)}$
M3	**~ 1 + Sex + Season + (1 | Individual)**	**808.2**	**37.5**	**0.0**	**0.667**
M5	~ 1 + Season + (1 | Individual)	809.5	36.6	-0.6	0.000
M4	~ 1 + Sex + (1 | Individual)	813.5	36.3	-2.6	0.000
M2	~ 1 + Sex * Season + (1 | Individual)	813.6	39.0	-2.7	0.000
M1	~ 1 + (1 | Individual)	813.8	35.2	-2.8	0.333

The raw data and model outcomes were in agreement and the optimal model depicted a higher probability of a mule deer kill for female pumas than males, and a considerably greater probability of an elk kill for males (Figure 2 A). In each season, the probability of pumas killing either mule deer or elk was similar and substantially higher than other species categories (Figure 2 B). Additionally, the optimal model revealed that individual puma, modelled as a random effect, had a strong influence on all prey species categories killed (Table 2).

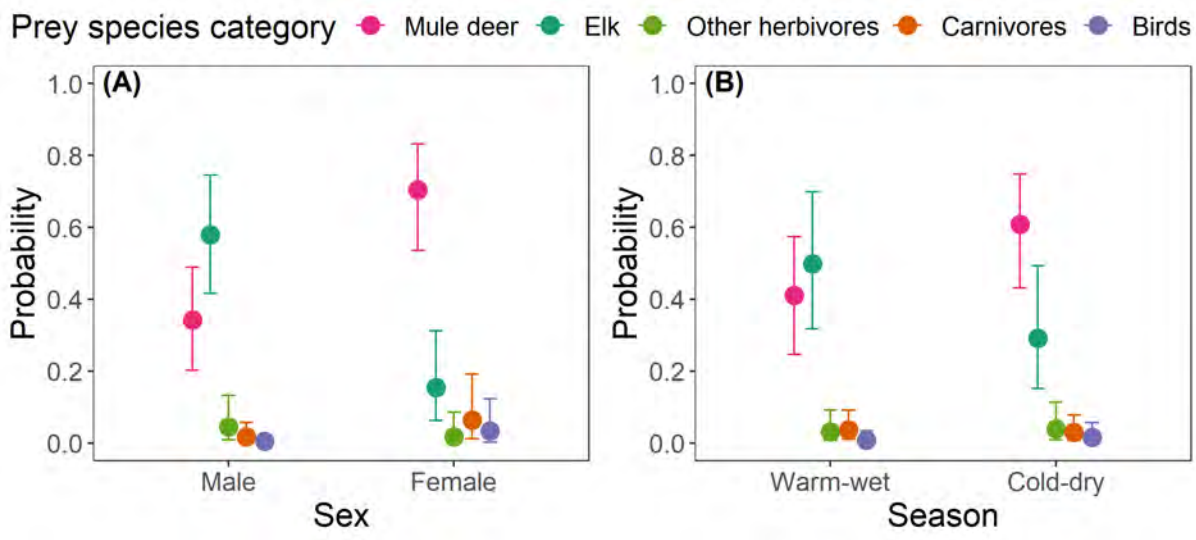

Figure 2. Probability of prey species categories being killed by a male or female puma (A), or by both puma sexes combined in each season (warm-wet, cold-dry; B) in south-west New Mexico. Data are probabilities with 95% confidence intervals.

Table 2. Estimated coefficients for the optimal Bayesian hierarchical multinomial model evaluating the probability of prey species categories killed by male and female pumas in the warm-wet and cold-dry seasons in south-west New Mexico. Estimate (Est.), estimated error (EE), lower and upper 95% confidence intervals, potential scale reduction factor (Rhat), and bulk and tail effect sample sizes (ESS) are given for each coefficient.

	Est.	**EE**	**L 95% CI**	**U 95% CI**	**Rhat**	**Bulk ESS**	**Tail ESS**
Group-Level Effects							
~ Individual (Levels: 16)							
sd(muElk_Intercept)	0.93	0.29	0.48	1.59	1.00	2527	2251
sd(muOtherherbivores_Intercept)	1.58	0.58	0.76	2.99	1.00	2636	2532
sd(muCarnivores_Intercept)	1.25	0.50	0.51	2.42	1.00	2705	2719
sd(muBirds_Intercept)	1.63	1.04	0.17	4.11	1.00	2026	1933
Population-Level Effects							
muElk_Intercept	-0.60	0.30	-1.20	-0.02	1.00	2789	2902
muOtherherbivores_Intercept	-2.93	0.66	-4.37	-1.84	1.00	2534	2392
muCarnivores_Intercept	-2.78	0.51	-3.88	-1.89	1.00	2651	2789
muBirds_Intercept	-3.97	0.88	-6.12	-2.70	1.00	2363	2226
muElk_Sex.L	-1.50	0.45	-2.45	-0.68	1.00	2493	2693
muElk_Season.L	-0.67	0.19	-1.03	-0.30	1.00	2928	2694
muOtherherbivores_Sex.L	-1.20	0.86	-2.87	0.44	1.00	2580	2084
muOtherherbivores_Season.L	-0.16	0.31	-0.77	0.45	1.00	2179	2617
muCarnivores_Sex.L	0.36	0.68	-0.99	1.73	1.00	2550	2011
muCarnivores_Season.L	-0.42	0.41	-1.23	0.36	1.00	2778	2586
muBirds_Sex.L	0.91	1.07	-1.12	3.12	1.00	2335	2545
muBirds_Season.L	0.28	0.59	-0.88	1.42	1.00	2874	2768

Prey size categories killed

In terms of prey size categories killed, the raw data revealed that pumas killed prey of all size categories (Appendix B), and that females specialised on prey of a medium size, while males killed more extra-large prey than females. The optimal model retained both predictor variables (puma sex and season) without an interaction term (M3), indicating that the effect of season on prey size category killed was independent of puma sex, and vice versa (Table 3).

Table 3. Bayesian hierarchical multinomial models evaluated probabilities of prey size categories killed by male and female pumas in the warm-wet and cold-dry seasons in south-west New Mexico. The Widely Applicable Information Criterion (WAIC), standard error (seWAIC), difference in the expected predictive accuracy (elpd_diff; ΔWAIC), and model weight (loo_model_weight; $WAIC_{(i)}$) are presented for each candidate model.

Models		WAIC	seWAIC	ΔWAIC	$WAIC_{(i)}$
M3	**~ 1 + Sex + Season + (1 | Individual)**	**966.9**	**25.6**	**0.0**	**0.682**
M5	~ 1 + Season + (1 | Individual)	969.9	24.9	-1.5	0.000
M2	~ 1 + Sex * Season + (1 | Individual)	971.1	26.0	-2.1	0.000
M4	~ 1 + Sex + (1 | Individual)	971.5	24.9	-2.3	0.000
M1	~ 1 + (1 | Individual)	973.4	24.4	-3.3	0.318

The results from the optimal model supported the raw data and suggested a higher probability of a medium-sized kill for female pumas than males, and a substantially greater probability of an extra-large kill for males (Figure 3 A). There were no clear trends of prey selection by size category between seasons (Figure 3 B), and individual puma strongly influenced all prey size categories killed (Table 4).

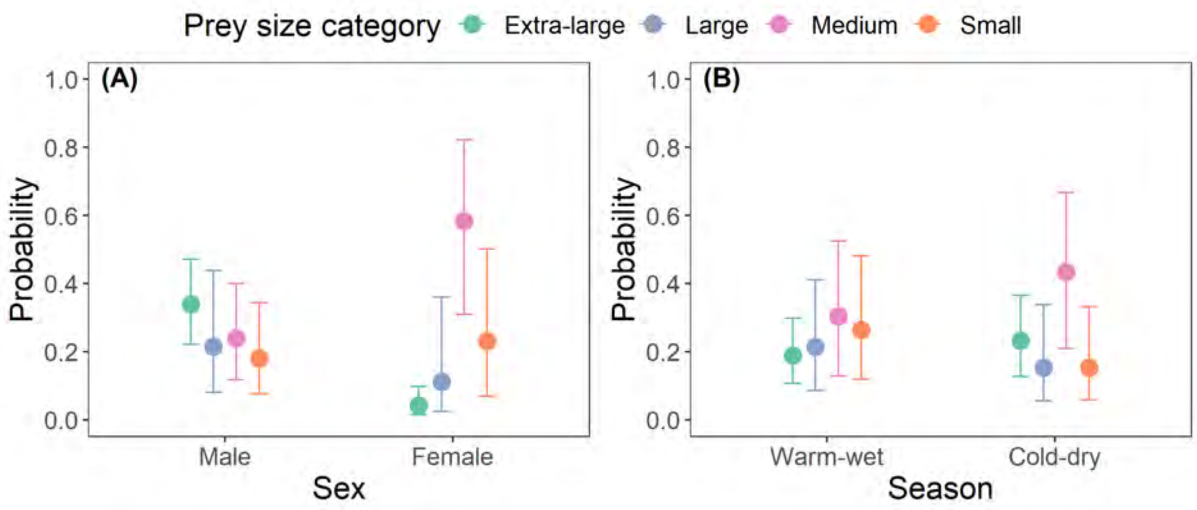

Figure 3. Probability of prey size categories being killed by a male or female puma (A), or by both sexes combined in each season (warm-wet, cold-dry; B) in south-west New Mexico. Data are probabilities with 95% confidence intervals.

Table 4. Estimated coefficients for the optimal Bayesian hierarchical multinomial model evaluating the probability of prey size categories killed by male and female pumas in the warm-wet and cold-dry seasons in south-west New Mexico. Estimate (Est.), estimated error (EE), lower and upper 95% confidence intervals, potential scale reduction factor (Rhat), and bulk and tail effect sample sizes (ESS) are given for each coefficient.

	Est.	EE	L 95% CI	U 95% CI	Rhat	Bulk ESS	Tail ESS
Group-Level Effects							
~ Individual (Levels: 16)							
sd(muLarge_Intercept)	1.47	0.49	0.73	2.62	1.00	2647	2729
sd(muMedium_Intercept)	0.89	0.34	0.34	1.70	1.00	2238	2375
sd(muSmall_Intercept)	1.20	0.36	0.66	2.04	1.00	2569	2297
Population-Level Effects							
muLarge_Intercept	0.21	0.49	-0.79	1.17	1.00	2853	2527
muMedium_Intercept	1.15	0.35	0.49	1.88	1.00	2841	2607
muSmall_Intercept	0.46	0.43	-0.38	1.25	1.00	3041	2458
muLarge_Sex.L	1.05	0.70	-0.33	2.48	1.00	2816	2527
muLarge_Season.L	-0.37	0.26	-0.88	0.14	1.00	2976	2527
muMedium_Sex.L	2.15	0.52	1.26	3.29	1.00	2650	2751
muMedium_Season.L	0.11	0.22	-0.32	0.55	1.00	2837	2682
muSmall_Sex.L	1.66	0.62	0.47	2.90	1.00	2770	2649
muSmall_Season.L	-0.52	0.24	-1.02	-0.06	1.00	2965	2756

DISCUSSION

The results of this study met the prediction that puma sex would influence prey species and prey size categories killed, and support the size-nested strategy with the diet of the smaller female puma being nested within that of the larger male (Sinclair et al. 2003). The data showed that both mule deer and elk were preyed upon considerably more than other species categories by both puma sexes combined and by males, while females exhibited a strong reliance on mule deer. These findings mirror a broader pattern of puma preference for deer species throughout their distribution (Iriarte et al. 1990, Logan and Sweanor 2001, Villepique et al. 2011, Clark et al. 2014, Wilckens et al. 2016, Prude and Cain 2021, LaBarge et al. 2022).

The optimal model results were in agreement with the raw data and revealed that the probability of an extra-large kill such as elk was higher for male pumas than for females, while the probability of a medium-sized kill such as mule deer was greater for females. Similar results have been found in previous research on the effect of puma sex on diet (Elbroch and Wittmer 2013, Clark et al. 2014, Elbroch and Quigley 2019). The larger body mass of male pumas allow them to successfully hunt extra-large prey such as elk (Iriarte et al. 1990), while the smaller bodied female puma successfully hunts medium-sized mule deer (Logan and Sweanor 2001, Murphy and Ruth 2009). Additionally, compared to female pumas, males may share more of their higher elevation habitat with elk, thus increasing the likelihood of detecting and hunting this species (Sawyer et al. 2005, Smith 2007). Differences in diet between sexes is recorded for other sexually dimorphic large felids, for example male African lions (*Panthera leo*) kill more African buffalo (*Syncerus caffer*), a larger sized bovid compared to females that specialize on smaller antelopes (e.g., blue wildebeest *Connochaetes taurinus*) (Radloff and du Toit 2004, Davidson et al. 2013).

In the two analyses of this study, both predictor variables (puma sex and season) were kept in the most parsimonious models, suggesting that season affected prey species and size categories killed by pumas. Additionally, the second-best model in each analysis included only season as a predictor variable. However, the outputs of the optimal models showed no clear effects of season on prey killed, particularly in the size category analysis. Nevertheless, the raw data suggested that pumas killed more small-sized prey, including elk and mule deer new-borns in the warm-wet season compared to the cold-dry season when they killed more extra-large prey such as adult elk. This pattern of puma predation between seasons is exhibited by individuals throughout their range, and corresponds to the ungulate birth pulse in the warm-wet season and the resource scarce cold months, respectively (Knopff et al. 2010, Allen et al. 2014, Elbroch et al. 2014, Wilckens et al. 2016).

In addition to mule deer and elk, pumas killed a range of other species of different sizes and this result is matched by previous findings (Clark et al. 2014, Elbroch and Quigley 2019, LaBarge et al. 2022). Male pumas on the Ladder Ranch killed more ‘other herbivores’ such as collared peccary than females, while females killed more ‘carnivores’ including skunks. Additionally, there was considerable variation between secondary prey killed by individual pumas, and the optimal models depicted a strong influence of individual on prey species and size categories killed, which is supported by previous work (Lowrey et al. 2016). Similarly, the Indochinese leopard (*Panthera pardus delacouri*) exhibited individual variation between secondary prey killed, but specialised on large ungulates of a similar body mass to its own (Rostro-GarcÍa et al. 2018). For large felids like the puma and leopard, their short-range, adaptable hunting strategies allow for energetic efficiency when hunting small-sized prey, which offsets the energy trade-off in hunting these smaller-sized animals (Murphy and Ruth 2009, Clements et al. 2014). Therefore, the potential impact of puma predation on populations of secondary prey, including smaller ungulates and mesocarnivores should not be overlooked as predation pressure may be sufficient to exert top-down control, as reported in other systems (Levi and Wilmers 2012, Allen et al. 2015).

The relationship between the abundance of mule deer and elk, and the frequency of kills of these species is an important aspect to include in future research on puma diet. However, due to the lack of prey abundance estimates on the Ladder Ranch, the current study was unable to assess the effect of prey abundance on prey killed.

Furthermore, to get a better understanding of the ecological impacts of puma predation on both primary and secondary prey, future studies should include kill rate data (kg/day) and biomass of prey killed (Elbroch et al. 2014, Wilckens et al. 2016).

The results from this study elucidate the primary and secondary prey of pumas in south-west New Mexico and contribute to local research on the effect of sex and season on puma diet in this region. Because the puma sexes occur at different densities on the landscape, it may be expected that male and female pumas have significantly different impacts on prey population dynamics and community structure, of not just primary prey but also of smaller herbivores and mesocarnivores, and this should be investigated in future research.

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APPENDIX

Appendix A. Number of kills of each prey species, and of each prey species category by both puma sexes combined between February 2008 and July 2020 in south-west New Mexico.

Species	**No. kills**	**Species category**	**No. kills**
Mule deer	192	Mule deer	192
Elk	150	Elk	150
Collared peccary	29	Other herbivores	33
Pronghorn	3	Other herbivores	33
North American porcupine	1	Other herbivores	33
Coyote	5	Carnivores	21
Gray fox	2	Carnivores	21
Northern racoon	2	Carnivores	21
Bobcat	1	Carnivores	21
Puma	1	Carnivores	21
Western spotted skunk	1	Carnivores	21
Striped skunk	1	Carnivores	21
Skunk (unknown species)	8	Carnivores	21
Wild turkey	3	Birds	8
Gambel’s quail	1	Birds	8
Red-tailed hawk	2	Birds	8
Greater roadrunner	1	Birds	8
Bird (unknown species)	1	Birds	8
Total	404		404

Appendix B. Body mass and number of kills per age class category of each species preyed upon by pumas in south-west New Mexico between February 2008 and July 2020. Size category is included for each entry. NA is inserted for species where the adult mass lies within the small prey size category, or for individuals where no age class was assigned.

Prey species	Age class category	Mass (kg)	No. kills	Size category
Elk	Adult male	353	3	Extra-large
Elk	Adult unidentifiable to sex	309	6	Extra-large
Elk	Adult female	265	28	Extra-large
Elk	Unidentifiable to age class	199	50	Extra-large
Elk	Juvenile	120	35	Large
Mule deer	Adult male	102	37	Large
Mule deer	Adult unidentifiable to sex	84	43	Medium
Mule deer	Adult female	66	22	Medium
Mule deer	Unidentifiable to age class	50	50	Medium
Mule deer	Juvenile	50	26	Medium
Pronghorn	Adult female	44	1	Medium
Puma	Juvenile	35	1	Small
Pronghorn	Unidentifiable to age class	33	2	Small
Elk	Calf	20	28	Small
Collared peccary	NA	20	29	Small
Coyote	NA	13	5	Small
North American porcupine	NA	9	1	Small
Bobcat	Cub	9	1	Small
Wild turkey	NA	6	3	Small
Gray fox	NA	6	2	Small
Northern racoon	NA	6	2	Small
Mule deer	Fawn	3	14	Small
Striped skunk	NA	3	1	Small
Red-tailed hawk	NA	1	2	Small
Western spotted skunk	NA	0.45	1	Small
Greater roadrunner	NA	0.3	1	Small
Gambel’s quail	NA	0.19	1	Small
Skunk (unknown species)	NA	NA	8	Small
Bird (unknown species)	NA	NA	1	Small

CHAPTER THREE

VEGETATION AND RUGGEDNESS INFLUENCE PUMA (*PUMA CONCOLOR*) HABITAT USE IN SOUTH-WEST NEW MEXICO

ABSTRACT

Understanding large felid habitat use can direct conservation efforts to protect functional landscapes and contribute to their survival. This study aimed to determine the best environmental predictors of puma (*Puma concolor*) habitat use at the within home range and kill site scales, and assess differences between the sexes, on a private ranch in south-west New Mexico. Following the prey abundance and prey catchability hypotheses, it was expected that the best environmental predictors of puma habitat use would differ between scales, and between sexes as a result of the different habits of each sex. The findings from this study met the expectations, with vegetation being the strongest predictor of puma occurrence at the within home range scale, while topographic ruggedness best predicted kill sites. There was a high probability of pumas selecting vegetation types such as riparian desert, montane shrub, and desert grassland at the within home range scale compared to what was available on the Ranch. Between sexes, there was a greater probability of males selecting pine forest, and of females selecting desert grassland and desert shrubland. At the kill site scale, there was a strong probability of pumas killing prey in level to intermediately rugged terrain relative to the habitat used within their home ranges. These results concur with previous findings on the importance of grassy shrubland and riparian vegetation, and slightly rugged terrain within puma habitat, and may contribute to the conservation of pumas in this region.

Key words: carnivore, conservation, cougar, environment, home range, kill site, large felid, mountain lion, topography

INTRODUCTION

Large carnivores of the Family Felidae, such as the puma (*Puma concolor*) require extensive suitable habitat to sustain a territory or home range, successfully mate with genetically distant individuals, and access prey and water resources (Orians and Wittenberger 1991, Beier 1995, Logan and Sweanor 2001, Klaassen and Broekhuis 2018, Ashrafzadeh et al. 2020). Wide-scale habitat loss can therefore negatively impact populations of large felids (Woodroffe 2000, Ripple et al. 2014). When natural, suitable habitat becomes saturated by established populations of large felids, or degraded and transformed into unsuitable land, individuals may travel great distances and cross human-created boundaries, such as fences, highways, and agricultural land in search of prey, suitable habitat, and mates (Beier 1995, Nowell and Jackson 1996, Balme et al. 2007, Knopff et al. 2014, Elbroch and Kusler 2018, Gigliotti et al. 2019). Although this ability to traverse through unsuitable habitat can benefit the animal by allowing it to access resources, it can also put it at risk of being killed by humans to protect livestock and promote human safety (Knopff et al. 2014, Elbroch and Kusler 2018, Elbroch and Quigley 2019, Suraci et al. 2019). Understanding the components of suitable habitat for large felids is thus a critical conservation question that will aid in conserving the resources needed for the survival of pumas and other large felid species (Nowell and Jackson 1996, Logan and Sweanor 2001, Morrison et al. 2015, Gigliotti et al. 2019).

The puma occurs within a variety of habitats across its range in North and South America, from swamp forests (Belden et al. 1988) to desert ecosystems (Logan and Sweanor 2001). Despite this ecological plasticity, hunting by humans and habitat loss have restricted modern-day puma populations to the western States and Florida (Nowell and Jackson 1996, Ripple et al. 2014, Elbroch and Kusler 2018). Recently, however, subadult pumas have dispersed eastwards through the Midwest of North America, making research on their habitat use not only relevant for established puma populations, but also for ensuring the successful dispersal of subadults into new functional habitats out of their modern range (Morrison et al. 2015, Choate et al. 2018).

The habitats used by the puma are influenced by a range of factors including their feeding ecology, and individuals may select areas that are conducive to hunting their preferred and secondary prey (Beier et al. 1995). Pumas prey on a variety of species, but will specialise on the most abundant large ungulates in their range (Logan and Sweanor 2001, Prude and Cain 2021). When actively hunting and prey is detected, pumas stalk to within close distance of prey before quickly accelerating towards it (Robinette et al. 1959, Hornocker 1970). Pumas are solitary, ambush predators that require adequate cover to capture their preferred prey (Hornocker 1970, Logan and Sweanor 2001).

All large felid habitat use, including that of the puma, occurs in a hierarchy, being, (1) geographic range, (2) home range, (3) time spent within the home range, and (4) kill site (Johnson 1980). The pumas geographic range has spanned every vegetation type, at elevations from sea level to 4000 meters above sea level throughout the Americas (Logan and Sweanor 2009). Puma home range selection may be affected by habitat availability and intraspecific competition (Quigley and Hornocker 2009), while time spent within the home range may be positively influenced by prey abundance (Murphy and Ruth 2009). Puma kill site selection is predicted to occur in habitats that facilitate successful hunting (Murphy and Ruth 2009). At the within home range and kill site scales, the prey abundance and prey catchability hypotheses (Hopcraft et al. 2005) predict that large felids select habitat where there is easy access to resources and where habitat structure allows for a successful hunt (Hayward and Kerley 2005). Therefore, animals select habitat that will improve their fitness (Orians and Wittenberger 1991), which for pumas at the within home range scale may be habitat that supports their preferred ungulate prey, for example grassy shrubland and riparian vegetation (Logan and Sweanor 2001, Knopff et al. 2014, Smereka et al. 2020). The environmental features that support puma habitat use at the kill site scale may be slightly rugged terrain to aid in both camouflage and fast acceleration while hunting (Laundré and Hernández 2003, Balme et al. 2007, Murphy and Ruth 2009, Knopff et al. 2014, Smereka et al. 2020). These two hypotheses are likely co-dependent, and prey catchability at the kill site scale will be a function of prey abundance at the within home range scale (Sargent et al. 2021).

The purpose of this study was to determine the best environmental predictors of puma habitat use at the within home range and kill site scales, and to assess potential differences between the sexes, on a private ranch in south-west New Mexico. Following the prey abundance and prey catchability hypotheses, it was expected that the best predictors of puma habitat use would differ between scales (Hopcraft et al. 2005), and between the sexes due to the different habits of each sex (Logan and Sweanor 2001, Murphy and Ruth 2009). The results from this study will contribute to a better understanding of puma habitat use in south-west New Mexico, and ideally, inform local management decisions on puma conservation (e.g., Dickson and Beier 2006).

METHODS

Study site

The data were collected on the Ladder Ranch (33°01’57.68”N, 107°30’39.11”W), which is a private property situated on the eastern border of the Gila National Forest and the Aldo Leopold Wilderness, at the base of the Black Range mountains in Sierra County, south-west New Mexico (Figure 1). The Ranch spans an area of 633 km^2 and is characterised by Chihuahua desert grassland at low elevation (1300 meters above sea level), pinyon juniper at mid-elevation, and mixed conifer at the crest of the Black Range (2400 meters above sea level) (Pitman 2010). Four perennial streams run through the property (Animas Creek, Seco Creek, and the North Palomas and South Palomas creeks) and are flanked by dense riparian vegetation. The climate is considered as semi-desert, and the Ranch receives approximately 500 mm of rain per year, with most occurring at high elevation during the monsoons of the summer season (Rossettie 2019). Temperatures are mild, with an average maximum of 17 °C in the winter months, and 31 °C in summer (Rossettie 2019). Besides puma, the American black bear (*Ursus americanus*) is the other apex predator on the Ranch, and mesocarnivores include the bobcat (*Lynx rufus*), coyote (*Canis latrans*), and gray fox (*Urocyon cinereoargenteus*). Common prey of puma include elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), collared peccary (*Tayassu tajacu*), and several skunk species (*Mephitis macroura, M. mephitis, Conepatus leuconotus,* and *Spilogale gracilis*) (Rossettie 2019, Bernard et al. in prep).

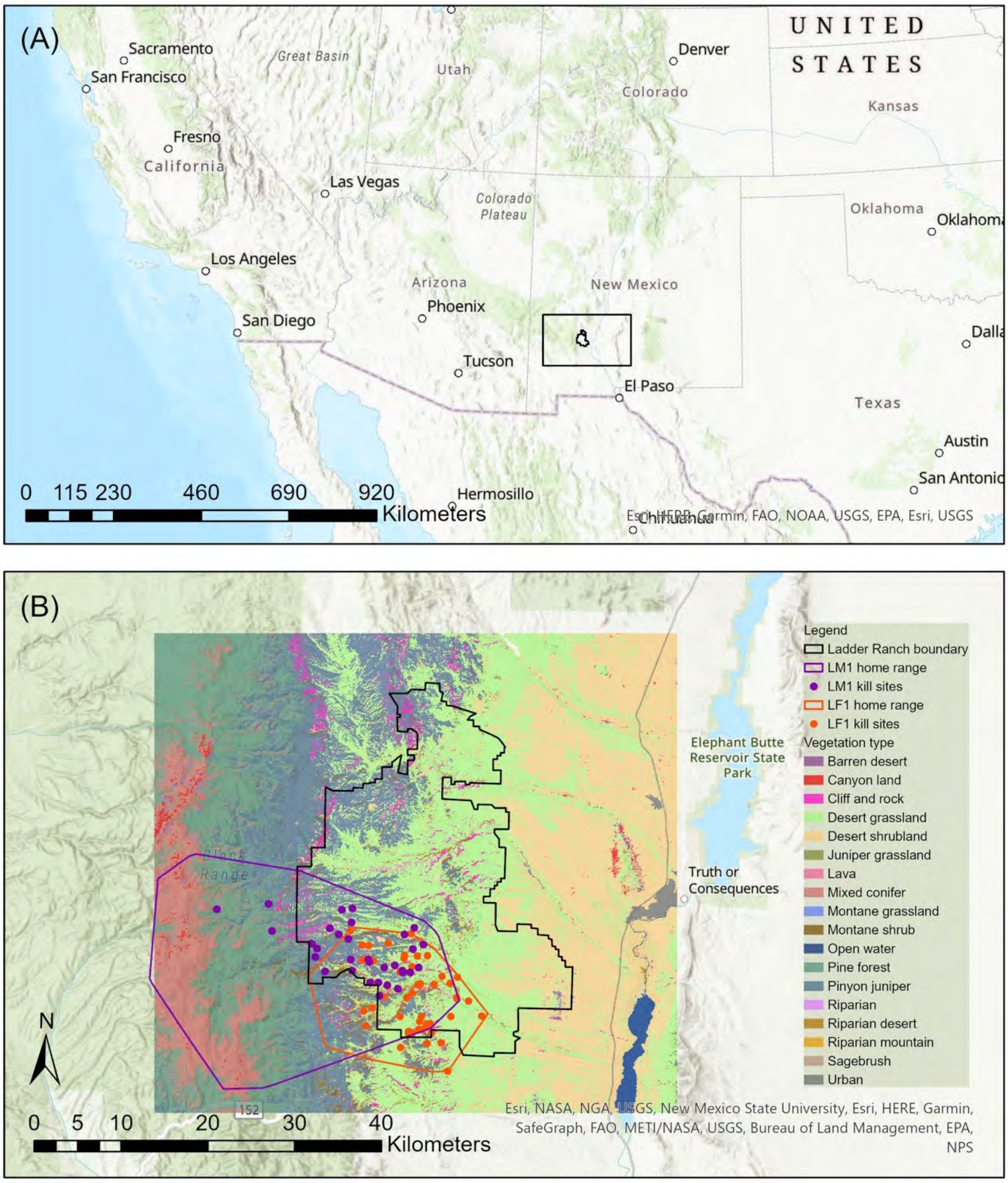

Figure 1. The Ladder Ranch study site in south-west New Mexico (A), with the vegetation depicted, and the home range (colored solid line) and kill sites (colored dots) of one male (LM1) and one female puma (LF1; B).

Data collection

Ethical clearance

This study was approved by the Institutional Animal Care and Use Committee (IACUC) at Furman University, the New Mexico Department of Game and Fish (permit number: 3456), and the Rhodes University Animal Research Ethics Committee (reference: 5009).

Collaring pumas to identify kill sites

Global Positioning System (GPS) collars were fitted to sixteen pumas (10 males and six females) between February 2008 and July 2020 (Appendix A). Pumas were captured in foothold cables (Logan et al. 1999) monitored by field cameras, and darted for immobilization with Ketamed (2 mg / kg ketamine + 0.075 mg / kg medetomidine; Kreeger et al. 2002) approximately two and a half hours after capture, as recorded by the camera. Once immobilized, the puma was carried to a flat surface, and the eyes were lubricated with gel and covered with a cloth for protection. The collar was fitted with a minimum two finger width space between the neck and collar, and several standard observations and body measurements were recorded (i.e., puma sex, reproductive status, presence of scars, length of body and canines (mm), and body mass (kg)). During collar fitting and observations, the respiration of the anaesthetised puma was monitored, eye lubricant was re-applied every 15 minutes, and body temperature was recorded every two minutes. After the collar was fitted, and observations and measurements were recorded, the immobilization was reversed with 0.3 mg / kg atipamezole (Kreeger et al. 2002). Collars fitted were an average mass of 900 g, and brands were Lotek, Northstar, Telonics, and Followit. The collars recorded location (i.e., one GPS fix) every two or three hours depending on the brand of collar and its battery life, between 07:00 and 19:00 when pumas are most active (Beier 1995, Logan and Sweanor 2001).

The GPS fixes per collared puma were assessed in RStudio (RStudio Team 2020), and clusters of fixes with at least two consecutive recordings occurring within

100 m of the first point in the cluster were investigated in the field as a potential kill site (Anderson and Lindzey 2003, Logan and Sweanor 2009, Stoner et al. 2021). At each confirmed kill site, species killed and habitat characteristics (e.g., vegetation, slope, and aspect) were noted.

Creating environmental raster files

Environmental features known to be important predictors of puma habitat use were chosen to characterise male and female puma occurrence at the within home range and kill site scales, and included vegetation, elevation (m), slope (%), solar gain (watts/hour/meter-squared), topographic ruggedness (Terrain Ruggedness Index; Appendix B), and distance to drainage (m; Dickson and Beier 2006, Morrison et al. 2015, Angelieri et al. 2016, Gigliotti et al. 2019, Smereka et al. 2020, Stoner et al. 2021). Data for all environmental variables were obtained from the USGS 10 m National Elevation Dataset for New Mexico (website https://rgis.unm.edu/), and were extracted from raster layers in ArcGIS 10.8.1 (ESRI 2011).

Vegetation type contained 15 categories (Appendix C), elevation was measured as meters above sea level at a scale of 10 m, and slope was calculated as a percentage at a scale of 10 m using the Spatial Analyst tool. Solar gain was measured using the Area Solar Radiation tool, which derived incoming solar radiation from a raster surface in watts per hour per meter-squared, and topographic ruggedness was measured in meters as the variance in elevation at scales of 50 m, 100 m, and 250 m. Distance to drainage was measured in meters at a scale of 100 m using the Spatial Analyst Hydrology tool.

The choice of scale was informed by previous research indicating that puma habitat use is best explained by environmental variables at fine spatial scales (Knopff et al. 2014, Smereka et al. 2020). Therefore, this study used the finest spatial scales available, except for ruggedness, where the appropriate scale was assessed statistically (Lindsay et al. 2019).

Data manipulation

Selecting GPS fixes

The GPS fixes of collared pumas and puma kill locations were uploaded into ArcGIS Pro (ESRI 2020). To investigate puma habitat use at the within home range scale, the Kernel Density tool was used to map the 95% home range of each puma. In order to minimize autocorrelation due to the large number of GPS fixes, only 50% of all collar points per puma were used (Klaassen and Broekhuis 2018). These fixes were randomly selected from the total number of GPS collar points within each puma’s home range using the random function (Eddelbuettel 2017) in R (RCore Team 2021). Due to the smaller sample size of the kill locations, all GPS fixes were used for the kill site analysis (Appendix D). Pumas occupied territories or home ranges that extended past the boundary of the Ladder Ranch (Figure 1), and these collar points were included in this study.

Creating random points and characterising the environment

The tool Create Random Points in ArcGIS Pro was used to generate 5000 available points on the Ladder Ranch. To examine puma habitat use at the within home range scale, the number of GPS fixes within each pumas home range was randomly applied to the 5000 available points on the Ranch so that there was a 1:1 ratio of used to available points per puma (Stabach et al. 2016, Klaassen and Broekhuis 2018, Stoner et al. 2021). To create the 1:1 ratio of puma habitat use at the kill site scale, the number of kill sites per puma was randomly applied to the GPS fixes within the home range of the puma. All available points were randomly selected with the random function in R.

Only fixes that intersected with all of the raster files were used. This resulted in a total of 8325 GPS fixes for 10 male pumas and 4864 GPS fixes for six female pumas at the within home range scale, with the same number of available points created per individual (Appendix D). For the kill site analysis, 244 GPS fixes for the kill sites of 10 male pumas and 147 GPS fixes for the kill sites of six females were used, with the corresponding number of random points created per puma (Appendix D).

The tool Extract Multi Values to Points was used in ArcGIS Pro to retrieve information from the environmental raster files for each used and available point per puma at both the within home range and kill site scales, and the data were saved in Microsoft Excel using the Conversion tool in ArcGIS Pro.

Statistical analyses

To examine the influence of puma sex and the environmental variables on puma occurrence at the within home range and kill site scales, the data were analysed in Bayesian hierarchical Bernoulli logistic regression models (e.g., Koster and McElreath 2017, dos Anjos et al. 2022, Lancaster et al. 2022, Bernard et al. in prep). All statistical analyses were conducted in RStudio (RStudio Team 2022). The Bayesian models were performed via the program *RStan v 2.21.2* (Stan Development Team 2021) in R version 4.0.3 using the package *brms v 2.17.0* (Buerkner 2017, 2018).

To enable successful running of the Bayesian models in *brms* all data corresponding to vegetation types that were not used by and available to both puma sexes were removed from the two analyses (analysis 1: within home range; analysis

2: kill site), and all numeric predictor variables (elevation, slope, solar gain, ruggedness, and drainage) were standardised using the function scale in the package *base* (RCore Team 2020). Additionally, sagebrush was excluded due to the extremely low number of data points (n = 9) in comparison to the remaining vegetation types (Appendix C). Seven levels were thus included for the vegetation predictor variable at the within home range scale (Appendix C), and six were retained for the kill site analysis.

To select the best predictor variables of puma habitat use at the within home range and kill site scales, a full model was created for each analysis and included all environmental variables and puma sex, as well as individual puma as a random effect. Due to the large quantity of data in these analyses (in particular the within home range analysis), the models would not run and thus a step-wise approach was performed and is described below.

Selecting the best ruggedness scale

To establish the best ruggedness scale, the used and available fixes in each analysis were entered as the response variable (Binomial response; two levels: used and available) per model. Puma sex (two levels: male and female) and one ruggedness variable (50 m, 100 m, 250 m scales) were entered as the predictor variables in each model. This resulted in three models per analysis (Appendix E). Additionally, individual puma (16 levels: 10 males and six females) was included as a random effect to account for potential preference individuals may have for different habitats.

Each model contained three chains of 500 burn-in samples and 1500 iterations, and mixing was successful to result in Rhat values of 1.0. The Widely Applicable

Information Criterion (WAIC; Watanabe 2010) was obtained for each model, and was compared between models by the predictive expected accuracy (elpd_diff), using the call loo_compare in the package *brms*. The model with the lowest WAIC (100 m scale; Appendix E) was chosen as the optimal model, and this variable was used as the ruggedness predictor in the subsequent statistical analysis.

Choosing the best environmental predictors

To determine the best environmental predictors of puma habitat use at the within home range and kill site scales, Bayesian models contained presence and absence data as the response variable, and puma sex and one environmental variable (vegetation, elevation, slope, solar gain, ruggedness, or drainage) as the predictor variables per model. This resulted in six models per analysis, each including individual as a random effect (Appendix F).

The warmup and iterations per model were increased to 1000 and 2000, respectively, and the chains remained at three. The WAICs of each model were obtained and compared using the predictive expected accuracy of each output. Vegetation was the best predictor of puma habitat use at the within home range scale, while ruggedness was the strongest predictor of kill sites (Appendix G), and these two variables were used in the final analysis.

Characterising puma habitat use

To examine the influence of puma sex and vegetation or ruggedness on puma habitat use at the within home range and kill site scales, respectively, five candidate models were created: (1) a null model containing only the intercept, (2) a model containing both predictor variables with an interaction term, (3) a model containing both predictor variables with no interaction, (4) a model containing only puma sex, and (5) a model containing only the best environmental predictor variable (Table 1, 3). The interaction model (model 2) was included to test if the effect of puma sex on habitat use was dependent on the environmental variable, and vice versa. Presence and absence data were inserted as the response variable in each model, and individual puma was included as a group-level factor (random effect).

In these analyses, the models contained four chains, with 1500 burn-in samples and 5000 iterations per model. Mixing was successful for all models and converged to a minimum Rhat value of 1.0. Model validation was performed using approximate leave-one-out cross-validation, and model outputs were compared using the predictive expected accuracy of each WAIC. To further define each model, model weights were obtained using the function loo_model_weights in the package *brms*. Probabilities with 95% confidence intervals for puma habitat use at the within home range and kill site scales were predicted from the optimal model outputs using the call conditional_effects in the package *brms*, and plotted for each analysis using ggplot2 (Wickham 2016).

RESULTS

Within home range scale

The raw data suggested that pumas in south-west New Mexico used desert grassland, pinyon juniper, riparian desert, montane shrub, and cliff and rock in a greater proportion to what was available on the Ranch (Appendix C). The optimal model contained both predictor variables (puma sex and vegetation) with an interaction term (M2; Table 1), suggesting that the effect of sex on habitat use at the within home range scale was dependent on vegetation, and vice versa.

Table 1. Bayesian hierarchical Bernoulli models evaluated probabilities of habitat use at the within home range scale as a function of puma sex and vegetation in south-west New Mexico. The Widely Applicable Information Criterion (WAIC), standard error (seWAIC), difference in the expected predictive accuracy (elpd_diff; ΔWAIC), and model weight (loo_model_weight; WAIC$_{(i)}$) are presented for each candidate model.

Models		**WAIC**	**seWAIC**	**ΔWAIC**	**WAIC$_{(i)}$**
M2	**~ 1 + Sex * Vegetation + (1 | Individual)**	**29404.7**	**115.0**	**0.0**	**0.972**
M3	~ 1 + Sex + Vegetation + (1 | Individual)	29635.7	113.6	-115.5	0.022
M5	~ 1 + Vegetation + (1 | Individual)	29636.2	113.8	-115.7	0.004
M1	~1 + (1 | Individual)	33273.1	25.4	-1934.2	0.001
M4	~ 1 + Sex + (1 | Individual)	33274.1	25.4	-1934.7	0.000

The raw data and model results were well matched, and the optimal model revealed a strong probability of pumas selecting riparian desert, montane shrub, desert grassland, cliff and rock, and pinyon juniper at the within home range scale compared to what was available within the study area (Figure 2). Additionally, the optimal model depicted a higher probability of male pumas selecting pine forest compared to females, and of females selecting desert grassland and desert shrubland (Figure 2). Individual puma, modelled as a random effect, influenced the vegetation types used at the within home range scale (Table 2).

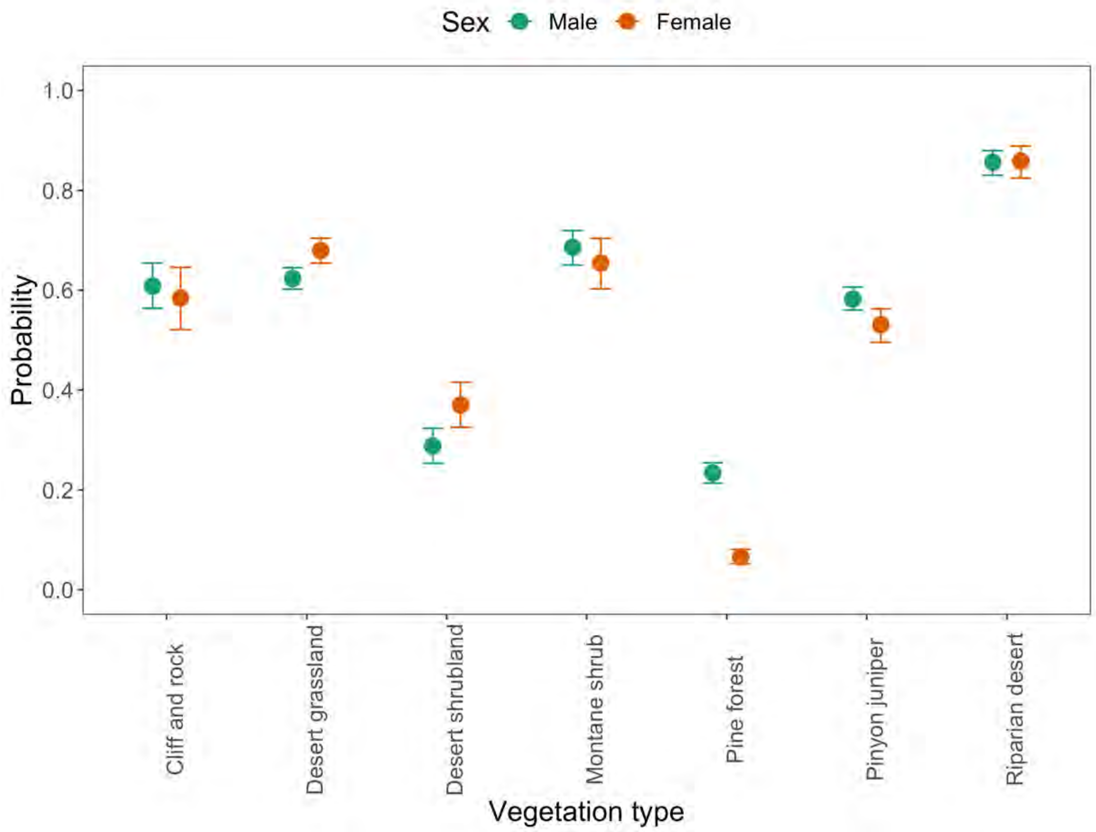

Figure 2. Probability of male and female pumas selecting vegetation types at the within home range scale compared to what was available in south-west New Mexico. Data are probabilities with 95% confidence intervals.

Table 2. Estimated coefficients for the optimal Bayesian hierarchical Bernoulli model evaluating the probability of puma habitat use at the within home range scale as a function of puma sex and different vegetation types in south-west New Mexico. Estimate (Est.), estimated error (EE), lower and upper 95% confidence intervals, potential scale reduction factor (Rhat), and bulk and tail effect sample sizes (ESS) are given for each coefficient.

	Est.	EE	L 95% CI	U 95% CI	Rhat	Bulk ESS	Tail ESS
Group-Level Effects							
~ Individual (Levels: 16)							
Sd(Intercept)	0.11	0.03	0.06	0.18	1.00	2383	2604
Population-Level Effects							
Intercept	0.39	0.08	0.23	0.55	1.00	2688	2615
Sex	-0.07	0.12	-0.30	0.16	1.00	2324	2404
Desert grassland	0.24	0.08	0.08	0.39	1.00	2683	2499
Desert shrubland	-1.11	0.10	-1.30	-0.93	1.00	2754	2674
Montane shrub	0.32	0.10	0.12	0.52	1.00	2694	2579
Pine forest	-2.32	0.10	-2.51	-2.13	1.00	2730	2650
Pinyon juniper	-0.16	0.08	-0.33	-0.01	1.00	2706	2596
Riparian desert	1.41	0.11	1.19	1.61	1.00	2699	2655
Sex : Desert grassland	0.25	0.11	0.02	0.46	1.00	2441	2672
Sex : Desert shrubland	0.34	0.14	0.07	0.60	1.00	2480	2392
Sex : Montane shrub	-0.03	0.14	-0.31	0.24	1.00	2371	2438
Sex : Pine forest	-0.97	0.14	-1.24	-0.70	1.00	2483	2402
Sex : Pinyon juniper	-0.08	0.12	-0.31	0.14	1.00	2306	2537
Sex : Riparian desert	0.09	0.15	-0.22	0.39	1.00	2397	2621

Kill site scale

The summary statistics of the primary data revealed that pumas killed prey in less rugged terrain (TRI; Mean ± Standard Deviation: 153.64 ± 149.51) compared to the habitat used at the within home range scale (202.54 ± 217.67; Appendix G). The most parsimonious model contained only ruggedness (M5; Table 3), suggesting that the effect of ruggedness on puma kill sites was consistent between sexes.

Table 3. Bayesian hierarchical Bernoulli models evaluated probabilities of puma kill sites as a function of sex and ruggedness in south-west New Mexico. The Widely Applicable Information Criterion (WAIC), standard error (seWAIC), difference in the expected predictive accuracy (elpd_diff; ΔWAIC), and model weight (loo_model_weight; $\text{WAIC}_{(i)}$) are presented for each candidate model.

Models		**WAIC**	**seWAIC**	**ΔWAIC**	**$\text{WAIC}_{(i)}$**
M5	**~ 1 + Ruggedness + (1 | Individual)**	**1029.9**	**7.5**	**0.0**	**0.922**
M3	~ 1 + Sex + Ruggedness + (1 | Individual)	1031.9	7.7	-1.0	0.000
M2	~ 1 + Sex * Ruggedness + (1 | Individual)	1033.6	7.7	-1.9	0.000
M1	~ 1 + (1 | Individual)	1041.7	1.7	-5.9	0.078
M4	~ 1 + Sex + (1 | Individual)	1043.7	1.9	-6.9	0.000

The observations from the primary data were supported by the most parsimonious model, which depicted a strong probability of pumas killing prey in level to intermediately rugged terrain relative to the habitat used at the within home range scale (Figure 3; Appendix B). Additionally, individual puma influenced the selection of kill sites in rugged habitat (Table 4).

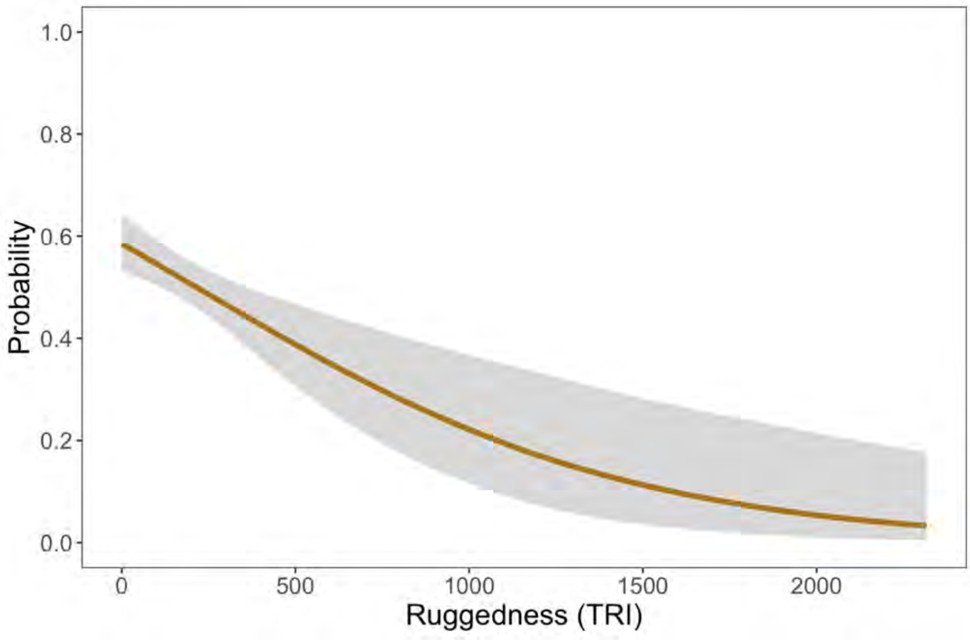

Figure 3. Probability of pumas killing prey in rugged terrain relative to the habitat used within their home ranges in south-west New Mexico. Data are probabilities (depicted by the solid brown line), with 95% confidence intervals (depicted by the grey wrap).

Table 4. Estimated coefficients for the optimal Bayesian hierarchical Bernoulli model evaluating the probability of puma kill sites in rugged terrain in south-west New Mexico. Estimate (Est.), estimated error (EE), lower and upper 95% confidence intervals, potential scale reduction factor (Rhat), and bulk and tail effect sample sizes (ESS) are given for each coefficient.

	Est.	EE	L 95% CI	U 95% CI	Rhat	Bulk ESS	Tail ESS
Group-Level Effects							
~ Individual (Levels: 16)							
Sd(Intercept)	0.11	0.08	0.004	0.31	1.00	2588	2617
Population-Level Effects							
Intercept	0.06	0.08	-0.1	0.22	1.00	2794	2727
Ruggedness	-0.30	0.08	-0.46	-0.14	1.00	2598	2459

DISCUSSION

The results from this study met the expectation that the best environmental predictors of puma habitat use would differ between the within home range and kill site scales (e.g., Hopcraft et al. 2005), and between the sexes (e.g., Logan and Sweanor 2001, Murphy and Ruth 2009). Vegetation was the strongest predictor of puma occurrence at the within home range scale, while topographic ruggedness best predicted kill sites.

At the within home range scale, the raw data revealed that pumas used desert grassland, pinyon juniper, riparian desert, montane shrub, and cliff and rock more than what was available on the Ranch. The optimal model showed similar findings with a high probability of pumas selecting the above-mentioned vegetation types, particularly riparian desert, and this result is mirrored by previous studies revealing puma preference for riparian vegetation (Laundré and Hernández 2003, Holmes and Laundré 2006, Knopff et al. 2014, Morrison et al. 2015, Guerisoli et al. 2019). Desert grassland was used the most by both puma sexes on the Ladder Ranch and this result is likely due not only to the abundance of this vegetation type within the study area (Figure 1 B), but also this habitat being preferred by ungulate prey such as mule deer, and providing cover for successful hunting. Similarly, cheetahs (*Acinonyx jubatus*) in the Maasai Mara, Kenya (Klaassen and Broekhuis 2018) selected habitat that provided thicket for cover and grassland supporting ungulate prey species (Balme et al. 2007), while African lions (*Panthera leo*) in Hwange National Park, Zimbabwe, preferred bushed grassland that supported an abundance of prey species (Davidson et al. 2012). These results can be explained in relation to the prey abundance hypothesis predicting large felid occurrence at the within home range scale in response to high densities of ungulate prey inhabiting grassy shrubland and riparian vegetation (Hopcraft et al. 2005).

The primary data for the within home range analysis additionally revealed differences between the vegetation types used by each sex, and this result is supported by previous studies (Morrison et al. 2015). The raw data suggested that male pumas used pinyon juniper, pine forest, montane shrub, and cliff and rock more than females, while females frequented desert grassland, riparian desert, and desert shrubland more than males. The optimal model in the within home range analysis contained interactive effects of sex and vegetation, and revealed a higher probability of male pumas selecting pine forest, and of females selecting desert grassland and desert shrubland. These results are likely affected by the placement and size of puma home ranges on the Ladder Ranch, with males having larger territories expanding into the western regions of the property at higher elevations containing more pine forest, and females occurring in the desert grassland foothills of the central and eastern sections of the Ranch (Figure 1 B). Additionally, this result could reflect the collaring effort during data collection, as pumas were only captured in the mid to lower elevations of the Ranch. It is therefore, unlikely that the smaller home ranges of female pumas would extend into the higher elevations and forested vegetation types, relative to the larger territories of male pumas that would encompass both the trapping sites and the higher elevation, forested habitat.

Contrastingly, puma sex was not retained in the most parsimonious model predicting the probability of kill sites in rugged habitat in south-west New Mexico. The summary statistics of the primary data revealed that pumas killed prey in less rugged terrain than the habitat used at the within home range scale, and this trend was evident in the optimal model, which depicted a strong probability of pumas killing prey in level to intermediately rugged terrain compared to their occurrence within their home ranges. Moderately to extremely rugged habitat may limit the pumas ability to observe prey and accelerate to catch it, and may thus be avoided due to providing too many obstacles during the hunt (Logan and Sweanor 2001).

Conversely, level to intermediately rugged terrain may be associated with grassy shrubland and riparian vegetation, both supporting a high abundance of prey and enabling a successful stalk and hunt (Beier et al. 1995, Logan and Sweanor 2001, Dickson and Beier 2006, Morrison et al. 2015). The results from the kill site analysis may thus be understood in relation to the prey catchability hypothesis (Hopcraft et al. 2005), where pumas select slightly rugged habitat in order to enhance hunting ability.

Research that examines the environmental features of puma habitat use can improve conservation planning and success (Dickson and Beier 2006, Stoner et al. 2021). The results from this study demonstrate the benefits of investigating male and female puma habitat use at the within home range scale to appropriately conserve the environmental features important for each sex, whereas, important environmental features at the kill site scale seem to be consistent between sex. Ultimately, these results demonstrate the significance of large tracts of intact wildland containing grassy shrubland and riparian vegetation, and slightly rugged terrain to support puma conservation in this region. An interesting addition to this study would be the inclusion of prey species killed and prey abundance to more closely examine the possible drivers of puma habitat use in south-west New Mexico.

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APPENDIX

Appendix A. Dates (day.month.year) of Global Positioning System (GPS) collar tracking per puma in south-west New Mexico.

Puma ID	Puma sex	Start GPS collar	End GPS collar
LM1	Male	22.03.2008	27.04.2009
LM1	Male	04.07.2012	13.02.2013
LM2	Male	15.10.2009	10.11.2010
LM3	Male	04.11.2009	07.01.2010
LM3	Male	21.06.2010	02.02.2011
LM4	Male	14.03.2012	17.02.2013
LM5	Male	14.12.2014	30.09.2015
LM6	Male	31.12.2014	17.03.2016
LM6	Male	26.06.2016	06.06.2017
LM8	Male	18.03.2016	28.12.2016
LM9	Male	28.04.2016	26.11.2016
LM10	Male	23.02.2017	27.06.2018
LM11	Male	01.05.2017	27.06.2018
LF1	Female	19.02.2008	25.12.2009
LF3	Female	25.10.2009	11.03.2011
LF4	Female	10.11.2009	07.10.2010
LF6	Female	03.06.2010	22.11.2010
LF8	Female	21.03.2011	19.05.2012
LF9	Female	12.12.2019	01.04.2021

Appendix B. Terrain Ruggedness Index (TRI) as described by ESRI.

TRI (m)	Description of surface
0-80	Level terrain
81-116	Nearly level
117-161	Slightly rugged
162-239	Intermediately rugged
240-497	Moderately rugged
498-958	Highly rugged
959-4367	Extremely rugged

Appendix C. Vegetation types used by and available to male and female pumas at the within home range scale in south-west New Mexico. Data are the number of GPS fixes per habitat type with percent occurrence per category (male: used, available; female: used, available) in brackets (%). Asterisks (*) depict the data used in the statistical analysis.

	Males		Females	
Habitat type	**Used**	**Available**	**Used**	**Available**
Desert grassland *	3430 (41%)	2115 (25%)	2558 (53%)	1223 (25%)
Pinyon juniper *	2261 (27%)	1603 (19%)	1125 (23%)	942 (19%)
Riparian desert *	699 (8%)	121 (1.5%)	446 (9%)	74 (2%)
Pine forest *	660 (8%)	2122 (25.5%)	87 (2%)	1212 (25%)
Montane shrub *	581 (7%)	267 (3%)	284 (6%)	145 (3%)
Cliff and rock *	314 (4%)	205 (2.5%)	154 (3%)	108 (2%)
Desert shrubland *	234 (3%)	583 (7%)	209 (4%)	353 (7%)
Mixed conifer	140 (2%)	1230 (15%)	0	751 (15%)
Canyon land	3	42 (1%)	0	32 (1%)
Sagebrush	2	4	1	2
Juniper grassland	1	0	0	0
Montane grassland	0	15	0	11
Barren desert	0	13	0	8
Riparian	0	3	0	1
Riparian mountain	0	2	0	2
Total	8325	8325	4864	4864

Appendix D. Number of Global Positioning System (GPS) fixes per puma at the within home range (HR) and kill site (Kill) scales in south-west New Mexico.

Individual	Sex	HR	Kill
LM1	Male	1220	32
LM2	Male	1018	23
LM3	Male	799	49
LM4	Male	747	27
LM5	Male	300	5
LM6	Male	944	47
LM8	Male	826	5
LM9	Male	576	10
LM10	Male	1050	15
LM11	Male	845	31
Total male		**8325**	**244**
LF1	Female	1441	53
LF3	Female	1412	22
LF4	Female	203	21
LF6	Female	549	25
LF8	Female	316	24
LF9	Female	943	2
Total female		**4864**	**147**
Overall total		**13189**	**391**

Appendix E. Bayesian hierarchical Bernoulli models evaluated puma habitat use as a function of sex and different ruggedness scales (50 m, 100 m, 250m scales) in south-west New Mexico. The Widely Applicable Information Criterion (WAIC), standard error (seWAIC), and difference in the expected predictive accuracy (elpd_diff; ΔWAIC) are presented for each candidate model.

Models **Within home range**		**WAIC**	**seWAIC**	**ΔWAIC**
M2	**~ 1 + Sex + Ruggedness100 + (1 | Individual)**	**32935.3**	**44.3**	**0.0**
M1	~ 1 + Sex + Ruggedness50 + (1 | Individual)	32939.0	44.6	-1.8
M3	~ 1 + Sex + Ruggedness 250 + (1 | Individual)	33010.5	41.2	-37.6
Kill site				
M2	**~ 1 + Sex + Ruggedness100 + (1 | Individual)**	**1031.4**	**7.6**	**0.0**
M1	~ 1 + Sex + Ruggedness50 + (1 | Individual)	1032.9	7.1	-0.8
M3	~ 1 + Sex + Ruggedness250 + (1 | Individual)	1037.2	6.2	-2.9

Appendix F. Bayesian hierarchical Bernoulli models evaluated puma habitat use as a function of sex and different environmental variables (vegetation, elevation, slope, solar gain, topographic ruggedness, and distance to drainage) in south-west New Mexico. The Widely Applicable Information Criterion (WAIC), standard error (seWAIC), and difference in the expected predictive accuracy (elpd_diff; ΔWAIC) are presented for each model.

Models				
Within home range		**WAIC**	**seWAIC**	**ΔWAIC**
M1	**~ 1 + Sex + Vegetation + (1 | Individual)**	**29635.7**	**113.5**	**0.0**
M2	~ 1 + Sex + Elevation + (1 | Individual)	31560.8	86.7	-962.5
M5	~ 1 + Sex + Ruggedness + (1 | Individual)	32935.3	44.3	-1649.8
M6	~ 1 + Sex + Drainage + (1 | Individual)	33167.4	32.9	-1765.8
M4	~ 1 + Sex + Solar + (1 | Individual)	33219.5	29.8	-1791.9
M3	~ 1 + Sex + Slope + (1 | Individual)	33247.9	27.7	-1806.1
Kill site				
M5	**~ 1 + Sex + Ruggedness + (1 | Individual)**	**1031.6**	**7.5**	**0.0**
M6	~ 1 + Sex + Drainage + (1 | Individual)	1035.7	6.7	-2.0
M3	~ 1 + Sex + Slope + (1 | Individual)	1040.1	4.9	-4.2
M4	~ 1 + Sex + Solar + (1 | Individual)	1040.4	4.9	-4.4
M2	~ 1 + Sex + Elevation + (1 | Individual)	1045.5	2.0	-6.9
M1	~ 1 + Sex + Vegetation + (1 | Individual)	1046.9	6.1	-7.7

Appendix G. Summary statistics (Mean ± Standard Deviation) of the habitat used by and available to pumas at the kill site scale in south-west New Mexico. The variable used in the final analysis is depicted in bold text.

Habitat variable	**Used**	**Available**
Elevation	1740.52 ± 150.06	1741.54 ± 151.31
Slope	13.84 ± 9.00	15.39 ± 9.91
Solar	1651665 ± 138873.9	1626999 ± 158508.6
Ruggedness	**153.64 ± 149.51**	**202.54 ± 217.67**
Drainage	40.66 ± 45.26	51.81 ± 51.31

CHAPTER FOUR
CONCLUSION

The puma (*Puma concolor)* occupies the broadest latitudinal range of all native extant mammals in the Americas (Walker and Paradiso 1975, Culver 2009), inhabiting diverse landscapes (Benson et al. 2020) and preying upon a wide variety of species (Karandikar et al. 2022, LaBarge et al. 2022). Site-specific research on puma ecology is thus important for conservation initiatives, both within and between states and countries. This study assessed puma diet and habitat use on a private ranch in south-west New Mexico and contributes to local research on puma ecology and may inform management plans for this apex predator in the region.

The results from the two data chapters revealed that pumas in south-west New Mexico specialised on mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) for prey, and selected vegetation types such as riparian desert, montane shrub, and desert grassland at the within home range scale compared to what was available on the Ranch. At the kill site scale, pumas selected level to intermediately rugged terrain relative to the habitat used within their home ranges. Apart from mule deer and elk, pumas killed a variety of prey of different sizes, including birds such as the wild turkey (*Meleagris gallopavo*), skunks (e.g., *Mephitis mephitis*), coyote (*Canis latrans*), and collared peccary (*Pecari tajacu*), and these results are supported by previous studies (Karandikar et al. 2022, LaBarge et al. 2022). Sex influenced puma diet, and the probability of a male making an extra-large kill such as elk was substantially greater than for females, while the probability of a medium-sized kill such as mule deer was higher for females. Sex also influenced puma habitat use at the within home range scale, and there was a greater probability of males selecting pine forest, and of females selecting desert grassland and desert shrubland.

However, this result was likely an artefact of an interaction between puma home range size and the location of puma capture on the Ranch. Nevertheless, the results from this study demonstrate that large tracts of wildland containing grassy shrubland and riparian vegetation, suitable for both pumas and their prey, and habitat of slightly rugged terrain should be conserved within puma home ranges to support their existence in this region. Additionally, careful attention should be attributed to the conservation of mule deer and elk which form the major components of puma diet.

Although the results from the current study focus only on the best predictors of puma habitat use in south-west New Mexico, as detected by the Bayesian models, a landscape level approach should be adopted when assessing puma habitat and determining environmental suitability for conservation initiatives. Vegetation, elevation, slope, solar gain, topographic ruggedness, and distance to drainage will all be correlated in one way or another and may all be important within puma habitat. For example, proximity to drainage is likely to be associated with lower elevation, gentler slope, reduced ruggedness, and a riparian vegetation type. The recommended landscape level approach holds true with regards to the wide-ranging habits of the puma and the importance of inter-state agreements on reliable conservation measures to protect pumas and other species over long distances across boundaries and borders.

A useful addition to this study would be the assessment of puma diet in relation to the presence of other apex predators in the study area, for example, the American black bear (*Ursus americanus*) and gray wolf (*Canis lupus*), in order to better understand whether competition within the carnivore guild affects puma habitat use and prey selection (Gonzalez-Barajo et al. 2017, Elbroch and Kusler 2018, Elbroch et al. 2020). The results from this assessment would better direct puma conservation in south-west New Mexico, as well as the preservation of other important apex predators in the area.

The current study did not include human presence as a potential factor driving puma habitat use in the region, as the study site is remote and largely left as wildland. The Ladder Ranch is thus a good model study site for puma ecology in a natural environment, and research in this area could be compared to other sites of similar environmental characteristics that are impacted by human development, in order to test the effect of human presence in different forms on the spatial ecology of this species. Results from this study would help to promote wildland ecosystems and direct urban and industrial development in ways that can promote both human development and species conservation.

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