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Cougar Predation Behavior in North-Central Utah

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COUGAR PREDATION BEHAVIOR IN NORTH-CENTRAL UTAH

by

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ABSTRACT

Cougar Predation Behavior in North-Central Utah

by

Dustin L. Mitchell, Master of Science

Utah State University, 2013

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Cougar (*Puma concolor*) predation has been identified as being one of several factors contributing to the decline of mule deer (*Odocoileus hemionus*) throughout the Western United States. In order to better understand how these elusive felines utilize their surroundings and prey, I examined and analyzed cougar predation behavior in North-Central Utah, using global positioning systems (GPS) data from 2002-2010. Twenty-three cougars were fitted with GPS collars and monitored for prey caching behavior. In total 775 potential cache sites were visited and 546 prey remains found. Mule deer comprised the majority of prey at cougar cache sites, but 11 other species were also found. Collectively, adult female mule deer were killed more than any other demographic class. Proportionally there was no difference in the sex or age class of deer killed by cougars in three different population segments, but seasonal differences were found in the number of kills made between cougar groups. Female cougars with kittens had a higher predation rate than males or solitary females, and seasonally more kills were made in the winter vs. summer. Cougars spent an average of 3.3 days on deer kills, and

6.2 days on elk kills. Habitat analyses suggested that cougars preferentially used Gambel oak (*Quercus gambelii*) over other land cover types when caching prey, as well as selected unburned over burned areas for caching and foraging on prey. These results suggest that cougars utilize dense stands of vegetation cover when stalking and concealing their prey. Wildlife managers may want to consider the use of prescribed burns in areas of high cougar predation on mule deer. This habitat manipulation tool could simultaneously help mule deer populations by reducing the percent of stalking cover afforded to cougars when attempting to kill prey, along with increasing nutrient levels of newly burned foliage and allow for an increased diversity in forb and shrub species available to mule deer.

(55 pages)

PUBLIC ABSTRACT

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Today's ability to apply global positioning systems (GPS) collars to wild animals and track their movements, without inadvertently disrupting their daily routine, is a major benefit to wildlife research. Cougars are carnivorous predators that have been identified as being one of several possible causes for recent mule deer population declines throughout the Western United States. Past cougar predation studies have relied on snow tracking, radio-collar tracking, and modeling techniques to estimate cougar prey use and predation rates. These methods rely heavily on weather conditions, logistical availabilities, and broad assumptions, which have led to a wide range of predation rate estimates.

I studied cougar predation behavior in North-Central Utah, using GPS locational data collected from 2002-2010. Mule deer made up >80% of cougar kills, but a variety of species were found at kill sites. Female cougars with kittens made kills more frequently than did solitary females or males. There was no difference in the demographic structure of mule deer killed by cougars. Cougars preferentially used areas of thick, unburned vegetation to make kills and cache their prey.

This research provides wildlife managers with information concerning the interaction between cougars and their prey, while also providing supportive evidence that the use of prescribed burns, as a habitat manipulation tool, could potentially mitigate

cougar predation on mule deer in areas of high predation and simultaneously benefit both cougars and mule deer.

DEDICATION

This work is dedicated to the memory of my Great-Grandmother Mildred Giles, who always encouraged me to learn as much as possible. As she always said… "They can't take away from you what you know."

ACKNOWLEDGMENTS

First and foremost I would like to thank my wife, Danielle, for supporting me in my pursuit of obtaining a degree in wildlife biology. Her unselfish willingness to move away and put life on hold is something not a lot of women would do. I could not have done this without her. I would also like to thank my son McKay, who kept me sane through these times by taking me hunting, fishing, and hiking and keeping my engineering skills up-to-date by designing countless skyscrapers (Lego's). You two are truly magnanimous.

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I would like to recognize the Utah Division of Wildlife Resources for their financial and logistical contributions to the project, particularly Kevin Bunnell, Justin

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It has been a humbling experience to spend time with houndsman and friend McLain Mecham. His first-hand knowledge of cougars and nature far exceeds that of any scientific publication I've encountered. I have learned more by "trailing" him then I ever thought possible. I also give special thanks to all those who have contributed in fieldwork throughout the years, particularly G. Bailey, B. Bateman, B. Blackett, C. Hendrix, G. and C. Jacobson, C. Juran, T. Kogianes, D. Ranglack, L. Redd, J. Robins, K. Shaney, and B. Watt.

Finally, I thank my extended family for all the support, guidance, and experiences throughout my life. There are far too many of you to thank individually, but each of you has contributed something special in my life one way or another. As for my parents, I owe you guys everything. Without your love, guidance, support, and examples, there is no way I would be where I am today. Thank you!

Dustin L. Mitchell

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INTRODUCTION

Predator-prey relationships are of primary interest to agencies charged with management and conservation of big game populations (Ballard et al. 2001, MDWR 2004). Cougars (*Puma concolor*) represent an obligate carnivore species, preying primarily on large ungulates such as mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*), but are also known to consume a variety of alternative prey species (Murphy et al. 2011).

Connelly (1949) was among the first to study cougar predation, wherein snow-tracking methods were used to determine that cougars in Utah were killing primarily mule deer, at a rate of one deer every 9.6 days. Since then, investigators throughout North America have tried to quantify more precisely cougar predation through the use of Very High Frequency (VHF) telemetry as well as energetics models (Hornocker 1970, Ackerman et al. 1986, Murphy 1998, Laundré 2005, Cooley et al. 2008). Estimates produced by these methods have been debatable, given their limited sample sizes, short monitoring periods, and large locational fix intervals. These factors have contributed a broad range of predation rate estimates ranging from an ungulate kill every 4.5 – 25.9 days (Hornocker 1970, Ackerman et al. 1986), along with a vague understanding of total prey composition.

More recently, investigators have used Global Positioning Systems (GPS) collars for studying cougar predation behaviors (Anderson and Lindzey 2003, Mattson et al. 2007, Knopff et al. 2010, Ruth et al. 2010, White et al. 2011). This method provides researchers with a noninvasive approach for monitoring individual cougars annually at predetermined intervals. Potential predation events can then be determined by localization of cougar movement patterns, and field visitations can be directed for prey identification (Anderson and Lindzey 2003). In a comparative study between GPS and VHF methods, Ruth et al. (2010) found that 11% of cougar predation events were missed by VHF methods alone. This was largely due to a lack of nocturnal locations obtained. GPS technology allows for continual day and night monitoring (Knopff et al. 2009), ensuring improved identification of predation events and also increased accuracy of locational fixes (± 14.6 m) (Rieth 2009). This technology has also bolstered support of hypotheses regarding cougar predation with respect to prey vulnerability, seasonal changes in prey demographics, kill success based on predator experience, and differences in prey size according to cougar sex class (Knopff et al. 2010, White et al. 2011).

One aspect of the predation process that has received limited attention is cougar response to fire. This void is largely due to the fact that data sets including both fire histories and predation events are lacking (Ream 1981). Dees et al. (2001) investigated the Florida panther's (*Puma concolor coryi*) response to prescribed burns and found selective use of newly burned areas by the animals. However, the author's focus was on total use of burned and unburned areas and not their relation to predation events. It has been suggested that by utilizing prescribed burns as a habitat manipulation technique, declining cougar prey populations (e.g. mule deer) might benefit (Atwood et al. 2007, Rieth 2009). This treatment could reduce stalking cover for cougars and allow increased vigilance by the ungulates, with the added benefit of increased nutrient levels of browse species (Pendleton et al. 1992).

The primary objectives of this study were to determine: (1) cougar prey composition; (2) primary prey demographics for male cougars and females with and without kittens; (3) predation rates for males and females with and without kittens; and (4) whether cougars disproportionately use burned or unburned habitats when foraging for prey.

STUDY AREAS

The study was conducted on three mountain ranges within the Great Basin Eco-region in North-Central Utah (Fig. 1). The primary study site was the Oquirrh Mountains, with the Stansbury and the Sheeprock Mountains serving as ancillary sites. Salient features of the Oquirrh Mountains were taken from the USU/UDWR cougar study final report (Wolfe et al. 2004).

Oquirrh Mountains

The Oquirrh Mountain study site is a complex consisting of the Oquirrh Mountain range which has a north-south orientation and the Traverse range, which has an east-west orientation. The range is located south of the Great Salt Lake, and divides the Salt Lake Valley to the east from the Tooele Valley to the west. The center of the range is located near the intersection of Tooele, Salt Lake, and Utah counties (~ 40.5 ^{o} N, 112.2 ^{o} W). The range covers approximately 950 km^2, and is positioned on the eastern edge of the Basin and Range Ecoregion (Chronic 1990). Topography of this site consists of flatlands to rolling foothills, shallow draws and canyons, rocky cliffs, steep drainages, and rugged mountain tops. Elevation ranges from 1280 m to 3200 m. Average annual precipitation at the Rocky Basin-Settlement Canyon SNOTEL station (elev. = 2,713 m) is 103 cm (NRCS 2011). The majority of precipitation falls in the form of snow during the winter while 25% comes from summer thunderstorms. Temperatures range from a monthly average of -2° C in January to 22° C in July (Ashcroft et al. 1992). Vegetation at low to mid elevations is typified by sagebrush (*Artemesia spp*), Gambel oak (*Quercus gambelii*), big-toothed maple (*Acer grandidentatum*), and Utah juniper (*Juniperus osteosperma*).

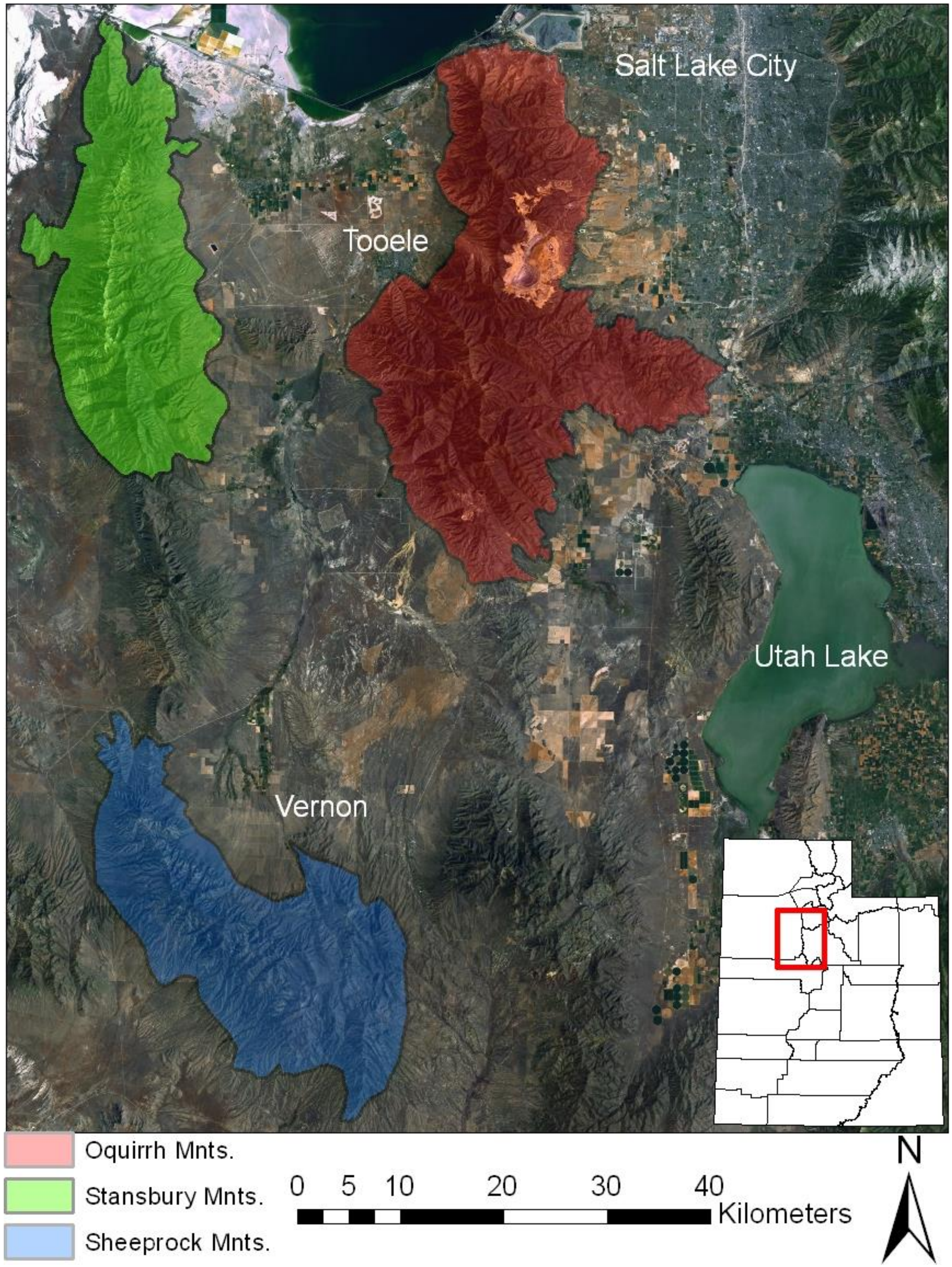

Figure 1. Locations of 3 mountain ranges used to study cougar predation in North-Central Utah 2002-2010.

Higher elevations are dominated by aspen (*Populus tremuloides*), mountain mahogany (*Cercocarpus spp.*), Douglas fir (*Pseudotsuga menziesii*), and limber pine (*Pinus flexilis*). Cougars are the largest carnivore species found on the Oquirrhs, although coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) are also present. The ungulate complement on the Oquirrhs consists of mule deer and elk. Pronghorn antelope (*Antilicapra americana*) are also present, though in relatively small numbers and at lower elevations. Livestock species such as cattle (*Bos taurus*), sheep (*Ovis aries*), goats (*Capra aegagrus hircus*) and horses (*Equus caballus*) seasonally inhabit the range.

Approximately 60% of the Oquirrh range is private land, of which the majority is owned and managed by the Kennecott Utah Copper Corporation, as well as the Utah Army National Guard (Camp W. G. Williams). The remaining area of the range is managed by The Bureau of Land Management. Big game hunting is allowed on the range, with the exception of privately owned lands. This range is part of the Oquirrh-Stansbury Cougar Management Unit and in accordance with the Utah Division of Wildlife Resources regulations, taking of cougars with radio-collars is prohibited (UDWR 2001).

Stansbury Mountains

The Stansbury Mountains (~ 40.5^{o} N, 112.6^{o} W) are located approximately 20 km west of the Oquirrh Mountains and divide the Tooele and Rush valleys on the east, from Skull Valley on the west. This range encompasses approximately 650 km^2 and ranges in elevation from 1,280 m to 3,362 m (Olson et al. 2008). Average annual precipitation at the Mining Fork SNOTEL station (elev. = 2,506 m) is 94 cm (NRCS 2011).

Major vegetation types of the range include sagebrush and juniper at lower elevations, with mountain mahogany, Douglas fir, Engelmann spruce (*Picea engelmanii*) and aspen at higher elevations. Gambel oak, which is commonly found on both the Oquirrh and Sheeprock Mountains, does not occur on the Stansbury Mountains (Taye 1983).

Like the Oquirrhs, cougars are the apex predator found on the range, although coyotes and bobcats are also present. The ungulate species occupying the Stansburys are mule deer, a small population of elk, and pronghorn antelope at lower elevations. Additionally a limited number of cattle seasonally graze portions of the range. In 2005 the Utah Division of Wildlife Resources initiated their first reintroduction of bighorn sheep (*Ovis canadensis*) to the mountain range with 12 individuals (UDWR 2008); currently there are an estimated 170 individuals on the mountain (T. Becker, UDWR, personal communication).

Sheeprock Mountains

The Sheeprock Mountains (~ 39.5^o N, 112.3^o W) are a rural mountain range in Tooele and Juab counties isolated by flat desert valleys. The range contains some moderately steep canyons along with gentle rolling foothills. Elevations range from 1,200 m in the valleys to 2,745 m at the highest peak. Average annual precipitation at the Vernon Creek SNOTEL station (elev. = 1,341 m) is 68 cm (NRCS 2011).

Major vegetation of the range includes sagebrush, juniper, Gambel oak, mountain mahogany, aspen and Douglas fir (Pekins et al. 1989).

Mule deer and pronghorn antelope are the only ungulates on the range. However, small bands of wild horses (*Equus ferus*) frequent the area, along with cattle which are grazed on the range seasonally. Big game hunting is allowed on this range. The Sheeprocks are part of the West Desert, Tintic-Vernon Cougar Management Unit. The taking of cougars with radio-collars is permitted.

METHODS

Captures

As part of a long-term study between Utah State University and the Utah Division of Wildlife Resources, cougars have and continue to be captured each winter (November – April) from 1996 to present. Cougar tracks were located using 4WD trucks, horses/mules, snowmobiles, ATV, and on foot. When a fresh track was located, trained hounds were released, which pursued and held the cougar at bay, until they could be reached (Hemker et al. 1986).

Cougars were immobilized with a combination of ketamine HCL and xylazine HCL (Logan et al. 1986) at a dosage of 10 mg ketamine plus 2 mg Xylazine per kg body mass. Immobilizing drugs were administered using a Palmer CO^2 pistol (Powder Springs, GA), jab-stick, or hand syringe. Once immobilized, cougars were sexed based on external genitalia characteristics (Logan and Sweanor 2001). Cougars were then aged (kittens <1.5 yrs, sub-adults 1.5-2.5 yrs, or adults >2.5 yrs) (Stoner et al. 2006), using gum-line recession measurements (Laundré et al. 2000) and visible physical condition. Each cougars was then weighed and ear-tattooed with a unique identification number (Fig. 2).

A subset of adult cougars was outfitted with GPS collars (Televilt, Lotek, ATS, or Telemetry Solutions) during the winters of 2002–2010. All animals were handled in accordance with Utah State University Institutional Animal Care and Use Committee (IACUC), Protocol No. 937-R.

Figure 2. Applying collar and recording measurements for F44 on the Oquirrh Mountains, Utah, 2009.

Locating Cache Sites

GPS collars were programmed to acquire satellite coordinates every 3 hours beginning at midnight, for a total of 8 location attempts/day. Coordinates were stored on internal (store-on-board) collar memory and retrieved approximately 1 year later when cougars were recaptured to replace collars, or upon their death. Once collars were retrieved, data points were downloaded into ArcMap version 9.2 (ESRI, Redlands, California) to produce a map of cougar use locations (Fig. 3). Cache site locations from predation events were identified on a map as ≥2 GPS locations (clusters) within 100 m on the same or consecutive nights (1700-0700 hrs); using methods similar to those described

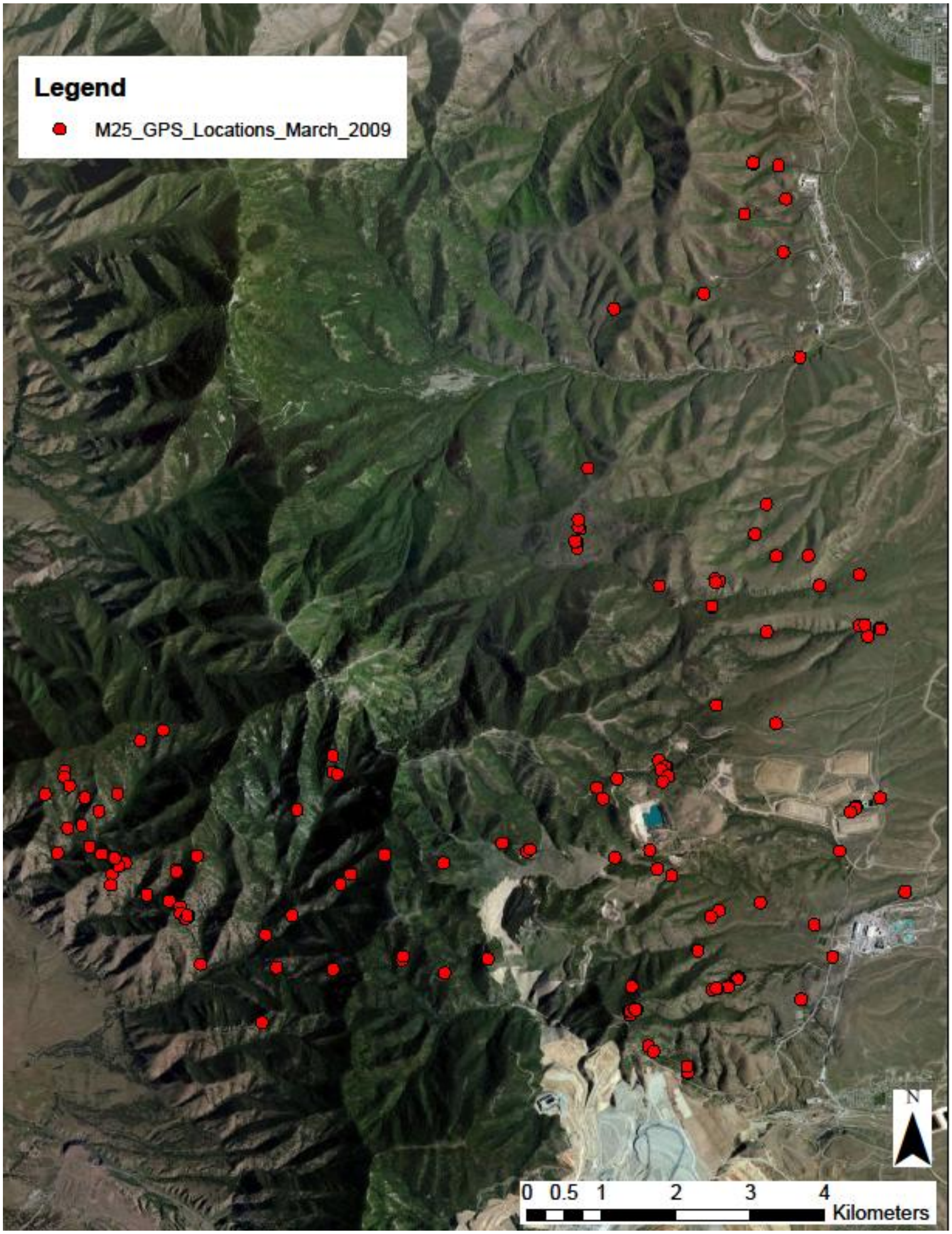

Figure 3. GPS locations (n=157) of M25 in March of 2009. Oquirrh Mountains, Utah.

by Anderson and Lindzey (2003) (Fig. 4). The mean of all GPS locations associated with a cluster location was then programmed into a handheld GPS unit and potential cache site locations were visited to determine if a kill had been made. If prey remains were not immediately found, a search was conducted for approximately 30 minutes, searching a radius of ≤100 m from the mean cluster location as identified on the map. When prey remains were found they were identified to species, sex, and age, when possible, from remaining skull and pelvic characteristics following methods described by (Schroeder and Robb 2005). For each identified kill, the date of discovery, time of discovery, persons present when remains were found, as well as search time to discovery was recorded. Site description characteristics were also recorded for each confirmed cache location, consisting of general geographic location, GPS coordinates (UTM), elevation, slope, aspect, distance to closest game trail, and vegetation characteristics including dominate vegetation species, and % canopy cover. Percent canopy cover was determined by standing at the cache location and visually estimating the percent of sky obscured by vegetation. I used logistic regression (SAS Institute 2008) in order to estimate the probability of successfully locating cache sites, based on the number of locational points associated with each GPS cluster. I used a binary response code of 1 for a carcass found and 0 for no carcass found.

Prey Use

I recorded prey species and age-sex class from each visited cache site where identifiable prey remains were located for all GPS collared cougars. I calculated prey species composition as percent frequency, by dividing the number of homogeneous species killed, by the total number of all kills (e.g. 67 deer/103 total kills =

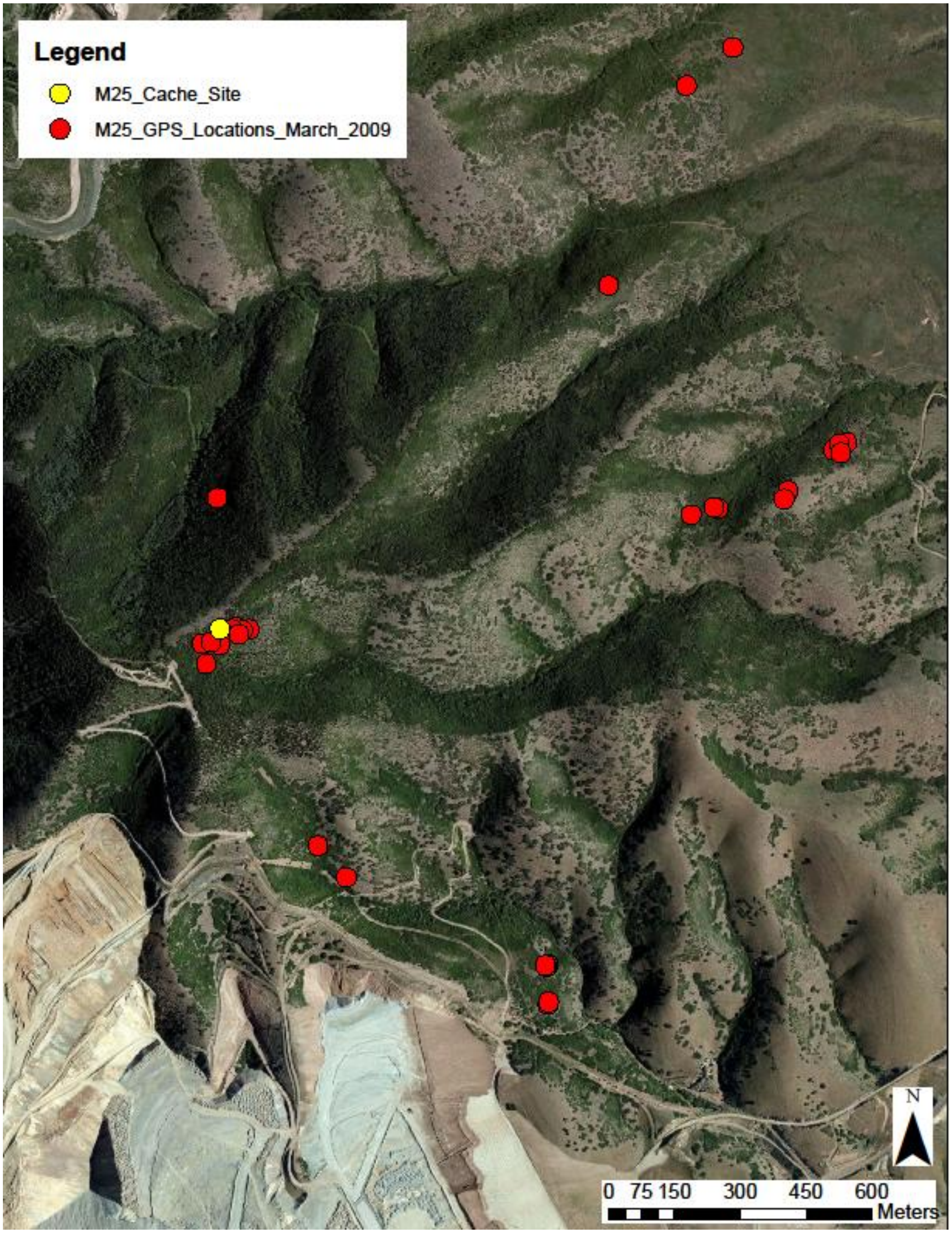

Figure 4. Clustered GPS locations illustrating potential cache sites, along with 1 confirmed cache location of M25 in March of 2009, Oquirrh Mountains, Utah.

65 % deer composition), for each cougar population segment (males, solitary females, females with kittens) and for all cougars combined. Any prey species found to be undeterminable at a cache site was recorded as unknown.

Given that mule deer tend to be the predominate (>80%) prey species taken by cougars in Utah (Ackerman et al. 1986, this study) I formally analyzed only those data pertaining to mule deer for examining selection of prey age and sex class along with any seasonal differences in cougar selection. I categorized deer prey by sex (male or female) using the presence or absence of antlers or antler pedicels for the respective sexes. If the sex was unattainable by cranial appendages (i.e. the skull was not found or was consumed beyond recognition), I used the presence or absence of suspensory tuberosities found on the pelvic girdle when available (Schroeder and Robb 2005). I categorized deer prey by age (adult ≥2 years, yearling 1 – 2 years, and juvenile ≤1 year) using dentition characteristics of the lower jaw, along with the ossification of pelvic joints when available (Schroeder and Robb 2005). If any of these variables were undeterminable I recorded them as unknown. For seasonal comparisons, I split deer kills into 2 seasons; summer (May – October) and winter (November – April).

I compared deer prey demographics (sex, age) between cougar population segments (male, female, female with kittens) and between seasons (summer, winter) using a generalized linear mixed model (PROC GLIMMIX; SAS Institute 2008) to test for statistical significance ($P \leq 0.05$). For this analysis, deer kills were my experimental unit.

Predation Rates

Predation rates were estimated for individual cougars by determining the number of days elapsed between two consecutive ungulate predation events. This time frame is defined as the inter-kill interval (IKI). To calculate the IKI, I subtracted the date and time of the first GPS fix for a confirmed predation event, from the date and time of the first GPS fix of the next confirmed predation event. I calculated IKI's for summer and winter seasons, as well as for combined seasons. I compared IKI estimates between cougar population segments and between seasons using a generalized linear mixed model (PROC GLIMMIX; SAS Institute 2008) with balanced means. For this analysis, each IKI was my experimental unit. In order to be consistent with other cougar predation studies using GPS data and to reduce sampling error, I excluded IKI's which did not meet the following criteria: (1) GPS collars had >45% fix success; (2) individuals were continuously monitored for ≥4 weeks in each season and reproductive class (Knopff et al. 2010); (3) IKI's could not contain a kill which was not validated in the field (Cavalcanti and Gese 2010, White et al. 2011). For this analysis, I excluded a single observation from F19 in the summer season when she was without offspring. This interval lasted for 82 days and did not closely match any of her other IKI's. Once this observation was excluded from the model, assumptions of normality and constant variance were met. The annual number of ungulates killed for each cougar class was calculated as:

$$\text{Annual \# of ungulates killed} = 52 * \text{\# kills/week}$$

Time Spent Feeding

Feeding intervals, or time spent on a kill, were calculated for deer and elk prey by subtracting the date and time of the first location on a confirmed kill from the date and time of the last location taken at the same cache site. I compared feeding intervals between cougar groups and among seasons using a generalized linear mixed model (PROC GLIMMIX; SAS Institute 2008). For this analysis, days fed (feeding interval) was my experimental unit. A square root transformation was applied to the days fed variable, so that assumptions of normality and constant variance were met.

Habitat Use

Due to limited sample sizes on the Sheeprock and Stansbury Mountain ranges, I analyzed land cover data for the Oquirrh Mountains only. For this analysis, I used Hawth's tools in ArcMap version 9.2 (ESRI, Redlands, California) to calculate a 95% fixed kernel density estimate of all acquired locations for all GPS-collared cougars on the Oquirrh Mountains between 2002–2010. I then masked vegetation classifications using 30-m South West Regional GAP (SWReGAP; USGS 2004) data to the study area, and condensed land cover classifications into similar categories. Land cover types were classified as agriculture, aspen, conifer, grassland, juniper, mahogany, maple, oak, other, and sage/shrub. The new SWReGAP raster served as the "available" land cover type. Confirmed cache sites were then overlaid on new land cover layers, and served as "used" land cover. I tested the hypothesis that cougars use all land cover types in exact proportion when caching prey, by using a Chi-square goodness-of-fit test. Chi-square values were calculated using the formula: $\sum$ (number of kills observed in each land cover type – expected number of kills observed in each land cover type)^2 / expected number of kills observed in each land cover type. Expected number of kills observed was calculated using the proportion of area for each land cover type, and multiplied by the total number of kills observed in each land cover type. For this analysis, each observed cache site was the experimental unit. In order to determine selection or avoidance of specific land cover types, I applied Bailey's simultaneous 95% confidence intervals using a continuity correction factor (Cherry 1996). Land cover types were considered preferred if they were used disproportionately more than they were available on the landscape and avoided if used disproportionately less than they were available (Johnson 1980).

Response to Fire

I analyzed historical fire data collected by personnel at Camp Williams National Guard training facility, along with confirmed cache sites from GPS collared cougars that traveled within Camp William's boundaries between 2002–2010. For this analysis, I used a Chi-square goodness-of-fit test to determine if cougars were using burned and unburned areas in exact proportions when caching prey. McKell (1950) found that Gambel oak, in which > 55% of cache sites were discovered, grew back to 75% of its original cover after 18 years following a fire disturbance. I therefore defined burned areas as an area having succumbed to fire ≤ 20 years prior to kill dates. Using ArcMap 10.0 (ESRI, Redlands, California) I overlaid cougar cache sites on the Camp Williams boundary, and recorded the number of cache sites that were in burned and unburned areas. For the cache sites that fell within the burned locations, I calculated the number of years between the two events. If a cache site was located where ≥2 fires had occurred in differing years, I used the interval which corresponded most recently to the cache event. I tested the hypothesis that cougars use burned and unburned areas in exact proportion when caching prey, by using a Chi-square goodness-of-fit test. Chi-square values were calculated using the formula: ∑ (number of kills observed in burned and unburned areas – expected number of kills observed in burned and unburned areas)^2 / expected number of kills observed in burned and unburned areas. Expected number of kills observed was calculated using the proportion of the burned or unburned area, and multiplied by the total number of kills observed in each area. For this analysis, each observed cache site was the experimental unit. In order to determine selection or avoidance of the burned or unburned areas, I applied Bailey's simultaneous 95% confidence intervals using a continuity correction factor (Cherry 1996). The area was considered preferred if it was used disproportionately more than what was available on the landscape and avoided if used disproportionately less than what was available (Johnson 1980).

RESULTS

Captures, Monitoring, and Cache Site Investigation

Twenty-three cougars (5 adult males, 18 adult females) were captured and fitted with GPS collars. Monitoring duration of GPS collared cougars varied from 78–1,647 days ($\bar{x}$ = 433 days/cougar, SD = 373) for a total of 9,958 cougar-days. Acquired GPS locations for individual cougars varied from 227–6,586 fixes ($\bar{x}$ = 1,755 fixes/cougar, SD = 1,529) and GPS acquisition rate for individual cougars varied from 21.0%–86.1% ($\bar{x}$ = 56.4%, SD = 16.4) (Table 1).

Table 1. Individual data for 23 North-Central Utah cougars, 2002-2010.

Cougar ID	Age/sex class[a]	Reproductive status[b]	Days monitored	Acquired GPS fixes	Fix acquisition (%)	kills found	kill intervals used[c]
F06	Ad F	SOL/MA	360	1,859	86.1	10	5
F12	Ad F	SOL/MA	730	2,195	49.4	57	30
F18	Ad F	SOL/MA	1,647	6,586	77.5	75	46
F19	Ad F	SOL/MA	1,258	5,183	73.2	73	45
F20	Ad F	SOL/MA	334	806	48.3	20	15
F26	Ad F	SOL/MA	343	1,491	54.3	11	9
F37	Ad F	SOL	174	461	32.5	8	–
F43	Ad F	SOL/MA	332	557	21.0	15	–
F44	Ad F	SOL	551	1,528	57.7	24	21
F47	Ad F	SOL	233	1,320	64.0	14	6
F50b	Ad F	SOL/MA	327	1,937	74.0	27	26
F51b	Ad F	SOL	78	250	40.1	6	–
F52	Ad F	SOL	372	1,652	56.9	19	16
F58	Ad F	MA	662	1,894	50.1	3	–
F68	Ad F	SOL	107	535	53.4	10	5
FS01	Ad F	SOL/MA	242	1,867	71.4	18	10
FS04	Ad F	SOL	382	2,135	56.6	23	17
FS05	Ad F	SOL	326	1,502	72.3	29	22
M15a	Ad M	–	86	889	74.2	9	7
M16	Ad M	–	129	227	35.2	4	–
M25	Ad M	–	671	3,563	63.3	54	36
M33	Ad M	–	256	674	46.1	14	13
M41	Ad M	–	358	1,261	39.8	23	–

[a] Age/sex class is Ad F = adult female, Ad M = adult male.
[b] Reproductive status is SOL = solitary, MA = maternal, SOL/MA = transitioned between solitary and maternal group.
[c] The number of kill intervals used in calculating predation rates.

In total, 40,372 GPS locations were obtained, of which 911 were identified as potential cache site clusters. Of these potential cache sites, 775 clusters (85%) were visited however; due to temporal and logistical restraints 136 clusters (15%) were not visited. Of the 775 visited clusters, 517 (67%) had prey remains present, but 258 (33%) had no detectable prey remains. Cache sites were visited 2–889 days ($\bar{x}$ = 348, SD = 156) after a kill was made and an average of 8 minutes (range = 0–90 minutes, SD = 12) was spent searching for prey remains, once the cluster mean was located. When field validating identified cache sites, the probability of successfully finding a cache site increased as the number of GPS locational points associated with cache sites increased, with a >95% probability of success occurring once ≥50 points were clustered (Fig. 5).

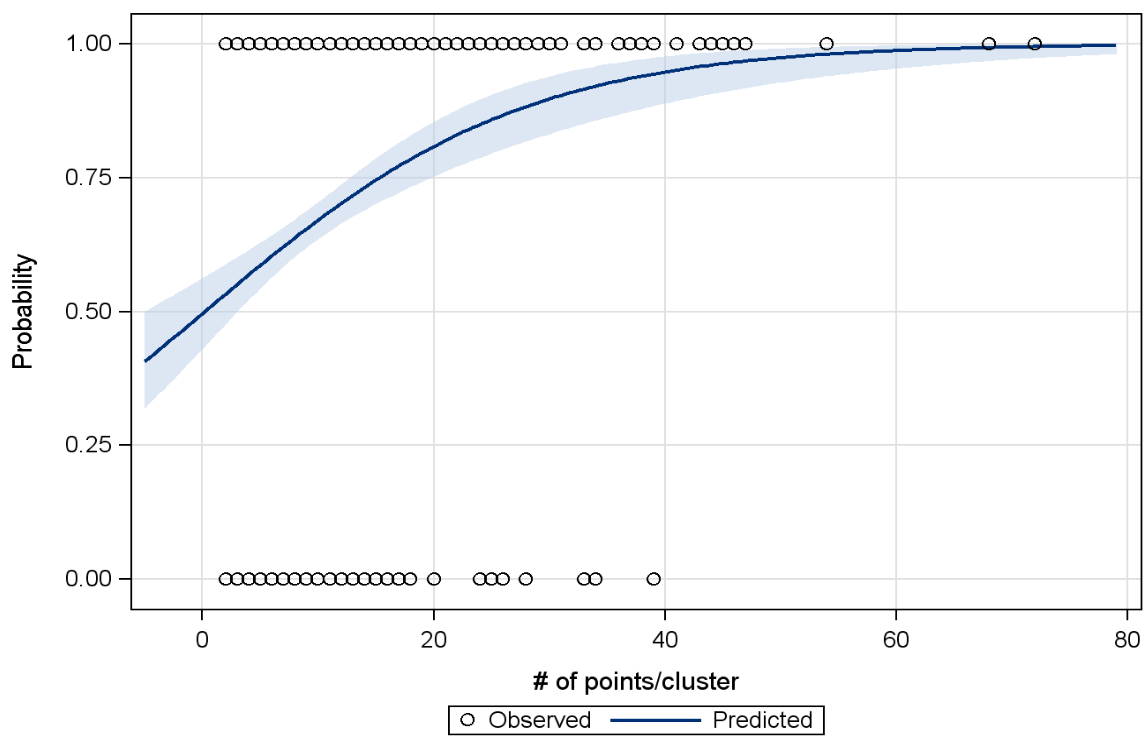

Figure 5. Probability of locating cougar cache sites based on the number of Global Positioning System (GPS) locations recorded at individual clusters. North-Central Utah, 2002-2010. 95% confidence intervals are illustrated by light blue buffer around the predicted values.

When prey remains were found, common characteristics included broken leg bones, chewed scapula and pelvic bones and when skulls were present they were typically chewed on, especially around the rostrum area. Large hair piles were also associated with most cache sites along with varying amounts of rumen contents. Scat piles were commonly found approximately 10–30 m from cache sites. At sites where no prey remains were detected, bed sites, den sites, or caves/culverts were found. However, it is likely that a predation event did occur at some of these sites but the remains were either totally consumed, drug away, or inconspicuous due to thick vegetation.

Of the 517 confirmed kill sites, remains of 546 prey items were found, ranging from 3 to 75 kills per individual cougar (Table 1). Twenty-three of these sites had ≥2 kills attributed to an individual cougar. These multi-prey sites were documented as being largely mother-offspring kills (doe and fawn), sibling kills (multiple fawns), or cache defense kills (deer and coyote). Additionally, 4 social interactions were documented (female and male (n = 2); female and female (n = 2)), where collared cougars spent corresponding time at a kill. Four scavenging events were also documented, where evidence suggested that a cougar was not responsible for the kill.

Prey Use

In total, 546 prey remains were detected, consisting of 12 different species. Mule deer were the majority of kills, comprising 87% (n = 477) of total kills. Elk were the next highest contributing species at 5% (n = 28) of all kills (Table 2). Interestingly, 79% (n = 22) of elk kills were made by male cougars. Less frequently used prey consisted of domestic cattle and sheep, coyote, cougar, turkey, skunk, bobcat, fox,

Table 2. Prey remains detected (n, [%]) at 517 cache sites of GPS collared cougars in North Central Utah, 2002 – 2010.

Prey	Solitary females (n = 329)	Females with kittens (n = 114)	Males (n = 103)	Total (n = 546)
Mule Deer	304 (92.4)	106 (93.0)	67 (65.0)	477 (87.4)
Elk	5 (0.2)	1 (0.1)	22 (21.4)	28 (5.1)
Livestock[a]	3 (0.1)	1 (0.1)	4 (0.4)	8 (1.5)
Cougar	0	0	3 (0.3)	3 (0.6)
Coyote	6 (0.2)	1 (0.1)	2 (0.2)	9 (1.7)
Bobcat	0	0	1 (0.1)	1 (0.2)
Skunk	2 (0.1)	0	0	2 (0.4)
Fox	0	1 (0.1)	0	1 (0.2)
Porcupine	1 (0.0)	0	0	1 (0.2)
Raccoon	1 (0.0)	0	0	1 (0.2)
Turkey	1 (0.0)	1 (0.1)	1 (0.1)	3 (0.6)
Unknown	6 (0.2)	3 (0.3)	3 (0.3)	12 (2.2)

[a] Includes 5 domestic cows and 3 domestic sheep.

porcupine, raccoon, and 12 unidentifiable species remains. Three hundred and twenty nine kills from solitary female cougars were found, along with 114 kills from females with kittens, and 103 kills from male cougars (Table 2).

Among deer kills, the proportion of bucks or does killed among cougar population segments did not differ significantly ($F_{4, 40} = 1.51$, $P = 0.218$). Nor was there a difference in the proportion of adults, yearling, or juveniles killed between cougar population segments ($F_{6, 40} = 1.09$, $P = 0.387$). Of the deer kills in which sex identification was determinable, solitary female cougars killed 36.9% male deer and 63.1% female deer. Females with kittens killed 42.9% male deer and 57.1% female deer, while male cougars killed 54.8% male deer and 45.2% females (Table 3). Additionally, solitary female cougars killed 63.6% adult, 16.1% yearling and 20.4% juvenile deer. Females with kittens killed 69.4% adult, 14.3% yearling and 16.3% juvenile deer and male cougars killed 75.1% adult, 4.9% yearling and 19.7% juvenile deer (Table 4).

Table 3. Sex composition (n, [%]) of 203 known sex mule deer found at GPS cluster locations for male cougars and females with and without kittens in North-Central Utah, 2002 – 2010.

	Cougar		
Mule deer sex class	Females	Females w/Kits	Males
Female	82 (63.1)	24 (57.1)	14 (45.2)
Male	48 (36.9)	18 (42.9)	17 (54.8)
Total	130	42	31

Table 4. Age composition (n, [%]) of 439 known age mule deer found at GPS cluster locations for male cougars and females with and without kittens in North-Central Utah, 2002 – 2010.

	Cougar		
Mule deer age class	Females	Females w/Kits	Males
Juvenile	57 (20.4)	16 (16.3)	12 (19.7)
Yearling	45 (16.1)	14 (14.3)	3 (4.9)
Adult	178 (63.6)	68 (69.4)	46 (75.1)
Total	280	98	61

The number of kills made seasonally differed among cougar population segments ($F_{2, 40}$ = 13.42, $P \leq 0.001$) with males and solitary females having proportionally more kills in the summer rather than the winter, and females with kittens making proportionally less kills in the summer rather than winter. The proportional age class structure of mule deer killed also differed between seasons ($F_{3, 40}$ = 4.84, P = 0.005) with yearling deer being killed proportionally more in the summer rather than the winter. The majority of juvenile mule deer were killed in the months of July, August, and September (Fig. 6).

The proportion of male and female mule deer killed did not differ significantly between seasons ($F_{2, 40}$ = 1.71, P = 0.193). However, monthly comparisons of male and female deer kills revealed there was some variation, with male deer comprising >50% of cougars diets in the fall months of October, November and December (Fig. 7).

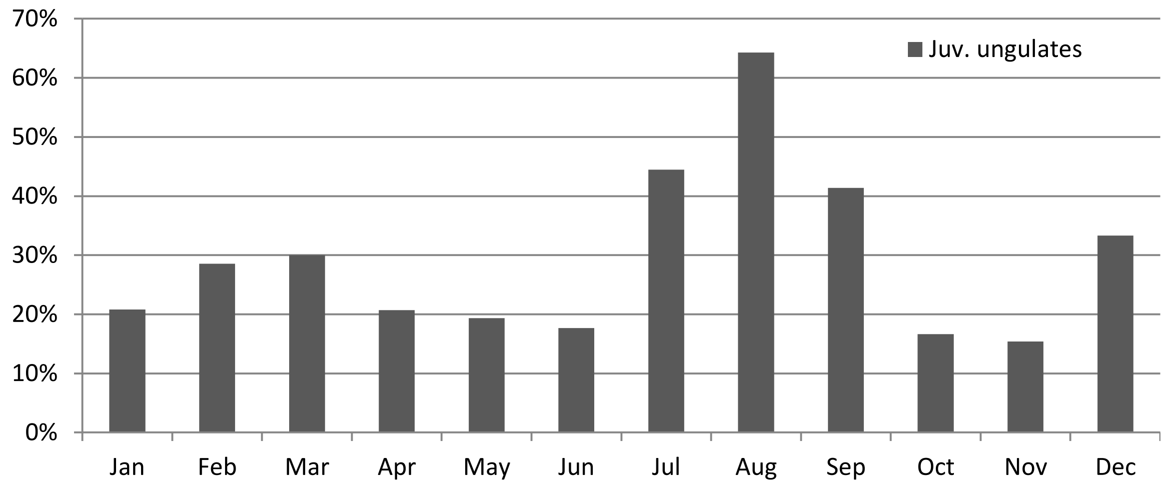

Figure 6. Monthly percentage of juvenile (≤1 yr. old) ungulates killed by cougars in North-Central Utah, 2002-2010.

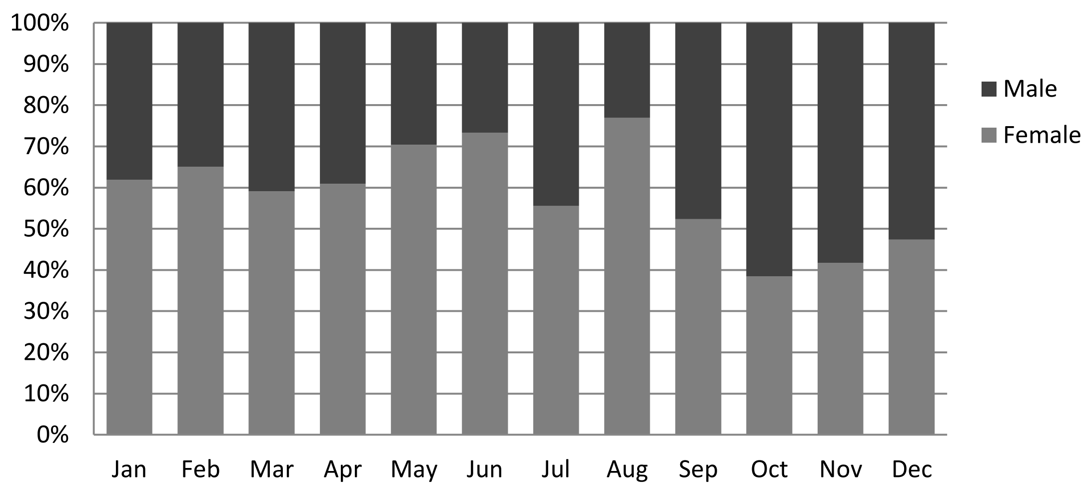

Figure 7. Monthly percentage of male and female ungulates killed by cougars in North-Central Utah, 2002-2010.

Predation Rates

The mean predation rate on all ungulate species killed for all cougars was 11.2 days/kill (95% CI = 9.9 – 12.5). Predation rates did differ among cougar population segments (females $\bar{x}$ = 12.2 days/kill; females with kittens $\bar{x}$ = 9.1 days/kill; males $\bar{x}$ = 12.4 days/kill; $F_{2, 22} = 3.46$, $P = 0.049$) (Fig. 8). Predation rates also differed

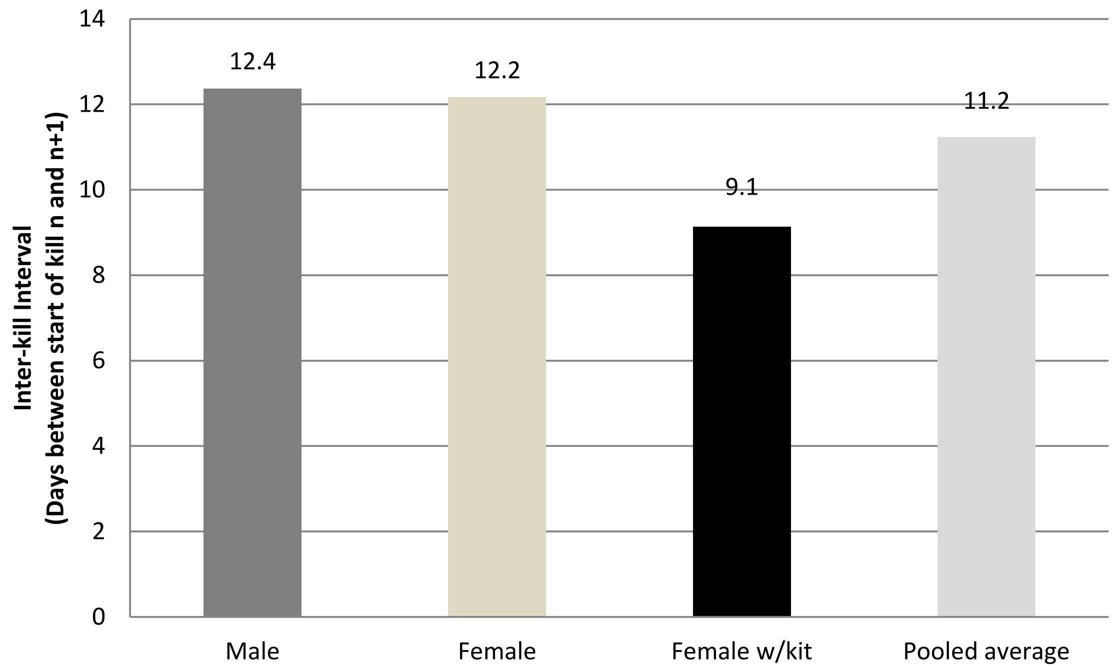

Figure 8. Predation rates for cougars of North-Central Utah, 2002-2010.

significantly between seasons (winter $\bar{x}$ = 9.5 days/kill; summer $\bar{x}$ = 12.9 days/kill; $F_{1, 14}$ = 7.18, P = 0.018). The mean annual number of ungulates killed was 29.9 for solitary females, 39.3 for females with kittens, and 29.4 for male cougars.

Time Spent Feeding

The mean time that cougars spent feeding on deer kills was 3.1 days/kill (95% CI = 2.9 – 3.2). There was no significant difference in time spent feeding on deer kills between cougar population segments (females $\bar{x}$ = 3.3 days/kill; females with kittens $\bar{x}$ = 2.9 days/kill; males $\bar{x}$ = 3.1 days/kill; $F_{2, 21}$ = 0.10, P = 0.902). Time spent feeding on deer kills did not differ between seasons (winter $\bar{x}$ = 3.2 days/kill; summer $\bar{x}$ = 2.9 days/kill; $F_{1, 21}$ = 0.50, P = 0.487). The mean time cougars spent feeding on elk kills was 6.2 days/kill (95% CI = 4.1 – 8.3).

Habitat Use

There was a significant difference between the occurrence of land cover types and the proportion cougars used when caching prey remains (χ^2 = 102.59, df = 9, $P \leq 0.001$) with the highest use occurring in Gambel oak land cover at 1.7 times higher than expected. Oak was the only land cover type found to be preferred, while conifer and other land cover types were avoided (Table 5).

Response to Fire

Burned and unburned areas comprised 63% and 37% of the Camp Williams study site respectively. There was a significant difference in the proportion of burned vs. unburned areas cougars used when caching prey remains (χ^2 = 67.62, df = 1, $P \leq 0.001$). Use in unburned areas was 1.8 times higher than expected, and use in burned areas was 1.9 times lower than expected (Table 6).

Table 5. Occurrence of cougar kills in differing land cover types on the Oquirrh Mountains, Utah, 2002-2010. Negative (-), positive (+) and neutral (o) signs signify occurrence less, greater than or in proportion to expected value, respectively.

Landcover	Area (Km^2)	Use	Observed kills	Expected kills	Available	Lower CI	Upper CI	Preference
Conifer	34	0.025	11	31	0.071	0.008	0.053	-
Aspen	41	0.083	36	37	0.086	0.049	0.126	o
Mahogany	22	0.021	9	20	0.045	0.006	0.047	o
Juniper	74	0.175	76	67	0.155	0.126	0.230	o
Oak	123	0.442	192	112	0.257	0.374	0.509	+
Maple	24	0.028	12	22	0.051	0.010	0.056	o
Sage/shrub	96	0.164	71	87	0.201	0.116	0.218	o
Grassland	25	0.028	12	23	0.052	0.010	0.056	o
Agriculture	6	0.000	0	5	0.012	0.000	0.013	o
Other	33	0.035	15	30	0.068	0.014	0.066	-
Total	477		434					

Table 6. Occurrence of cougar kills in burned vs. unburned habitat types on Camp Williams military installation, Utah, 2002-2010. Negative sign (-) signifies occurrence less than expected. Positive sign (+) signifies occurrence more than expected.

Habitat	Area (Km^2)	Use	Observed kills	Expected kills	Available	Lower CI	Upper CI	Preference
Burn	61	0.332	61	115	0.627	0.254	0.413	-
Unburn	36	0.668	123	59	0.373	0.583	0.743	+
Total	97		184					

DISCUSSION

Prey Use

The prey of GPS collared cougars in North-Central Utah consisted primarily of ungulates. This finding is consistent with a scat analysis conducted in the same geographical area (Wolfe et al. 2004), as well as with other cougar predation studies throughout North America (Iriarte 1990, Knopff et al. 2010). Mule deer comprised the majority of ungulates killed on the study sites and were likely the most abundant ungulate species available to cougars, although there were no reliable estimates of the area's density. Prey composition frequencies obtained using this detection methodology are likely biased towards larger prey species, because of their persistence rate in the environment (Cavalcanti and Gese 2010). That said, several smaller prey species were documented, providing further evidence that cougars are opportunistic feeders and consume a variety of prey species and size (Murphy and Ruth 2010). Both sexes of cougars killed elk, including mature bulls, but the majority of elk kills were made by male cougars. This is a common finding among cougar studies and further supports the hypothesis that comparatively, male cougars kill larger prey than females (White et al. 2011). Some evidence of intra-guild competition between cougars and coyotes or bobcats was observed at cache sites. The majority of these carnivore kills were found at sites where cougars had cached ungulate prey. It appears that cougars killed the competing carnivores to protect their cached prey (Boyd and O'Gara 1985, Murphy et al. 2011). Intraspecific competition was also documented, wherein adult male cougars had killed other adult (male and female) cougars as well as juvenile cougars. This phenomenon may occur in order to promote the males individual fitness by acquiring, or defending, a valuable territory (i.e. sustainable resources). When infanticide takes place, males may be increasing their reproductive fitness by inducing an early estrus in the maternal female, thereby increasing the male's opportunity to breed and reproduce (Logan and Sweanor 2001).

Data collected for this study suggests that cougars killed more adult female deer than other age/sex classes on the study site. These findings are similar to those of Pierce et al. (2000), Mattson et al. (2007), and Knopff et al. (2010). However, Hornocker (1970) found more adult bucks and fawns were killed by cougars on his study area. When deer kills were compared between cougar population segments, there was no difference in proportions of age or sex of deer prey. However, there was a seasonal difference in the proportion of deer kills between cougar population segments, wherein females with kittens made proportionally less kills in the summer than either males or solitary females. This finding differs from Knopff et al.'s (2010) results, in which all cougar demographic classes increased the proportion of large ungulates killed during the summer. This may be due to access to smaller prey on the landscape during warmer months (Hornocker 1970), which coincides with birth pulses for cougars (Rieth 2009). These maternal females may be taking smaller, easier prey to sustain their energetic needs while nursing, as well as decreasing the risk of injury by larger prey (Nowak 1999). Yearling age class deer were being taken by cougars proportionally more in the summer months than other age classes of deer. This could be happening because these younger deer are still somewhat naïve to predators and therefore more vulnerable to predation (Pierce et al. 2000, Knopff et al. 2010). Of the juvenile mule deer that were killed on the study sites, the majority of them were killed in the summer, just after May-June birth pulses, and likely when neonates become increasingly available on the landscape. Like Knopff et al. (2010), this study found there to be no difference in the proportion of sex classes of mule deer killed between seasons, but when looking at the percentages of male and female deer in cougar diets across the months of the year, there was some variation. Male deer comprised the majority of kills in the fall months corresponding with rutting behavior, which has been known to cause male ungulates to become more vulnerable to predation (Owen-Smith 2008, Metz et al. 2012). These findings lend support to the prey vulnerability hypothesis, suggesting that predators may exhibit temporal variation in prey selection given the prey's stage of reproductive and/or age class (Lima and Dill 1990, Pierce et al. 2000, Knopff et al. 2010).

Predation Rates and Time Spent Feeding

Females with kittens had the highest predation rates on this study. This finding supports Ackerman et al.'s (1986) prediction of increased predation rates for family groups, and is similar to findings by nearly all previous cougar predation studies (Murphy 1998, Anderson and Lindzey 2003, Laundre 2005, Cooley et al. 2008, Knopff et al. 2010). This result is intuitive, given that maternal females must consume increased amounts of food in order to meet their metabolic needs during lactation, as well as provide enough food for their dependant offspring (Ackerman et al. 1986).

Predation rates between males and solitary females did not significantly differ from one another, and therefore my results did not support McNab's (1988) hypothesis or Ackerman et al.'s (1986) prediction regarding increased predation rates with increased body mass. My results for these two classes of cougars were also different from those of

Murphy (1998), who found males to have a higher predation rate than solitary females, but were similar to those of Anderson and Lindzey (2003) who found similar rates between male and solitary female cougars. This may be attributed to an increased success in finding smaller prey remains (i.e. fawns), which female cougars tend to utilize more than male cougars (White et al. 2011, this study), given the higher precision of accuracy associated with GPS locations vs. traditional VHF telemetry (Table 7).

Cougars had a higher kill rate in the winter vs. summer seasons. This supports Hornocker's (1970) prediction that cougars may be killing smaller emerging prey in summer, which is not available in winter time. The smaller prey species may go undetected, given the methods used to define a cache site. This seasonal shift in prey could cause cougars to rely on making ungulate kills more often in winter months.

The annual number of ungulates killed by cougars from each population segment, from this study, fell near the average number of kills reported for studies conducted throughout North America (Knopff et al. 2010).

Both Murphy's (1998) and Mattson et al.'s (2007) data suggests that male cougars spent a shorter duration of time on a kill relative to female cougars with and without kittens. Their results support Pierce et al.'s (2000) assumption that male cougars may gorge themselves on a kill in order to patrol their large territories. Those findings differed from this study, wherein there was no significant difference between cougar population segments in the time spent on a kill. However, of these three population groups, females with kittens spent the least amount of time on kills, which may be explained by Pierce et al.'s (1998) suggestion that maternal females display behavioral traits that minimize encounters with conspecifics in order to protect their young.

Table 7. Cougar predation rates of ungulates from North American studies.

Source	Location	Primary prey[a]	Predation rate[b]	Cougar sex/age[c]	Technique
Hornocker (1970)	ID	MD, Elk	18.4–25.9	US	Energetics model
			4.5	FG	Snowtracking
Shaw (1977)	AZ	MD	6.8	FG	Radiotracking
			10.4	AF	
Ackerman et al. (1986)	UT	MD	8.5	AM	Energetics model
			16.1	AF	
			3.1–10.4	FG	
			4.5	FG	Radiotracking
Harrison (1990)	BC	BS, MD	2.7–6.4	FG	Radiotracking
Beier et al. (1995)	CA	MD	7.6	US	Radiotracking
Murphy (1998)	WY	Elk	7.5	AM	Radiotracking
		Elk, MD	11.1	AF	
		Elk, MD	7.2	FG	
		Elk, MD	11.0	SM	
		MD, Elk	10.3	SF	
Nowak (1999)	OR	MD, Elk	7.7	UF	Radiotracking
Anderson and Lindzey (2003)	WY	MD, Elk	7.0	US	GPS model
		Elk, MD	7.8	AM	
		MD, Elk	7.0	AF	
		MD	5.4	FG	
		Elk, MD	9.5	SM	
		MD, PH	7.3	SF	
Laundré (2005)	ID	MD	18.9	AM	Energetics model
			24.1	AF	
			8.2	FG	
Mattson et al. (2007)	AZ	Elk, MD	7.4	AM	GPS model
			8.0	SM	
			9.2	AF	
			6.0	SF	
Cooley et al. (2008)	WA	WTD, MD	9.5	UM	Radiotracking
			7.7	UF	
Laundré (2008)	ID	MD	14.9	AM	Radiotracking
			14.3	AF	
			11.9	FG	
Laundré (2008)	ID	MD	14.9	AF	Radiotracking
White et al. (2009)	WA	MD	6.5	US	GPS telemetry
		Elk	9.8	US	
Knopff et al. (2010)	AB	WTD, MD, MO	10.4	AM	GPS telemetry
			11.9	SM	
			8.8	AF	
			15.2	SF	
			5.4–7.8	FG	
This study	UT	MD, Elk	12.4	AM	GPS telemetry
			12.2	AF	
			9.1	FG	

[a] Primary ungulate prey found at kill sites. MD = mule deer, WTD = white-tailed deer, MO = moose, PH = pronghorn.

[b] Predation rate is days/kill.

[c] US = unspecified sex/age, AM = adult male, AF = adult female, SM = subadult male, SF = subadult female, FG = family group.

Although the sample size of elk kills for this study was too small to test for significance, cougars spent a longer time on elk kills than deer kills. This is probably due to the larger body mass of elk, allowing cougars to consume more biomass.

Habitat Use and Response to Fire

Although Gambel oak land cover was the most abundant land cover available on the Oquirrh Mountain study site, it was surprisingly used by cougars > 1.5 times more than what was available to them when caching prey. This highly selected land cover type grows in very dense stands (Stubbendieck et al. 2003), and is known to be an important year-round browse for mule deer and elk (Pendleton et al. 1992, Newmark and Rickart 2012). These traits may provide cougars with the perfect set-up for stalking and caching prey. Similarities in cougar selection for areas with increased cover when feeding on prey have also been documented in other felid studies (Dickson and Beier 2002, Cavalcanti and Gese 2010). The apparent avoidance of conifer land cover type, which typically lacks a dense understory, by cougars on this study site, gives further evidence to the importance of cover for cougars to be successful in predation attempts.

There is little literature pertaining to cougar response to fire, likely due to the lack of datasets containing both cougar locations and fire histories. This study's dataset, which includes GPS cougar locations and limited burn histories, suggests that cougars selectively use areas that have not been burnt, or at least have no effects from historical burns, when caching prey. This result supports Atwood et al.'s (2007) hypothesis that prescribed burns will reduce hunting success of stalking predators. Conversely, Dees et al. (2001) found that Florida panthers were selectively using <1-year-old burn stands, likely due to an increased usage by ungulate prey. However, their dataset consisted of

VHF telemetry locations recorded between 0600–1000 hr. and therefore may not have captured the full spectrum of predation events. These findings also support previously mentioned findings, indicating that increased cover appears to be a trait that cougars readily utilize.

MANAGEMENT IMPLICATIONS

My results indicate that the use of GPS collars may give a more precise estimate of cougar predation, at least for larger prey, than was previously possible. The technological advancement of GPS data to be delivered through remote downloads or weekly email will likely improve future estimates of predation rates and prey use by expediting the time between a kill and the investigation of kill sites.

I found that cougars in North-Central Utah, on average, make an ungulate kill every 11 days. This is a lower kill rate than the commonly perceived rate of 1 deer every 7 days. I have also shown that cougars selectively use dense stands of vegetation when caching, and likely killing prey. This information can benefit managers looking for solutions to reduce the amount of predation on limited ungulate populations, without overexploiting local cougar populations. Prescribed burns could simultaneously help mule deer populations by reducing the percent of stalking cover afforded to cougars when attempting to kill prey, along with increasing nutrient levels of newly burned foliage and allow for an increased diversity in desirable forb and shrub species.

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