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Abstract

Understanding predator-prey dynamics is a fundamental principle of ecology and an ideal component for management decisions. Across North America, the impact of cougars (*Puma concolor*) on their prey varies regionally. To document the relationships between cougars, bighorn sheep (*Ovis canadensis canadensis*), mule deer (*Odocoileus hemionus*), and feral horses (*Equus caballus*) on the Bighorn Canyon National Recreation Area and the Pryor Mountains, we deployed GPS collars on 6 cougars (the total number residing on the study area), and visited their clusters to determine predation rates and foraging patterns. We examined the composition of cougar kills by species, mule deer sex-age classes, prey size classes, season, and cougar sex. As a measure of selection, we examined the composition of prey killed relative to the composition of ungulates obtained during an aerial survey. We found mule deer were the primary prey, while bighorn sheep constituted secondary prey. While cougars selected for bighorn sheep, this was attributable to a single cougar. Among mule deer, female cougars killed more does and male cougars killed more bucks. Family groups had the highest predation rates (i.e., the shortest time intervals between kills), while adult males had the lowest rate. During the study, cougars were not depredating any feral horses in the area. Maintaining predator and prey numbers will require agencies to monitor and manage all fauna within this complex ecosystem. Habitat manipulations may be necessary to increase populations of deer and bighorn sheep, while continued management of feral horses will be required to reduce competition with native ungulates.

Keywords: predation, cougar, bighorn sheep, mule deer, feral horse

Introduction

Predators can potentially have profound impacts upon their prey populations (Caughley 1979, Sinclair 1989). Cougar (*Puma concolor*) predation has been implicated as a regulating factor in some ungulate populations (Ballard et al. 2001, Logan and Sweaner 2001, Robinson et al. 2002). However, the influence of predation can be difficult to understand when compounded by factors such as the presence of other predators, disease, climate, habitat quality, availability of secondary prey, or demographic vulnerability inherently present within small, isolated ungulate populations (Festa-Bianchet et al. 2006, Atwood et al. 2007, Cooley et al. 2008, Hurley et al. 2011). Managers concerned with the dynamics of prey populations under their auspices need information about the extent and impact of predation in those

ecosystems if they are to make sound management decisions. Specifically, they need reliable estimates of predation indices, including composition of kills and predation rates. Whether predation on ungulates by cougars is additive or compensatory requires additional knowledge on cause-specific mortality agents within the ungulate population (Hurley et al. 2011).

Due to their nocturnal, secretive hunting and prey consumption habits, cougar predation patterns are impossible to observe directly. The advent of GPS collars has allowed us to better understand cougar predation by enabling 24-hour monitoring of a cougar's location, thereby allowing scientists to identify cache sites and locate prey remains (Anderson and Lindzey 2003). With this advance, biologists have been able to more accurately estimate cougar predation metrics (e.g., Monroy-Vilchis et al. 2009, Knopff et al. 2010, Kunkel et al. 2013, Mitchell 2013). An understanding of the

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role of cougar predation is enhanced by knowledge of their selection for certain prey species and for sex-age classes within a prey population. If the composition of cougar kills reveals they disproportionately prey upon sex-age classes with higher reproductive values (often adult females), this could have a higher impact than if they do not select for particular prey classes (Rubin et al. 2002, Boukal et al. 2008). Some research has supported the reproductive vulnerability hypothesis (Lima and Dill 1990, Knopff et al. 2010, Mitchell 2013) which proposes that sex-age classes of prey vary in their vulnerability to predation based upon their reproductive state. That is, male ungulates should be most vulnerable during and after the rut, females during late gestation and shortly after giving birth while tending neonates, and juvenile ungulates shortly after their birth when they are inexperienced and less mobile. Researchers have also examined the interplay between predation patterns and the social class of cougars. In most instances, females supporting dependent kittens tend to kill more frequently than solitary adult females or males (Anderson and Lindzey 2003, Knopff et al. 2010, Mitchell 2013), thus having a greater impact on prey populations in terms of the number of individuals killed. Predation rates and handling times are also generally influenced by the biomass of prey (Mattson et al. 2007, Cavalcanti and Gese 2010). Finally, it has been demonstrated that dominant predators such as brown bears (*Ursus arctos*), black bears (*Ursus americanus*), and wolves (*Canis lupus*) may engage in kleptoparasitism by displacing subordinate felids from their kills (Ruth and Murphy 2010b, Krofel et al. 2012, Allen et al. 2014). Prey loss due to kleptoparasitism could increase the predation rates of cougars as they compensate for lost biomass of prey by resuming hunting earlier following usurped kills.

Previous studies have found cougar predation upon feral horses (*Equus caballus*) varies widely. Turner and Morrison (2001) found cougars limited feral horse populations in the White Mountains of California and Nevada, while in other studies cougar predation has been negligible, or attributable to a specialist individual (Knopff and Boyce 2007). While bighorn sheep (*Ovis canadensis*)

are typically thought to be a secondary prey item, cougar predation has been shown to impact small, isolated populations, sometimes even driving them to extinction (Wehausen 1996, Hayes et al. 2000, Kamler et al. 2002, Rominger et al. 2004, Festa-Bianchet et al. 2006). Predation pressures upon bighorn sheep vary between cougar populations and even among individual cougars (Ross et al. 1997, Logan and Sweanor 2001). The presence of cougars does not necessarily imply a threat to a bighorn sheep population (Hornocker 1970, Rominger et al. 2004), although there are indications predation pressures may increase with a change in the population of a primary prey species, or if an individual cougar learns to specialize in killing bighorn sheep. Cougars have sometimes been blamed for mule deer (*Odocoileus hemionus*) population declines, but the influence of cougar predation on a mule deer population is often complicated by the presence of secondary prey species, and additional predators such as black bears or coyotes (*Canis latrans*), and by whether the nature of predation is additive or compensatory (Ballard et al. 2001, Robinson et al. 2002, Hurley et al. 2011).

Cougars have been implicated in predation upon mule deer, bighorn sheep, and feral horses in the Pryor Mountains of Montana and Wyoming (Schoenecker 2004, C. Bromley, National Park Service, personal communication). Managers with an interest in maintaining healthy herds of all three prey species and their predator need insight into cougar predation patterns. Our objectives were to: 1) estimate predation rates and handling times for all cougars and by cougar social classes, seasons, and prey size classes, 2) document composition of cougar kills and determine differences in the proportion of prey species, prey sex-age classes, or prey size classes, killed by sex of cougars and by season, and 3) examine if cougars are selective for certain prey species or prey sex-age classes as compared to the composition of ungulates observed in an aerial survey. We hypothesized ungulate prey killed by cougars would be composed primarily of mule deer with smaller percentages of bighorn sheep and horses; we anticipated some predation of horses during foaling season (Turner et al. 1992). We expected higher predation rates among females

with kittens than with solitary cougars in response to increasing energetic demands of growing kittens. We expected shorter inter-kill intervals to follow those kills that were detected by black bears (i.e., kleptoparasitism) as the displaced cougar would need to kill again to meet its energetic needs. We also expected handling time to be shorter for adult males as mature males may be minimizing feeding to maximize reproductive opportunities, as postulated by Mattson et al. (2007). Lastly, we hypothesized differential prey use with selection for larger prey (mule deer bucks and bighorn rams) among male cougars, while female cougars would select for smaller prey (female and young mule deer and bighorn ewes and lambs), due to differing body size and the males ability to subdue larger prey (Anderson and Lindzey 2003, Knopff et al. 2010, White et al. 2011).

Study Area

We conducted this study in the southern portion of the Pryor Mountains of northcentral Wyoming and southcentral Montana. The 2553 km² study area included the Bighorn Canyon National Recreation Area (BCNRA), the Pryor Mountain Wild Horse Range (PMWHR), a portion of the Crow Indian Reservation, the Custer National Forest, Bureau of Land Management (BLM) property, and private properties (Figure 1). The study area was formed by creating a minimum convex polygon of all recorded cougar locations. Within this polygon were patches of habitat that were considered less suitable for cougars including grasslands, sagebrush, desert shrubland, developed areas, and in winter, areas above 2140 m elevation where only 5% of cougar locations in winter were documented.

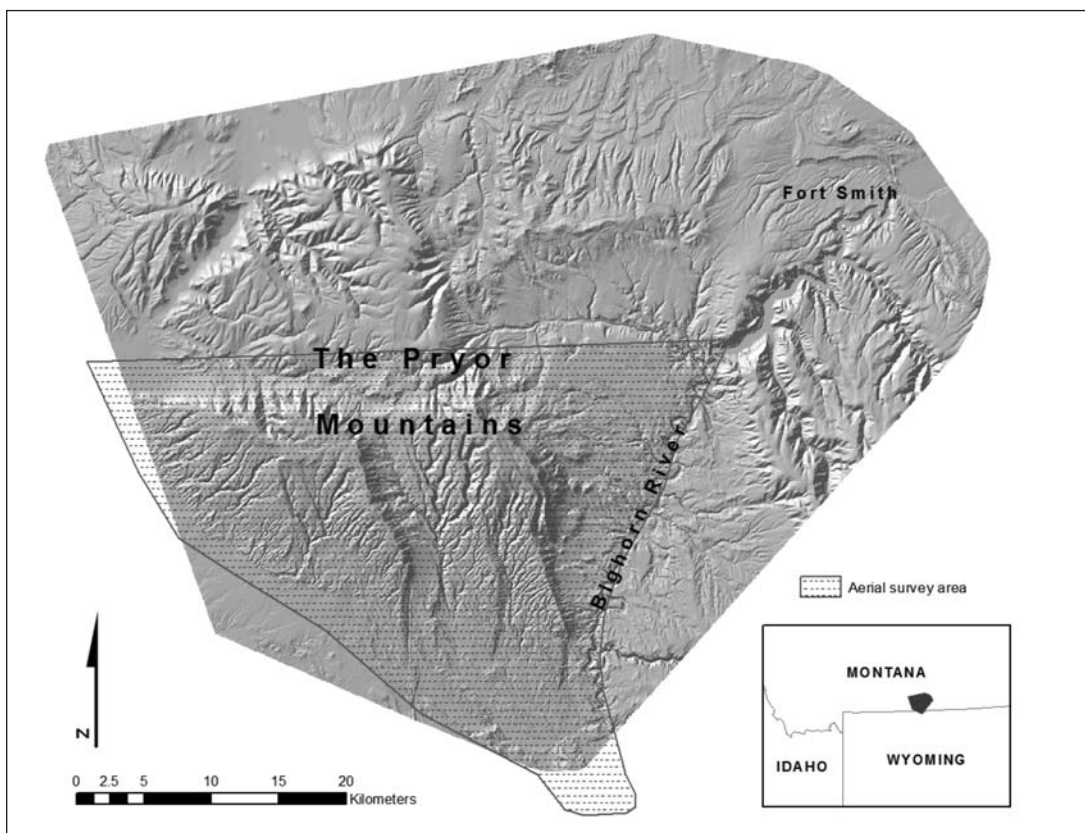


Figure 1. The 2553 km² study area in the southern Pryor Mountains of Wyoming and Montana with the 925 km² aerial ungulate survey area.

In the summer, 33% of the 2553 km² study area was considered suitable for cougars, while 28% was considered suitable in winter. The habitat and topography of the Pryor Mountains was extremely variable. One notable feature was Bighorn Canyon itself with cliffs up to 300 m high. Several creeks flowed through the study area, as well as several seasonal creeks, natural springs and anthropogenic water sources. The southern portion of the study area consisted of desert badlands, expanses of sagebrush (*Artemisia spp.*), and desert shrublands. The northern portion was characterized by steep timbered slopes, high alpine meadows, and sagebrush steppes. Rugged, incised canyons were prevalent throughout the area. Using the vegetation community classifications developed for the BCNRA (Knight 1987) and the nearby Bighorn Mountains (Logan and Irwin 1985), we classified vegetation as sagebrush, coniferous forest, juniper-mountain mahogany (*Juniperus spp.*, *Cercocarpus ledifolius*) woodland, desert shrubland, grassland, deciduous shrubland, riparian, or developed.

Elevations ranged from 950 to 2700 m. The climate was characterized by hot summers with temperatures exceeding 32 °C and cold winters with temperatures below −15 °C. There was a north-south precipitation gradient with an average total annual precipitation of 16.9 cm in the south and 45.8 cm in the north, with most precipitation falling as rain during May and June (Western Regional Climate Center 2013). Because the study site exhibited strong seasonality, we defined two seasons: summer (April 16–October 15) and winter (October 16–April 15).

Cougars and black bears were the apex predators of the area; grizzly bears (*Ursus arctos horribilis*) and wolves had not re-established in the area. Other mammals in the study area included coyote, red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), beaver (*Castor canadensis*), and porcupine (*Erethizon dorsatum*). The main ungulate species were mule deer, feral horses, and domestic cattle (*Bos primigenius*). Additional ungulates included a small population of Rocky Mountain bighorn sheep and a few white-tailed deer (*Odocoileus virginianus*). The bighorn sheep population in-

habited a subset of the study area (Schoenecker 2004; Figure 2) and was estimated to be 107 ewes (95% CI: 75–172) and a minimum of 14 lambs in 2012 (Kissell 2013). Schoenecker (2004) reported 39 rams:100 ewes in 2000, 58 rams:100 ewes in 2001, and 69 rams:100 ewes in 2002 from ground and fixed-wing aerial surveys. The feral horse population was approximately 170 individuals (J. Bybee, Bureau of Land Management, personal communication) and exceeded the management target of 90–120 individuals (Bureau of Land Management 2009).

Methods

We captured resident adult cougars using hounds (Hornocker 1970) or box traps (Shuler 1992) between January 2011 and March 2012. We immobilized cougars with ketamine hydrochloride and xylazine hydrochloride, and fitted them with Telonics GEN3 GPS collars (Telonics Inc., Mesa, AZ). We programmed the collars to record 8 GPS locations per 24-hour period with 7 locations recorded at 2-hour intervals during nocturnal periods (1800–0600) and 1 location recorded during diurnal periods (0601–1759). We retrieved collars following automatic drop-off; the drop-off was scheduled at the end of the field study (August 2012). Animal capture and handling protocols were reviewed and approved by the Institutional Animal Care and Use Committees of the National Wildlife Research Center (QA-1811) and Utah State University (#1516).

The GPS collars transferred their GPS locations through the Argos satellite system to the Argos Processing Center (CLS America Inc., Lanham, MD). Every three days, we downloaded the data from the Argos website and converted it into Universal Transverse Mercator (UTM) coordinates with the Telonics Data Converter (Telonics Inc., Mesa, AZ). Not all locations were successfully transmitted while the collars were on the animals. We acquired remaining locations from the collars at the time of an animal's death, or after the pre-programmed collars dropped off. We used a data screening protocol to minimize error by eliminating all locations within 48 hours of capture events or with only 2D accuracy. Home ranges of individual

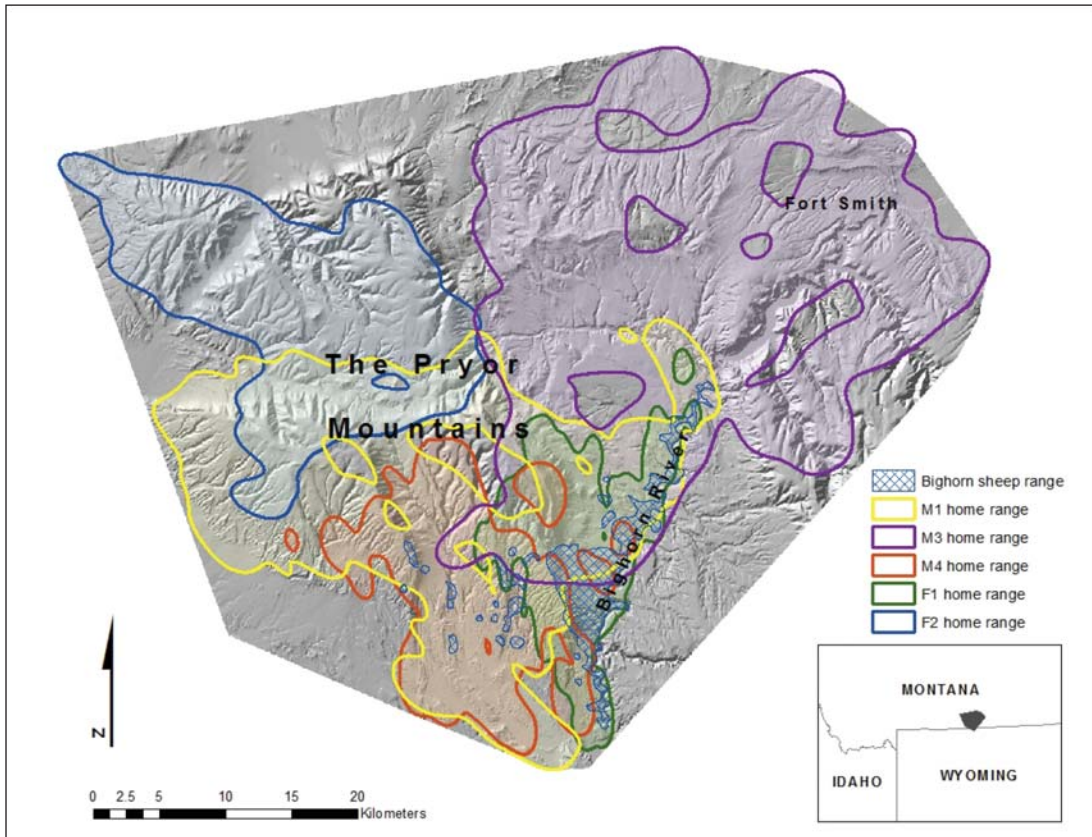


Figure 2. The 2553 km² study area in the southern Pryor Mountains of Wyoming and Montana with 95% KDE home ranges of the 5 radio-collared cougars and the range of bighorn sheep on the study area.

cougars (Figure 2) were developed using 95% kernel density estimators (Beyer 2012).

Cougars typically stay and feed on their kills for several days, thereby cougar kill sites can be identified by spatially and temporally clustered GPS locations (Beier et al. 1995, Anderson and Lindzey 2003). We examined our location data sequentially to identify clusters. Following Anderson and Lindzey (2003), we initially defined a cluster as ≥ 2 locations within 200 m during the same or consecutive nights. Because we were not having success finding prey remains at 2–3-location clusters, we modified our cluster definition to ≥ 4 locations within 150 m during the same or consecutive nights. To decrease our likelihood of missing a kill of a neonate ungulate, we still investigated 2–3-location clusters between May 23 and September 30 when fawns and lambs would

be small and consumed quickly. We visited these clusters and, if we did not find a kill immediately, searched a circle at least 100 m in diameter centered on the mean UTM's of the GPS locations of the cluster. We searched in concentric circles approximately 5–10 m apart depending upon visibility, with the goal of visually examining all of the ground within the search area. When we found prey remains, we recorded species, age, and sex. We divided prey into juvenile (< 1 -yr) or adult (≥ 1 -yr) classes based on dentition. We classified prey by size class as small (< 40 kg), medium (40–90 kg), or large (> 90 kg) based on typical biomass of the species. The small prey class consisted of mule deer fawns, bighorn sheep lambs, raccoon, coyote, beaver, porcupine, red fox, striped skunk, American marten, and mallard. Medium prey included mule deer does, bighorn

sheep ewes, and cougar, while large prey consisted of mule deer bucks, bighorn sheep rams, and elk. When sex or species could not be determined by physical characteristics, muscle, hide, or hair samples were collected and sent to the National Wildlife Research Center (Fort Collins, CO) for analysis of DNA using a polymerase chain reaction (Yamamoto et al. 2002). We examined sites for evidence of black bear activity (scat or tracks) within 100 m of prey remains. If black bear sign was of a similar age to the cluster, we considered the cluster to have been detected and possibly usurped by a black bear.

We determined composition of cougar kills as the percent frequency of total prey by species. We used Pearson's chi-square tests to determine statistically significant ($P \leq 0.10$) differences in the proportion of prey species (deer, sheep, other), prey size classes (small, medium, or large), or sex-age classes of mule deer (< 1-yr old, adult female, adult male) killed as a function of cougar sex and season. Due to small sample sizes, we were unable to examine the effect of cougar social classes upon prey composition beyond cougar sex. We also tested for increased proportions of sex-age classes of mule deer killed by all cougars during their vulnerable seasons as predicted by the reproductive vulnerability hypothesis (bucks: September–December, does: April–June, juveniles: June–August). We were unable to consider the sex-age classes of bighorn sheep killed in our analyses due to small sample sizes.

We conducted a winter aerial helicopter survey to determine herd size and composition of the ungulate species in the study area. We surveyed the study area as we initially defined it. This boundary, however, turned out to be a subset of the ultimate study area which was based on the home ranges of collared cougars (Figure 1). We divided the study site into 2.59 km² quadrats and randomly selected and surveyed approximately 10% of these quadrats. Perimeters of the quadrats were flown initially to 'capture' any animals leaving the quadrats due to the survey disturbance. Several transect lines were flown within each quadrat to ensure thorough coverage (Gill 1969). Transect spacing within the quadrat depended upon vegetative cover and density with spacing being closer

in quadrats with dense vegetation or tree cover. Counts of ungulate species, their age and sex, and a relative measure of habitat openness (one = most open, three = most visually obscured) was recorded for each quadrat. Helicopter aerial surveys, while generally more accurate than ground surveys, are subject to bias associated with imperfect detection (Caughley 1974). To address this, we used existing sightability correction factors from prior surveys conducted under similar conditions in similar habitats to derive population estimates (Keegan et al. 2011, Flesch and Garrott 2013).

Relative to our mule deer and bighorn population estimates, we looked for statistically significant ($P \leq 0.10$) selection of prey species (mule deer, bighorn) and of different demographic classes of mule deer killed by cougars with Pearson's χ^2 tests. We compared the proportion of species, or sex-age classes of mule deer derived from our aerial surveys (i.e., expected proportion) to the observed counts of animals killed by cougars. Because our aerial surveys were conducted on a subset of what would ultimately become our study area, we only included those mule deer and bighorn sheep kills within the area covered by the aerial survey.

To determine predation rates, we calculated the inter-kill interval between the first GPS location at a confirmed kill site cluster and the first GPS location at the next confirmed kill site cluster. In two instances we were unable to visit a cluster due to safety or logistical issues, so we eliminated the interval in which it occurred (White 2009, Cavalcanti and Gese 2010). We only used intervals during which the collar had a $\geq 45\%$ fix rate (Knopff et al. 2009) of nocturnal locations. We eliminated any intervals for which a cougar was collared ≤ 4 weeks in a given season and social class (Knopff et al. 2010), intervals in which we disturbed cougars on kills, or when they scavenged our bait carcasses. We used a natural log transformation to normalize the data and then analyzed predation rates with a one-way ANOVA to examine significant differences ($P \leq 0.10$) between the means of predation rates between individual cougars, social classes of cougars, by season, and between prey size classes. To examine if possible kleptoparasitism by black bears influenced predation rates, we used a square

root transformation to normalize the data and then tested for significant differences ($P \leq 0.10$) in inter-kill intervals following kills with and without indications of possible kleptoparasitism.

To determine handling time (i.e., the amount of time a cougar spent on a kill), we subtracted the time of the last nocturnal location at a kill cluster from the first nocturnal location at the same cluster. To be consistent with the predation rate analysis, we removed any clusters for which a cougar was collared ≤ 4 weeks in a given season and social class. We also removed two clusters at which a cougar consumed two kills simultaneously, dividing her time between them. We used a natural log transformation to normalize the data and then analyzed handling times with a one-way ANOVA to examine differences in handling times between individual cougars, social classes of cougars, seasons, and prey size classes.

Results

Cougar Capture and GPS Collaring

We captured and monitored six cougars (two adult females, three adult males, one sub-adult male) in the study area (Table 1). We spent a minimum of 188 days attempting to locate and capture cougars, and believe we captured and collared all resident adult cougars within the study area; investigations of cougar sign invariably led back to already-collared, or shortly-thereafter collared, cougars. Cougars were monitored between 98 and 416 days ($\bar{x} = 254.2 \pm 129.0$ SD) for a total

of 1525 cougar-days. Over that period of time, we acquired between 665 and 2664 locations per cougar ($\bar{x} = 1644.7 \pm 772.7$ SD) for a total of 9868 locations. The overall fix rate for the GPS collars was 80.9%. Individual fix rates for the GPS collars varied between 76.0% and 89.9% (Table 1). We identified 383 clusters and searched 381 of them for kills; 190 clusters had kills and 10 had 2 prey items for a total of 200 kills. Clusters were searched within an average of 68 (± 94 [SD]) days after initiation; 58% of clusters were searched within 6 weeks of cluster initiation. Delays in checking some clusters were due to access to private and tribal lands, snowfall covering prey remains, and limited personnel in the field. Black bears visited 18 clusters with kills (9.5%); 15 of those clusters (7.9%) were visited by bears soon enough to consider them kleptoparasitism events.

Composition of Cougar Kills

Of the 190 kill sites searched, mule deer were most commonly detected (71.5%), with bighorn sheep detected at the second highest frequency (8.0%; Table 2). We also found a single elk (*Cervus canadensis*) kill; the only indication we had of elk in the area. There was a variety of non-ungulate prey including beavers, raccoons, porcupines, and coyotes (Table 2). We found single instances of predation upon a striped skunk (*Mephitis mephitis*), American marten (*Martes Americana*), mallard (*Anas platyrhynchos*), and a red fox. Also of note was a GPS-collared female cougar that was killed and likely consumed by a GPS-collared

TABLE 1. Social class, monitoring duration, GPS location acquisition rates, number of kills, and predation rates of GPS-collared cougars, Pryor Mountains of Wyoming and Montana, 2011–2012. Notes: AF = solitary adult female, AFK = adult female with kittens, AM = adult male, SM = subadult male. M2 was F1's dependent kitten; we only analyzed kills from the period after he dispersed.

Cougar ID	Social class ¹	Days monitored	Number of GPS locations	Acquisition rate	Number of kills	Number of kill intervals used	Predation rates (days) \pm SD
F1	AF/AFK	416	2664	80.0%	67	52	5.95 (\pm 3.41)
F2	AFK	210	1510	89.9%	33	29	6.86 (\pm 3.86)
M1	AM	404	2456	76.0%	38	28	9.61 (\pm 5.04)
M2	SM	98	665	84.8%	6 ²	0	–
M3	AM	230	1450	78.8%	30	25	7.62 (\pm 4.06)
M4	AM	167	1123	84.1%	26	21	7.14 (\pm 4.10)

TABLE 2. Number of prey killed by each cougar in the Pryor Mountains of Wyoming and Montana, 2011–2012. Percentage of total kills for each cougar is indicated in parentheses.

Prey Species	F1	F2	M1	M2	M3	M4	Total
Mule deer	47 (70.1)	30 (90.9)	27 (71.1)	3 (50.0)	14 (46.7)	22 (84.6)	143 (71.5)
Deer (spp. unknown)	0	0	0	0	1 (3.3)	0	1 (0.5)
Bighorn sheep	16 (23.9)	0	0	0	0	0	16 (8.0)
Unknown (mule deer or bighorn sheep)Elk	1 (1.5) 0	0 0	0 1 (2.6)	0 0	0 0	0 0	1 (0.5) 1 (0.5)
Coyote	1 (1.5)	1 (3.0)	1 (2.6)	0	3 (10.0)	0	6 (3.0)
Raccoon	1 (1.5)	0	3 (7.9)	0	0	3 (11.5)	7 (3.5)
Beaver	0	0	3 (7.9)	0	9 (30.0)	1 (3.8)	13 (6.5)
Porcupine	0	1 (3.0)	1 (2.6)	3 (50.0)	2 (6.7)	0	7 (3.5)
Red fox	0	1 (3.0)	0	0	0	0	1 (0.5)
Striped skunk	0	0	1 (2.6)	0	0	0	1 (0.5)
American marten	1 (1.5)	0	0	0	0	0	1 (0.5)
Mallard	0	0	1 (2.6)	0	0	0	1 (0.5)
Cougar	0	0	0	0	1 (3.3)	0	1 (0.5)
Totals	67	33	38	6	30	26	200

male cougar. Despite their presence in the study area, cougars killed no feral horses or domestic livestock. Of the mule deer kills where we could identify age, 31.6% were juveniles and 68.4% were adults. Of the mule deer kills where we could identify sex, 37.5% were male and 62.5% were female. Bighorn sheep kills with identifiable age were 25% juveniles and 75% adults. Of the bighorn sheep kills where we could identify sex, 53.3% were male and 46.7% were female.

There was a significant difference between the proportion of prey species killed ($\chi^2 = 35.38$, $df = 2$, $P < 0.001$) by female and male cougars. Female cougars killed 16 (16.2%) bighorn sheep, 77 (77.8%) deer, and 6 (6.1%) other prey, while males killed 67 (67.0%) deer and 33 (33.0%) other prey. There was a significant difference in the proportion of prey species between the seasons ($\chi^2 = 5.55$, $df = 2$, $P = 0.062$). In summer, cougar prey consisted of 4 (4.0%) bighorn sheep, 79 (78.2%) deer, and 18 (17.8%) other prey, while in winter the composition of prey was 12 (12.2%) bighorn, 65 (66.3%) deer, and 21 (21.4%) other prey.

We found that female cougars killed proportionally more adult female mule deer, whereas male cougars killed more juvenile mule deer ($\chi^2 = 5.11$,

$df = 2$, $P = 0.078$). Among mule deer killed by female cougars, 23 (46.9%) were adult females, 11 (22.4%) were adult males, and 15 (30.6%) were juveniles. Among mule deer killed by male cougars, 8 (22.9%) were adult females, 12 (34.3%) were adult males, and 15 (42.9%) were juvenile mule deer. We found no significant difference in the proportion of sex-age classes of mule deer killed between seasons ($\chi^2 = 0.62$, $df = 2$, $P = 0.734$). We did not detect significant differences in the proportions of sex-age classes of mule deer killed during their vulnerable periods as predicted by the reproductive vulnerability hypothesis.

We found that prey size was more evenly distributed for female cougars, but males killed proportionally more small prey ($\chi^2 = 15.52$, $df = 2$, $P < 0.001$). Kills by female cougars were composed of 16 (23.5%) large, 27 (39.7%) medium, and 25 (36.8%) small prey, while kills by male cougars were 13 (19.1%) large prey, 9 (13.2%) medium prey, and 46 (67.6%) small prey. There was no influence of season on the proportion of prey size classes killed ($\chi^2 = 0.51$, $df = 2$, $P = 0.777$) with small prey being found at 34% of summer kill sites and 37% small prey found at winter kill sites.

TABLE 3. Aerial ungulate survey data from the Pryor Mountains of Wyoming and Montana, January 2012. Raw counts of ungulates were corrected for sightability bias with sightability correction factors.

	Sightability factor	Population segment	Raw count	Corrected count	Number per km ²	Total population estimate	Total herd estimate
Bighorn high visibility	0.90	All	0	0.00	0.00	0	67
Bighorn intermediate visibility	0.70	All	5	7.14	0.07	67	
Mule deer high visibility	0.75	Bucks	3	4.00	0.04	38	1159
		Does	7	9.33	0.09	88	
		Fawns	2	2.67	0.03	25	
Mule deer intermediate visibility	0.67	Bucks	4	5.97	0.06	56	
		Does	55	82.09	0.83	772	
		Fawns	7	10.45	0.11	98	
Mule deer low visibility	0.23	Bucks	1	4.35	0.04	41	
		Does	1	4.35	0.04	41	
		Fawns	0	0.00	0.00	0	

Ungulate Surveys

We flew 38 quadrats on January 12 and 20, 2012. Weather conditions prevented us from completing the survey in a shorter time frame. While the 8 days between surveys may have presented a problem in our estimates, we flew 24 quadrats on January 12, then 14 quadrats on January 20. During the first survey, we counted 78 deer in 7 quadrats representing 97.5% of all deer counted; only 2 deer were counted in second survey. Thus most of our survey counts on mule deer were completed in the first day of the survey. Similarly, the 5 bighorn sheep counted were all observed in 1 quadrat during the first survey. Thus it appears that the second day of surveying did not cause recounts of animals observed during the first survey. Raw counts revealed 5 bighorn sheep, 80 mule deer, and no feral horses. After applying sightability correction factors, we calculated population estimates of 67 (90% CI: 3–174) bighorn sheep and 1159 (90% CI: 389–1929) mule deer (Table 3). The confidence intervals were very large mainly due to only 8 (21%) of 38 quadrats had mule deer sighted, and only 1 (3%) of 38 quadrats had observations of bighorn sheep. The estimated fawn:doe ratio was 13.7 fawns:100 does. We did not estimate the ewe:lamb ratio because we could not distinguish between the sexes of all adult sheep and we did not observe any lambs. Our density estimates in the aerial survey area were 1.25 mule deer/km² and 0.07 bighorn sheep/km².

Prey Selection

A total of 122 ungulates were killed within the aerial survey area. Comparing these kills with our mule deer and bighorn sheep population estimates (i.e., available), we found cougars disproportionately killed bighorn sheep ($\chi^2 = 13.74$, $df = 1$, $P < 0.001$). However, all of these bighorn sheep kills were attributed to a single female cougar. We also found cougars selected for certain sex-age classes of mule deer when making kills ($\chi^2 = 86.23$, $df = 2$, $P < 0.001$). In comparison to availability as determined from the aerial survey, cougars selected for adult male (killed: 28.8%, available: 11.6%) and juvenile (killed: 40.7%, available: 10.6%) mule deer, and selected against adult females (killed: 30.5%, available: 77.8%).

Predation Rates

We retained 155 inter-kill intervals with which to analyze predation rates. To examine inter-kill intervals with respect to prey size class, we eliminated 54 of these intervals because, although we knew the species of some ungulate remains, without sex or age we were unable to assign them to a size class. The mean predation rate was 7.21 ± 0.33 (SE) days. Predation rates differed among individual cougars (Figure 3A) from 5.95 ± 0.47 to 9.61 ± 0.95 days ($F_{4, 150} = 3.20$, $P = 0.015$), and between social classes (Figure 3B) of cougars with adult females with kittens having the shortest intervals ($\bar{x} = 6.01 \pm 0.42$ days), adult males

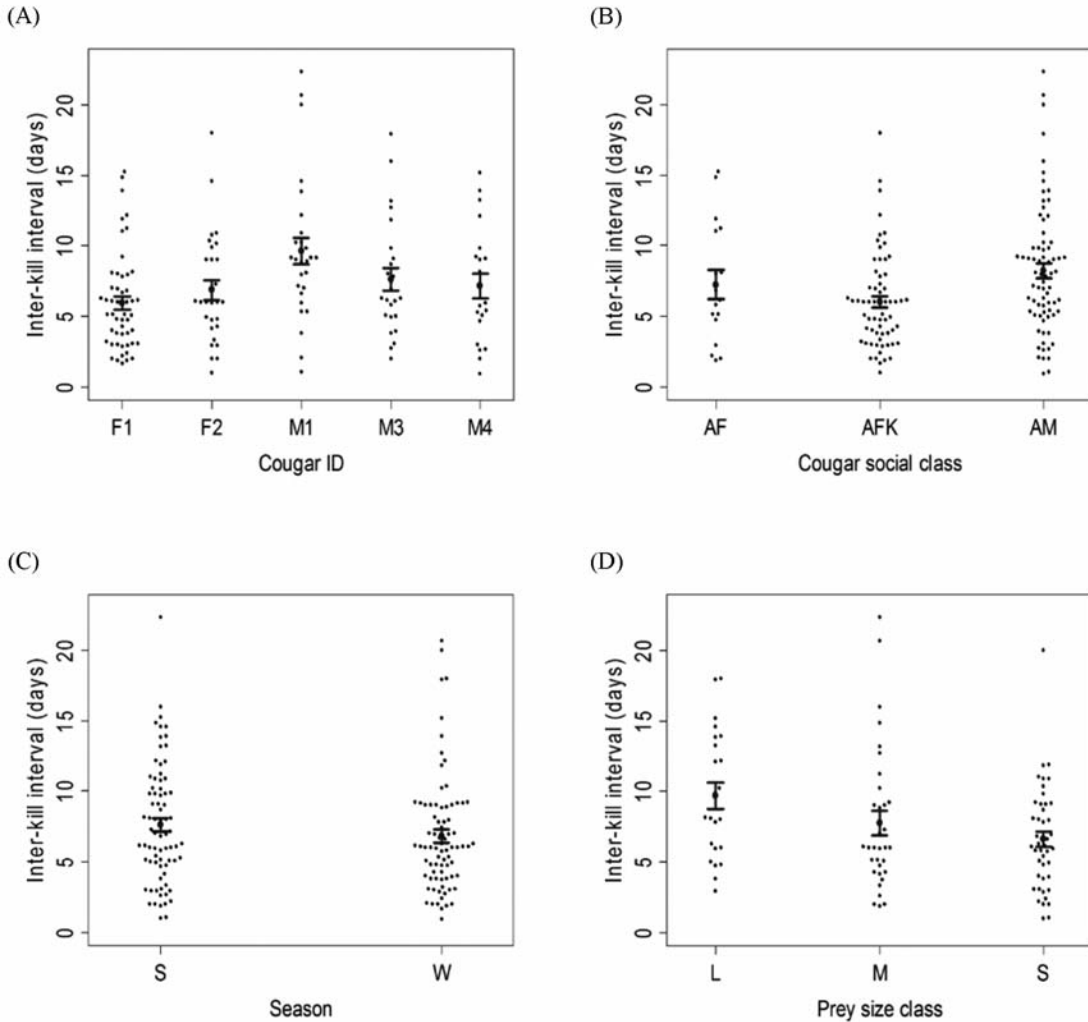


Figure 3. Predation rates of (A) individual cougars, (B) cougar social classes (AF: adult female, AFK: adult female with kittens, AM: adult male), (C) seasons (S: summer, W: winter), and (D) prey size classes (L: large, M: medium, S: small), Pryor Mountains of Wyoming and Montana, 2011–2012. Means and standard errors are indicated by the bars.

having the longest intervals ($\bar{x} = 8.24 \pm 0.53$ days), and solitary adult females having intermediate intervals ($\bar{x} = 7.25 \pm 1.04$ days; $F_{2,152} = 1.30$, $P = 0.016$). Predation rates did not differ by season ($F_{1,153} = 1.23$, $P = 0.270$; Figure 3C). Predation rates differed based upon the size of the prey item ($F_{2,98} = 3.86$, $P = 0.024$; Figure 3D). The shortest inter-kill intervals followed the consumption of the smallest prey ($\bar{x} = 6.61 \pm 0.54$ days), mid-length inter-kill intervals followed the killing of medium size prey ($\bar{x} = 7.75 \pm 0.88$ days), and cougars went the longest between kills after killing the large-

est prey ($\bar{x} = 9.68 \pm 0.94$ days). We detected no difference between inter-kill intervals following potential kleptoparasitism events and those with no indication of kleptoparasitism by black bears.

Handling Time

We retained 166 kills to examine with respect to handling time. With respect to prey size class, we only used 104 kills. The mean handling time was 2.52 ± 0.16 (\pm SE) days. Handling times differed among individual cougars (Figure 4A) from 1.52 ± 0.21 to 3.11 ± 0.36 days ($F_{4,161} = 3.34$, $P = 0.012$).

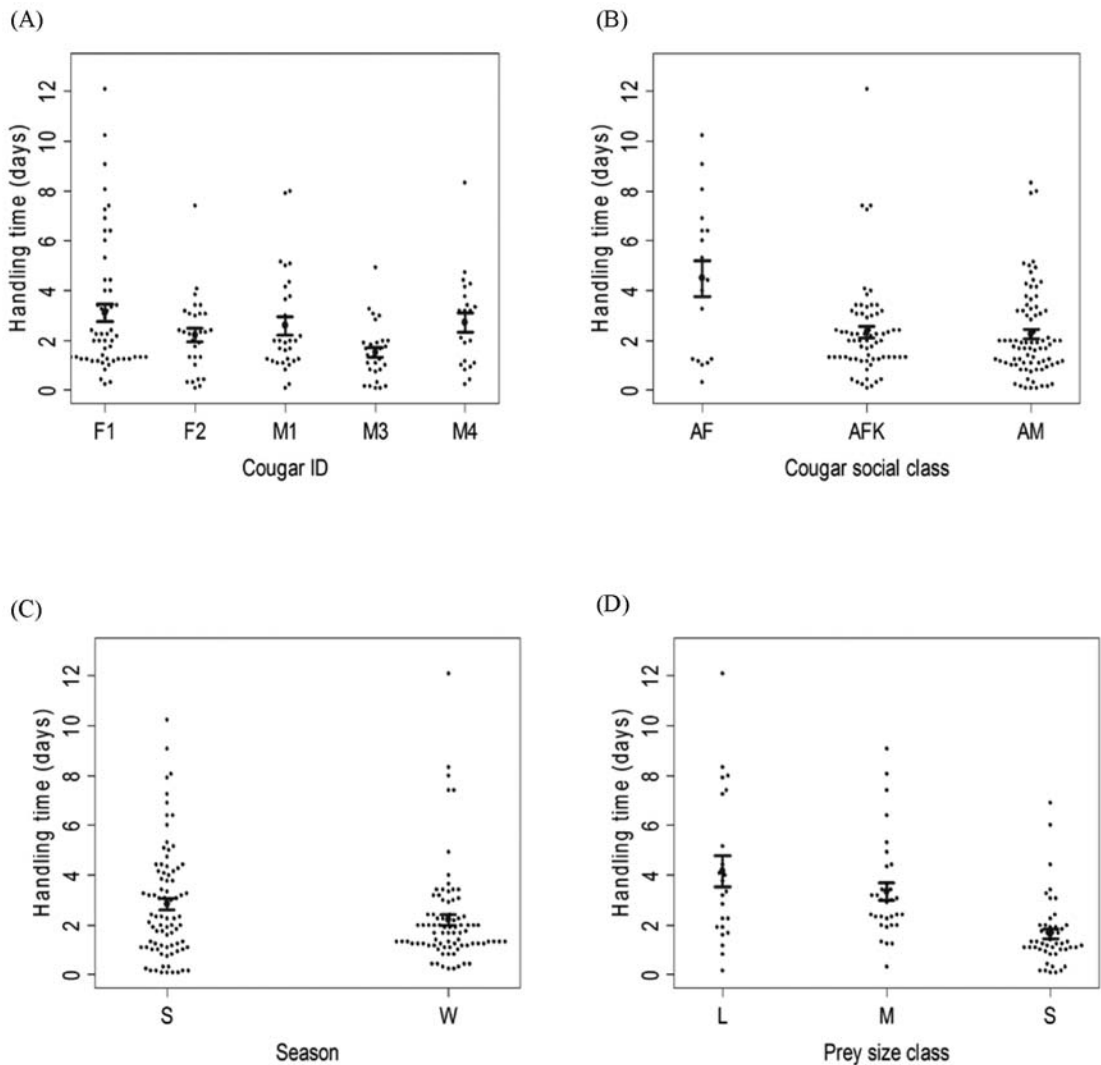


Figure 4. Handling times of (A) individual cougars, (B) cougar social classes (AF: adult female, AFK: adult female with kittens, AM: adult male), (C) seasons (S: summer, W: winter), and (D) prey size classes (L: large, M: medium, S: small), Pryor Mountains of Wyoming and Montana, 2011–2012. Means and standard errors are indicated by the bars.

Handling times also differed by social classes ($F_{2,163} = 5.93$, $P = 0.003$; Figure 4B). Adult males had the shortest handling times ($\bar{x} = 2.24 \pm 0.20$ days), while solitary adult females spent the most time on their kills ($\bar{x} = 4.48 \pm 0.72$ days), and adult females with kittens had handling times similar to adult males ($\bar{x} = 2.34 \pm 0.24$ days). Handling times did not differ by season ($F_{1,164} = 2.02$, $P = 0.157$; Figure 4C). Handling times also differed by prey size class ($F_{2,101} = 17.60$, $P < 0.001$; Figure 4D).

The smallest prey were only handled for 1.64 ± 0.20 days, while medium prey were handled for a mean of 3.35 ± 0.35 days, and the largest prey were handled for a mean of 4.15 ± 0.63 days.

Discussion

Congruent with other studies (e.g., Ackerman et al. 1984, Logan and Irwin 1985, Anderson and Lindzey 2003, Mitchell 2013), this cougar population subsisted primarily on the main resident ungulate

species on the study area, mule deer. Bighorn sheep served as a major secondary prey source for one individual. The single elk that was killed was probably a lone individual that had travelled into the study area. Cougars incorporated an important amount (19%) of non-ungulate prey into their diets, including a notable amount of beavers which represented 30% of the kills made by one male cougar. In most cases, the consumption of prey was near complete (in some cases, probably due to some consumption by scavengers) and, in the case of ungulate prey, often just the skeleton, hide, and rumen remained for examination. Due to this lack of evidence, we possibly classified some scavenging events as kills. We observed five instances of scavenging in our study site in which cougars scavenged deer carcasses that we had brought in for trapping efforts. Our study design was also biased towards the detection of larger kills. We could have missed smaller prey that were either consumed within the < 2 hours between locations, or entirely consumed and thereby classified as non-kill clusters (Cavalcanti and Gese 2010).

Male cougars killed and consumed more items from the other prey species class; but this was mainly due to one male killing many beavers. In contrast, one female was responsible for all of the bighorn sheep killed which composed 16.2% of the diet of female cougars. Interestingly, while this female's territory had the greatest overlap with bighorn sheep range, three of the four other cougars spent significant amounts of time in bighorn sheep habitat without killing them (Figure 2). Similar studies have also shown certain cougars may develop individual prey preferences (Elbroch and Wittmer 2013). Cougars specializing on bighorn sheep have been observed to sometimes have a profound impact upon a small bighorn population (Ross et al. 1997, Logan and Sweanor 2001).

More bighorn sheep and other prey were killed in winter and more mule deer were killed in summer. While this might appear to suggest an increased vulnerability of neonate deer to cougar predation (Knopff et al. 2010, Mitchell 2013), we found no increase in juvenile mule deer among cougar prey following the birth pulse.

Females killed proportionally more medium-sized and less small-sized prey than males; but we

again emphasize that one male was responsible for many beaver kills. We found that the proportion of large-sized prey killed by males and females did not differ contrary to the differential prey use hypothesis in which the sexual dimorphism of cougars leads to females generally taking smaller prey than males presumably because males are more capable of subduing larger prey (Ross and Jalkotzy 1996, Anderson and Lindzey 2003, White et al. 2011). However, our study area lacked populations of larger prey such as elk and moose (*Alces alces*). Reduced predation of small-sized prey by female cougars may be due to their increased energetic needs associated with raising kittens. The time and effort needed to hunt and kill small prey may not meet the energetic demands of family groups. We also may have missed finding small prey of female cougars because they would have been consumed faster and more completely by females associated with a family group. Our finding that males killed more small prey than females is in contrast to some previous studies (Anderson and Lindzey 2003, Knopff et al. 2010). This may be a unique strategy of the male cougars in our study area if they are prey switching and supplementing their diets with small prey due to a low density mule deer population, or an individual selectively preying on small prey (i.e., one male cougar killing many beaver).

Female cougars killed proportionally more mule deer does while male cougars killed more bucks and juveniles. In contrast to our findings amongst all prey killed, these findings amongst just mule deer kills could support the differential prey use hypothesis. We did not find that cougars selected differently for mule deer sex-age classes between seasons.

Our surveys showed that the mule deer population had a relatively low density with low recruitment. A review of mule deer densities (Innes 2013) reported mule population densities between 0.1–29 deer/km². Our density of 1.25 deer/km² falls on the lower end of this spectrum. For comparison, in the prairie breaks and badlands of Montana, densities ranged from 1.4–4.4 deer/km² (Hamlin and Mackie 1989). About 16 deer/km² were found in the mountain-foothill areas in Utah (Robinette et al. 1977), while the moun-

tainous pinyon pine-Utah juniper (*Pinus edulis*, *Juniperus osteosperma*) Piceane Basin of Colorado supported 14–24 mule deer/km² (Unsworth et al. 1999). Our fawn:doe ratio of 13.7:100 is also on the low end of reported ranges. In their review of mule deer population demographics, Unsworth et al. (1999) reported fawn:doe ratios of 42–48:100 in Colorado, 49–77:100 in Idaho, and 25–51:100 in Montana. We did not research the mule deer population directly, but a myriad of factors could be limiting mule deer density and recruitment including additional predation by coyotes and black bears, severe weather, human hunting, disease, competition with native and non-native ungulates, and habitat quality (Unsworth et al. 1999, Ballard et al. 2001).

We observed selection by cougars for bighorn sheep over mule deer, but all of these bighorn were killed by a single cougar. While we only documented this behavior by a single cougar, it is reasonable to assume selection for bighorn sheep will develop again based on past instances of cougar predation in BCNRA and the intersection of cougar and bighorn habitat. Additionally, the mule deer herd is sympatric with the bighorn sheep herd and during times when the deer herd is declining, it is possible predation on bighorn sheep will increase through prey switching (Kamler et al. 2002, Ruth and Murphy 2010a). Conversely, cougar predation on bighorn sheep could increase through apparent competition if the mule deer population increases (Roemer et al. 2002, DeCesare et al. 2010). Considering 16 bighorn were killed over a 416-day monitoring period by a single cougar, predation could be influencing this small bighorn population. Information on the sex-specific and age-specific vital rates of this bighorn sheep population (e.g., fecundity, recruitment, survival, etc.) in combination with the sex-age classes of all killed sheep would be needed to further understand the effect of this cougar's predation upon this population's long-term growth rate. However, our data suggest that a single cougar could contribute to a bighorn sheep decline. At the conclusion of our study, the female cougar responsible for the bighorn sheep kills had died, and to our knowledge, cougar predation upon bighorn had ceased. This situation highlights the

unpredictable and erratic impacts of even a single individual that selectively preys upon a small population of a rare prey species. Similarly, one cougar was responsible for killing 9% of a bighorn sheep population during a single winter in Alberta (Ross 1997). However, it is important to note that bighorn sheep population growth rates are affected by factors aside from cougar predation including direct and indirect interspecific competition, other predator species (e.g., black bear, golden eagle [*Aquila chrysaetos*], coyote), disease, selenium levels, and forage availability (Risenhoover et al. 1988, Goodson et al. 1991, Sawyer et al. 2002, McKinney et al. 2006).

We observed cougars killing disproportionately more adult male and juvenile mule deer, and less adult female mule deer than were available to them. A lack of selection for female mule deer should be less limiting to the deer population if they are the primary reproductive class but it is difficult to understand the impact of cougar predation on mule deer without understanding the specific vital rates and additional pressures to this population (Ballard et al. 2001).

Our mean predation rates ranged from 6.01 ± 0.42 (\pm SE) to 8.24 ± 0.53 days between social classes of cougars. These rates were within the previously reported ranges of 5.4–15.2 days (Anderson and Lindzey 2003, Mattson et al. 2007, Knopff et al. 2010, Ruth et al. 2010, Mitchell 2013). Other studies have had larger prey (i.e., elk, moose) and some included predation rates for sub-adults which may exhibit longer predation intervals between kills than adults. The predation rates we observed were on the lower end of this spectrum. As expected, female cougars with dependent kittens had the highest predation rates, consistent with the greater energetic requirements of a family group (Laundre 2005). Adult males had the lowest predation rates. As we also hypothesized, the longest kill intervals followed predation of a large prey item. The shortest intervals followed kills of smaller prey. We did not detect shorter inter-kill intervals following kills with evidence of kleptoparasitism, but our small sample size of kills with evidence of kleptoparasitism may have prevented detecting this effect.

Adult males were the social class with the shortest handling times, while solitary females displayed the longest handling time. This is consistent with findings of Mattson et al. (2007) that adult males have a life strategy focused on travelling long distances quickly and spending less time on kills, with the hypothesis that males are maximizing reproductive opportunities. Also expected was that cougars handled larger prey for longer periods of time than smaller prey. We had expected shorter handling times in summer than winter due to increased spoilage, scavenging, and displacement by bears, but we did not find any difference.

Our ungulate survey suggested low density and low recruitment of mule deer (Innes 2013). Increased predation upon a secondary species, like this bighorn population, is consistent with the prey switching that can occur when a primary prey species, mule deer in this case, experiences a population decline. While one approach would be to investigate ways to enhance the mule deer population, we recommend this approach with caution, as the relationships between two prey species' densities and their predator can be complicated and shift over time. Another approach might be to examine those habitat factors whose alteration could reduce predation pressures on bighorn sheep. Whether cougar predation is additive or compensatory to either the bighorn sheep or mule deer population is unknown as we did not have information on cause-specific mortality of these species, only predation rates. In southeastern Idaho, Hurley et al. (2011) reported cougar predation was mostly additive among mule deer in the short term as evidenced by increased survival of adults and fawns following mountain lion removal. However, they also reported that cougar predation appeared to be compensatory in the long term as evidenced that when cougar predation was reduced through cougar removals, natural causes of mortality increased (Hurley et al. 2011).

Regardless, managers should be aware that maintaining small isolated populations of ungulates (in this case, bighorn sheep) is often difficult and costly, and may require management interventions including translocations of sheep, habitat manipula-

tions to increase forage and reduce predation risk, or even focused removal of individual mountain lions that are specializing on the bighorn sheep. This last tactic should be approached with caution as lethal removals can present special challenges. If neither cougars nor their rare prey are radio-collared, capturing an offending individual will be extremely difficult or impossible. The accidental removal of a cougar that does not prey upon bighorn sheep may then open up a territory to an unknown cougar who may engage in sheep predation (Ernest et al. 2002, Knopff and Boyce 2007). Further research will benefit from a better understanding of what drives individual cougars to select for a secondary species and whether this behavior is passed on to their young. An alternative approach to reducing predation upon bighorn sheep may be to modify habitat in areas where cougars and sheep overlap to decrease those factors associated with predation of bighorn sheep, such as low horizontal visibility (Blake 2014). We note that feral horses were absent from the prey killed by cougars during this study. While there was some evidence cougars have preyed on foals before in the area, our study showed cougar predation cannot be consistently counted on to limit this horse population and continued management will be necessary to maintain this population within herd objectives.

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