

# Cougar Prey Selection in a White-Tailed Deer and Mule Deer Community

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**ABSTRACT** Widespread mule deer (*Odocoileus hemionus*) declines coupled with white-tailed deer (*O. virginianus*) increases prompted us to investigate the role of cougar (*Puma concolor*) predation in a white-tailed deer, mule deer, and cougar community in northeast Washington, USA. We hypothesized that cougars select for and disproportionately prey on mule deer in such multiple-prey communities. We estimated relative annual and seasonal prey abundance (prey availability) and documented 60 cougar kills (prey usage) from 2002 to 2004. White-tailed deer and mule deer comprised 72% and 28% of the total large prey population and 60% and 40% of the total large prey killed, respectively. Cougars selected for mule deer on an annual basis ( $\alpha_{md} = 0.63$  vs.  $\alpha_{wt} = 0.37$ ;  $P = 0.066$ ). We also detected strong seasonal selection for mule deer with cougars killing more mule deer in summer ( $\alpha_{md} = 0.64$ ) but not in winter ( $\alpha_{md} = 0.53$ ). Cougars showed no seasonal selection for white-tailed deer despite their higher relative abundance. The mean annual kill interval of 6.68 days between kills varied little by season (winter = 7.0 days/kill, summer = 6.6 days/kill;  $P = 0.78$ ) or prey species (white-tailed deer = 7.0 days/kill, mule deer = 6.1 days/kill;  $P = 0.58$ ). Kill locations for both prey species occurred at higher elevations during summer months (summer = 1,090 m, winter = 908 m;  $P = 0.066$ ). We suspect that cougars are primarily subsisting on abundant white-tailed deer during winter but following these deer to higher elevations as they migrate to their summer ranges, resulting in a greater spatial overlap between cougars and mule deer and disproportionate predation on mule deer. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):99-106; 2008)

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Within the last 10 years, a major change in the species distribution and abundance of deer in several areas in western North America has taken place. Mule deer (*Odocoileus hemionus*) populations have declined (Workman and Low 1976, Bleich and Taylor 1998, Gill 1999), whereas white-tailed deer (*Odocoileus virginianus*) have increased in numbers and expanded in range (Swanson 1950, Soper 1964, Spalding 1968, Kamps 1969, Livingston 1987). Although white-tailed deer were once rare in eastern Washington (Dalquest 1948), USA, they now outnumber mule deer 2:1 to 4:1 in our study area (Cruickshank 2004). Reasons for this shift in species composition are presently unclear, but investigators suggest that habitat change (Roseberry and Woolf 1998, Gill 1999), competition (Anthony and Smith 1977, Stewart et al. 2002), climate (Unsworth et al. 1999b), or predation (Bleich and Taylor 1998, Ballard et al. 2001, Robinson et al. 2002) may be responsible.

As part of a larger study looking into mule deer declines and white-tailed deer increases, our objectives were to investigate the influence of cougars (*Puma concolor*) on local deer populations in Northeast Washington and to determine whether predation is acting as a stabilizing density

dependent (proportional prey switching) or destabilizing density-independent (disproportional prey selection) force on prey populations in the area. Specifically, we sought to 1) estimate relative proportions of white-tailed deer and mule deer available to cougars annually and seasonally, 2) estimate the relative proportions of cougar-killed white-tailed and mule deer, 3) estimate annual and seasonal selection (use vs. availability) for white-tailed deer and mule deer, and 4) estimate species-specific cougar kill rates for white-tailed and mule deer.

## STUDY AREA

Our 3,800-km<sup>2</sup> study area in northeastern Washington extended across a patchwork of federal, state, and privately owned lands west from the Okanogan-Ferry County line to the Columbia River and south from the Canadian-United States border to the Colville Indian Reservation. The study area was part of the Okanogan Highlands physiographic province, a glacially subdued mountainous region (400–2,130 m elevation) occupying a transitional position between the east-slope Cascades and northern Rocky Mountain forests (Bailey et al. 1994). Upland canopy species included Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Most of the annual precipitation (46 cm) fell as snow and mean temperatures ranged from –6° C in

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January to 21° C in July. An average of 136 cm of snow fell from mid-November to mid-April annually.

White-tailed deer and mule deer were the most abundant and second most abundant ungulates in the region, respectively (Cruickshank 2004). Moose and elk were also present in very low densities (H. S. Robinson, Washington State University, unpublished data). White-tailed deer and mule deer congregated on separate winter ranges between December and April. Winter ranges were typically gentle, south- to west-facing slopes at elevations of 900 m to 1,220 m in dense canopy timber, which provided refuge from wind and snow (Pauley et al. 1993, Armeleder et al. 1994). Higher elevation winter ranges (>900 m) were used almost exclusively by mule deer, whereas lower elevation ranges (<900 m) were used mainly by white-tailed deer. White-tailed deer migrated to higher elevations and integrated with mule deer during summer months (Anthony and Smith 1977).

Field efforts were concentrated in 2 areas separated by the Kettle River. The Wedge (a triangular shaped area bounded by the Kettle River, Columbia River and Canadian border) rested to the east of the high mountain Kettle Crest and Kettle River; the Republic area rested to the west. We conducted analyses on each area separately.

## METHODS

We searched the study area for cougar tracks in snow each year (Nov to Apr) from 2002 to 2004. We released hounds on fresh tracks to tree cougars (Hornocker 1970). We immobilized treed cougars by injecting a mixture of ketamine hydrochloride (200 mg/mL) and xylazine hydrochloride (20 mg/mL), at a dosage of 0.4 mL per 10 kg of body mass, with a projectile dart in the hindquarter (Ross and Jalkotzy 1992, Spreadbury et al. 1996). We fitted cougars with mortality-sensing very high frequency radio-collars and classified them either as kitten (0–1 yr), yearling (1–2 yr), or adult (>2 yr), based on their general appearance and tooth wear (Ashman and Greer 1976). We handled all animals in accordance with Washington State University Animal Care (IACUC permit 3133), and Animal Welfare Assurance Committee (permit A3485-01).

### Prey Availability

We determined relative prey availability for collared cougars using a ground-sampling technique that followed cougar movements throughout their home ranges. While radio-monitoring collared cougars, we conducted a year-round ground count along forest service roads of white-tailed deer and mule deer (Cruickshank 2004). At each observation, we recorded the date, time, Universal Transverse Mercator coordinates, species, number of deer, habitat, and the straight-line distance from the transect. We classified habitat types as open ponderosa pine, dense mixed forest, clear-cut, or agricultural. Of these variables, we identified 3 that had the highest potential to affect the probability of detection for each deer species and, therefore, the accuracy of our survey (i.e., group size, habitat type, and perpendicular distance from the transect [road]; Buckland et al. 2001).

We examined whether sighting probabilities were the same for white-tailed deer and mule deer by testing for differences in independent variables between species.

To determine sighting probabilities for deer we conducted sightability trials, with standardized controllable factors (i.e., no. and experience of observers, driving speed), and measured the biases of sightability caused by environmental factors (i.e., group size, distance, vegetation cover). Beginning in August 2003, we daily placed 6 McKenzie HD30 deer decoys (McKenzie Targets, Granite Quarry, NC) along secondary roads in the study area. We placed decoys in groups of 1 to 6 individuals, in 1 of 4 habitat types (open ponderosa pine, dense mixed forest, clear-cut, and agricultural), from 0 m to 130 m from transects. A second researcher, unaware of decoy locations, drove the road later that day and recorded the decoys observed.

We used logistic regression (LR) analyses (Proc Logistic; SAS Institute, Cary, NC) to test for effects of independent variables (i.e., group size, habitat, distance) on sightability, then used that LR model to calculate corrected relative numbers of live white-tailed deer and mule deer on survey transects (Cruickshank 2004). To test the accuracy of our ground count, we conducted a late-winter helicopter survey on the Wedge following the methods of Unsworth et al. (1999a). We compared the proportions of white-tailed deer and mule deer from the corrected winter ground survey on the Wedge to that from the aerial survey. We also compared the proportions of deer species in the entire study area versus the 2 sub-areas (the Wedge, Republic) and among seasons. We used the chi-square test of homogeneity for all comparisons.

### Cougar Kills or Prey Usage

We located cougars using fixed-wing aircraft, ground telemetry, and snow-tracking. We located all cougars with aerial telemetry during daylight hours 1–2 times per week in summer and less frequently in winter (typically 2–3 times/month) because of inclement weather. We monitored individual cougars with ground telemetry during daylight hours for 21-day sampling periods (Murphy 1998, Nowak 1999) to document predation. For each day in a sequence, we collected  $\geq 3$  convergent bearings to determine a cougar's location within 1,000 m<sup>2</sup>. We established error polygons with LOAS (Location of a Signal) telemetry triangulation software (Ecological Software Solutions, Sacramento, CA), and we plotted potential kill sites (sites where a cougar spent >24 hr) on 1:24,000 United States Geological Survey topographic maps.

We discovered cougar kills by visiting these sites on the day following cougar presence, often with the help of a dog. When we successfully located a kill, we determined whether the radiocollared cougar was responsible by comparing the kill location to recent telemetry records and field sign (e.g., cougar bed sites, tracks, scat, and evidence that the carcass had been covered or cached; Shaw 1987). We examined carcasses for morphological traits to differentiate between deer species (antlers, tails, and metatarsal glands; Verts and Carraway 1998). When we

could not determine species in the field, we collected tissue samples and sent them to the Washington Department of Fish and Wildlife Genetics Laboratory for mitochondrial DNA analysis. We assigned a kill date to each carcass (the first day we located the cougar at the site), calculated a predation sequence (the interval [days] between 2 consecutive kills), and recorded the position with a handheld Global Positioning System unit.

### Prey Selection and Predation Rates

Thomas and Taylor (1990) identified 3 general study designs for evaluating selection at various scales. In design I, all data are collected at the population level; individual animals are not identified. Design II identifies the individual and compares individual use to availability at the population level. In design III, all data are measured with respect to the individual animal and comparisons are made between individuals.

We calculated 2 measures of preference: standardized forage ratios (i.e., a selection index; Manly et al. 2002) and Manly's  $\alpha$  (i.e., a preference index; Manly 1974). We defined selection as any deviation from random use of prey (Chesson 1978) and evaluated selection using Design types I and II.

*Population prey selection.*—Our first objective was to estimate population selection ratios for each prey type regardless of differences in selection among individuals (design I). Because we sampled the available prey, but did not conduct a complete census, we used the following estimator to calculate a selection index for each prey species:

$$\hat{w}_i = o_i/\pi_i \quad (\text{Manly et al. 2002, eq 4.9})$$

where  $\hat{w}_i$  is the selection index for species  $i$ ,  $o_i$  is the proportion of species  $i$  in the diet, and  $\pi_i$  is the proportion of species  $i$  available in the environment. The index ranges from zero to one (avoidance) and from one to infinity (preference). We standardized the ratios so that they sum to one:

$$\beta_i = \frac{\hat{w}_i}{\sum_{i=1}^n \hat{w}_i} \quad (\text{Manly et al. 2002, eq 4.10})$$

where  $\beta_i$  is the standardized selection ratio for species  $i$ . In our 2-prey species system a ratio of 0.5 indicates no preference. Ratios below the threshold indicate relative avoidance and ratios above indicate relative preference.

We calculated Manly's  $\alpha$ , assuming constant prey populations:

$$\alpha_i = \frac{r_i}{n_i} \left( \frac{1}{\sum (r_j/n_j)} \right) \quad (\text{Manly 1974, eq 3})$$

where  $\alpha_i$  is Manly's preference index for prey type  $i$ ,  $r_i$ ,  $r_j$  is the proportion of prey type  $i$  or  $j$  in the diet, and  $n_i$ ,  $n_j$  is the proportion of prey type  $i$  or  $j$  in the environment. This method automatically standardizes the index as described above. A comparison of the above formulas reveals that the 2 methods (standardized selection index and Manly's  $\alpha$  for

constant prey populations) result in the same output. We estimated standard errors as:

$$se(\hat{w}_i) = \hat{w}_i \sqrt{\{(1 - o_i)/(o_i u_+) + (1 - \hat{\pi}_i)/(\hat{\pi}_i m_+)\}} \quad (\text{Manly et al. 2002, eq 4.23})$$

where  $o_i$  is the proportion of species  $i$ ,  $u_+$  is the total number of prey killed,  $\hat{\pi}_i$  is the proportion of prey type  $i$  available, and  $m_+$  is the total number of available prey sampled. We used Bonferroni-corrected 95% confidence limits and a chi-squared log-likelihood statistic to test the null hypothesis that cougars select prey at random.

We performed the above design I selection analyses on the Wedge and Republic separately to determine year-round prey selection. Because the 2 areas were representative of the larger Okanogan Highlands region (Bailey et al. 1994), we combined the data for the 2 study areas and performed a regional prey selection analysis in order to increase sample size and decrease Type II errors (Zar 1999). To analyze seasonal selection, we used summer and winter observed and expected values. We considered summer 1 May through 31 October and winter 1 November through 30 April. These seasonal designations ensured that the greatest snowfall occurred in one season and coincided with deer migrations.

*Individual prey selection.*—Our second objective was to estimate selection for individual cougars compared to population-level availability (design II) and determine the amount of variation in selection among individuals. For each cougar, we computed the selection ratio for prey species  $i$  by cougar  $j$ :

$$\hat{w}_{ij} = u_{ij}/(\hat{\pi}_i u_{+j}) \quad (\text{Manly et al. 2002, eq 4.37})$$

where  $u_{ij}$  is the number of prey species  $i$  killed by cougar  $j$ , and  $u_{+j}$  is the total prey killed by cougar  $j$ . We calculated standard errors (as above), Bonferroni confidence limits, and a chi-squared log-likelihood statistic for each analysis. We also used a 1-tailed, paired  $t$ -test to test the null hypothesis that mean selection ratios were stronger for mule deer than for white-tailed deer.

To better understand how individual cougars might affect selection at the population scale, we calculated 2 additional chi-square tests. First, we tested the null hypothesis that individual cougars used resources in the same proportions as other cougars, regardless of whether selection occurred. We compared individual use to availability in the study area for each cougar:

$$X_{L1}^2 = 2 \sum_{j=1}^n \sum_{i=1}^I u_{ij} \log_e(u_{ij}/E(u_{ij})) \quad (\text{Manly et al. 2002, eq 4.26})$$

Where  $df = (I - 1)(n - 1)$ ,  $I$  is the number of prey categories, and where  $E(u_{ij})$  is the expected number of prey type  $i$  used by the  $j$ th cougar if that animal uses the resources in the same way as the other cougars. Second, we tested selection by comparing individual use with prey availability at the population level:

**Table 1.** Prey availability and prey use by cougars in northeastern Washington, USA, 2002–2004. We show estimated numbers of deer ( $n$ ) from corrected ground counts and percent of total large prey population for each species, white-tailed deer (WT) and mule deer (MD).

Season	Study area	Available WT		Killed WT		Available MD		Killed MD	
		$n$	%	$n$	%	$n$	%	$n$	%
Annual	Wedge	1,130	0.82	27	0.71	255	0.18	11	0.29
	Republic	482	0.56	8	0.40	384	0.44	12	0.60
	Regional	1612	0.72	35	0.60	639	0.28	23	0.40
Summer	Wedge	783	0.85	17	0.74	138	0.15	6	0.26
	Republic	356	0.56	4	0.33	278	0.44	8	0.67
	Regional	1,139	0.73	21	0.60	416	0.27	14	0.40
Winter	Wedge	400	0.78	9	0.75	114	0.22	3	0.25
	Republic	73	0.40	4	0.50	109	0.60	4	0.50
	Regional	473	0.68	13	0.65	223	0.32	7	0.35

$$\chi_{L2}^2 = 2 \sum_{j=1}^n \sum_{i=1}^I u_{ij} \log_e(u_{ij}/E(u_{ij}))$$

(Manly et al. 2002, eq 4.27)

Where  $df = n(I - 1)$ ,  $I$  is the number of prey categories, and where  $E(u_{ij})$  is the expected number of prey type  $i$  used by the  $j$ th cougar if use is proportional to availability. A significant result would indicate nonrandom selection by at least some individuals. The difference  $(X_{L1}^2 - X_{L2}^2)$ , where  $df = I - 1$ ,  $I$  is the number of prey categories, tested if cougars were on average using prey in proportion to availability, regardless of whether individuals were selecting consistently.

To estimate kill rate (days between kills) from predation sequences, we assigned a kill date by considering the first day we located the cougar at the site. We then calculated the number of days between 2 consecutive deer kills (Murphy 1998). We averaged kill rates to determine summer, winter, and mean annual kill rates. We used a  $t$ -test to compare seasonal predation rates and species-specific predation rates (predation rate following a white-tailed deer kill vs. predation rate following a mule deer kill).

## RESULTS

### Prey Availability

Raw counts of deer available to collared cougars suggested that white-tailed deer were more abundant than mule deer across the entire study area (70% for white-tailed vs. 30% for mule deer), when observed both as groups (317 vs. 150) and as individuals (843 vs. 355). Our sightability model corrected the raw counts of white-tailed deer from 843 to 1,612 (+91%) and mule deer from 355 to 639 (+80%). The final corrected relative prey availability for the entire study area was 72% white-tailed deer and 28% mule deer (Table 1). Helicopter survey data confirmed ground counts and indicated that white-tailed deer were more abundant than mule deer in the Wedge (80% vs. 20%) during winter ( $\chi^2_1 = 610.4$ ,  $P < 0.001$ ). The helicopter sightability survey estimated white-tailed abundance at 1,384 (90% CI = 221) and the mule deer at 354 (90% CI = 83). There was no difference between proportions of deer species from the corrected winter ground survey (78% white-tailed deer, 22% mule deer) and winter helicopter survey on the Wedge

( $\chi^2_1 = 0.816$ ,  $P = 0.37$ ). We detected significant differences in seasonal ( $\chi^2_1 = 6.59$ ,  $P < 0.025$ ) and spatial ( $\chi^2_1 = 176.33$ ,  $P < 0.001$ ) deer availability across the study area. White-tailed deer comprised 68% (vs. 32% for mule deer) of the regional deer population in winter and 73% (vs. 27% for mule deer) of the deer during summer. Year-round availability for white-tailed deer was 82% and 56% for the Wedge and Republic, respectively. The corresponding mule deer availability was 18% and 44% (Table 1).

### Cougar Kills or Prey Usage

During April 2002 through August 2004, we captured and monitored 14 adult cougars (12 F and 2 M) and completed 27 21-day monitoring sequences. Fourteen additional sequences remained incomplete due to cougar movements out of the study area. We found 60 cougar-killed deer: 35 (58%) white-tailed deer, 23 (38%) mule deer, and 2 (4%) unknown deer species. Cougars killed more white-tailed deer during both winter (65% white-tailed vs. 35% mule deer;  $\chi^2_1 = 5.14$ ,  $P = 0.02$ ) and summer seasons (60% white-tailed vs. 27% mule deer, 3% unknown;  $\chi^2_1 = 3.5$ ,  $P = 0.06$ ; Table 1). In the Wedge, summer kill sites occurred at higher elevations (1,090 m, SE = 66) than winter kill sites (908 m, SE = 68;  $t_{31} = 1.91$ ,  $P = 0.07$ ).

### Kill Rates

Mean annual kill rate from all cougars was 6.68 days per deer kill (SD = 3.12 days, range = 2.0–14.0 days,  $n = 22$  inter-kill intervals). Kill rate from females with kittens averaged 5.93 days per deer kill (SD = 3.28 days, range = 2.0–14.0 days,  $n = 15$ ), solitary females averaged 7.8 days per kill (SD = 2.17 days, range = 6.0–11.0 days,  $n = 5$ ), and solitary males averaged 9.5 days per kill (SD = 2.12 days, range = 8.0–11.0 days,  $n = 2$ ). Kill rates did not differ between seasons (6.6 days/kill for summer and 7.0 days/kill for winter;  $t_{20} = -0.29$ ,  $P = 0.78$ ) or deer species (7.0 days/kill for white-tailed deer and 6.1 days/kill for mule deer;  $t_{19} = 0.58$ ,  $P = 0.58$ ).

### Prey Selection

*Population prey selection.*—Cougars did not show statistically significant selection for mule deer (MD) over white-tailed (WT) deer in the Wedge (MD selection ratio [sr] = 1.61, WT sr = 0.87;  $P = 0.12$ ) or Republic (MD sr =

**Table 2.** Prey species killed by cougars annually and associated selection indices, from population level use and availability, in northeastern Washington, USA, 2002–2004.

Area	Inputs			Selection ratios		SEs, CLs, and $\chi^2$ tests				
	Prey	Obs <sup>a</sup>	Exp <sup>b</sup>	$w_i^c$	$\beta_i^d$	SE( $w_i$ )	CI Lower	CI Upper	$\chi^2$ LL <sup>e</sup>	P
Wedge	WT <sup>f</sup>	27	31.01	0.866	0.350	0.091	0.667	1.075	2.414	0.116
	MD <sup>g</sup>	11	11.20	1.611	0.650	0.409	0.655	2.490		
Republic	WT	8	6.99	0.714	0.344	0.198	0.275	1.163	1.928	0.161
	MD	12	8.80	1.364	0.656	0.252	0.787	1.919		
Regional	WT	35	11.20	0.833	0.368	0.090	0.640	1.045	3.302	0.066
	MD	23	8.80	1.429	0.632	0.231	0.879	1.915		

<sup>a</sup> Obs no. of kills for each prey species.

<sup>b</sup> Exp no. of kills (total kills  $\times$  proportion available prey for each species).

<sup>c</sup> Selection index (Manly et al. 2002).

<sup>d</sup> Standardized selection index.

<sup>e</sup>  $\chi^2$  log-likelihood statistic.

<sup>f</sup> White-tailed deer.

<sup>g</sup> Mule deer.

1.36, WT sr = 0.71;  $P = 0.16$ ) but showed selection for mule deer regionally (MD sr = 1.43, WT sr = 0.83;  $P = 0.07$ ; Table 2). During summer, cougars did not show selection for mule deer over white-tailed deer in the Wedge (MD sr = 1.73, WT sr = 0.87;  $P = 0.17$ ) or Republic (MD sr = 1.52, WT sr = 0.60;  $P = 0.11$ ) but cougars showed selection for mule deer regionally (MD sr = 1.48, WT sr = 0.82;  $P = 0.9$ ; Table 3). Selection ratios and chi-square results indicate lack of selection during winter in all areas ( $P > 0.50$ ).

*Individual prey selection.*—Nine of 14 cougars selected in the direction of (selection ratio  $> 1.0$ ) mule deer; however, selection was statistically significant ( $P > 0.10$ ) for only 3 cougars (Table 4). Five cougars selected in the direction of (selection ratio  $> 1.0$ ) white-tailed deer;

however, no cases were significant ( $P > 0.10$ ). The mean selection ratio for mule deer was 1.55 (SD = 1.45, SE = 0.39) and the mean selection ratio for white-tailed deer was 0.813 (SD = 0.498, SE = 0.13;  $t = -1.80$ ,  $P = 0.09$ ). Individual cougars did not show consistency when choosing resources ( $\chi_{L1}^2 = 42.419$ ,  $P < 0.001$ ), with some more selective than others ( $\chi_{L2}^2 = 39.101$ ,  $P < 0.001$ ). The difference between the 2 statistical scales of analysis ( $\chi_{L1}^2 - \chi_{L2}^2 = 3.318$ ,  $df = 1$ ,  $P = 0.069$ ) indicated that cougars were, on average, strongly selecting for mule deer.

## DISCUSSION

Our results indicated that cougars selected for (disproportionately prey upon) mule deer in our study area. Although

**Table 3.** Prey species killed by cougars seasonally, and associated selection indices, from population-level use and availability in northeastern Washington, USA, 2002–2004.

Area	Inputs			Selection ratios		SE( $w_i$ )	Lower CI	Upper CI	$\chi^2$ LL <sup>e</sup>	P
	Prey	Obs <sup>a</sup>	Exp <sup>b</sup>	$w_i^c$	$\beta_i^d$					
Summer										
Wedge	WT <sup>f</sup>	17	19.55	0.871	0.334	0.108	0.627	1.112	1.841	0.171
	MD <sup>g</sup>	6	3.45	1.733	0.666	0.626	0.337	3.145		
Republic	WT	4	6.72	0.595	0.282	0.243	0.048	1.139	2.484	0.111
	MD	8	5.28	1.515	0.718	0.318	0.808	2.330		
Regional	WT	21	26.29	0.822	0.357	0.114	0.564	1.074	2.815	0.089
	MD	14	8.71	1.481	0.643	0.316	0.787	2.203		
Winter										
Wedge	WT	9	9.36	0.962	0.458	0.162	0.600	1.327	0.053	0.814
	MD	3	2.64	1.136	0.542	0.571	0	2.408		
Republic	WT	4	4.80	1.250	0.600	0.455	0.227	2.267	0.306	0.588
	MD	4	3.20	0.833	0.400	0.300	0.164	1.506		
Regional	WT	13	12.55	0.956	0.466	0.159	0.600	1.313	0.077	0.778
	MD	7	7.45	1.094	0.534	0.338	0.334	1.851		

<sup>a</sup> Obs no. of kills for each prey species.

<sup>b</sup> Exp no. of kills (total kills  $\times$  proportion available prey for each species).

<sup>c</sup> Selection index (Manly et al. 2002).

<sup>d</sup> Standardized selection index.

<sup>e</sup>  $\chi^2$  log-likelihood statistic.

<sup>f</sup> White-tailed deer.

<sup>g</sup> Mule deer.

**Table 4.** Prey species killed by cougars annually, and associated selection indices, from individual use and population-level availability, in northeastern Washington, USA, 2002–2004.

Cougars no.	Inputs		Total		Selection ratios		SEs, CIs, and $\chi^2$ tests					
	Prey	Season killed		Obs <sup>a</sup>	Exp <sup>b</sup>	$w_i^c$	$\beta_i^d$	SE( $w_i$ )	CI Lower	CI Upper	$\chi^2$ LL <sup>e</sup>	P
		Summer	Winter									
F 102	WT <sup>f</sup>	3		3	2.45	1.22	1	0.016	1.191	1.261	1.219	0.27
	MD <sup>g</sup>			0	0.55	0	0	0	0	0		
F 223	WT	3	2	5	6.53	0.76	0.27	0.210	0.295	1.237	1.592	0.20
	MD	3		3	1.47	2.08	0.73	0.937	0	4.137		
F 293	WT	5	2	7	6.53	1.07	0.61	0.144	0.750	1.395	0.204	0.66
	MD	1		1	1.47	0.69	0.39	0.636	0	2.105		
M 402	WT			0	0.82	0	0	0	0	0	3.381	0.06
	MD		1	1	0.18	5.56	1	0.307	4.743	6.120		
F 423	WT	2	1	3	4.90	0.61	0.18	0.250	0.052	1.174	3.039	0.08
	MD	2	1	3	1.10	2.78	0.82	1.119	0.207	5.225		
F 473	WT	1		1	0.82	1.22	1	0.016	1.191	1.261	0.407	0.53
	MD			0	0.18	0	0	0	0	0		
F 662	WT	1	4	5	5.71	0.87	0.35	0.210	0.406	1.345	0.425	0.52
	MD		2	2	1.29	1.59	0.65	0.932	0	3.640		
M 683	WT	2	1	3	3.26	0.92	0.40	0.266	0.324	1.515	0.106	0.74
	MD		1	1	0.74	1.39	0.60	1.178	0	4		
F 145	WT			0	0.56	0	0	0	0	0	1.625	0.20
	MD		1	1	0.44	2.27	1	0.086	2.063	2.448		
F 154	WT		1	1	3.90	0.26	0.12	0.238	0	0.790	5.150	0.02
	MD	4	2	6	3.10	1.95	0.88	0.307	1.244	2.622		
F 191	WT	1		1	0.56	1.79	1	0.055	1.675	1.919	1.171	0.28
	MD			0	0.44	0	0	0	0	0		
F 261	WT	2	2	4	3.34	1.19	0.61	0.348	0.418	1.977	0.300	0.59
	MD	2		2	2.66	0.76	0.39	0.435	0	1.727		
F 341	WT	1		1	1.11	0.89	0.44	0.636	0	2.324	0.026	0.87
	MD	1		1	0.89	1.14	0.56	0.799	0	2.918		
F 593	WT		1	1	1.67	0.60	0.28	0.489	0	1.696	0.604	0.56
	MD	1	1	2	1.33	1.52	0.72	0.617	0.122	2.885		
$\bar{x}$	WT					0.81	0.45	0.130	0.410	1.216		
	MD					1.55	0.55	0.390	0.522	2.581		

<sup>a</sup> Obs no. of kills for each prey species.

<sup>b</sup> Exp no. of kills (total kills  $\times$  proportion available prey for each species).

<sup>c</sup> Selection index (Manly et al. 2002).

<sup>d</sup> Standardized selection index.

<sup>e</sup>  $\chi^2$  log-likelihood statistic.

<sup>f</sup> White-tailed deer.

<sup>g</sup> Mule deer.

selection for mule deer appeared more pronounced in the eastern area (the Wedge) where mule deer proportions were lower in relation to white-tailed deer, cougars selected for mule deer over white-tailed deer throughout the year in both areas. Seasonally, cougars selected for mule deer only during summer months and never selected for white-tailed deer despite their much higher abundance. In other words, cougars within our study area preyed upon white-tailed deer in direct proportion to their availability throughout the year but killed mule deer in greater proportion than availability during summer. This suggests that cougars winter at lower elevations on the gentle slopes near concentrated herds of white-tailed deer (Pauley et al. 1993) but shift to higher elevations during summer months, following the white-tailed migration to summer ranges. Cougars moving to higher terrain are more likely to overlap areas used by mule deer during summer (Armeleder et al. 1994). As a result, encounters between mule deer and cougars increase. Katnik (2002) documented such a situation in the nearby Selkirk

Mountains, where cougar preyed upon white-tailed deer, mule deer, and mountain caribou (*Rangifer tarandus*). Katnik (2002) linked increased predation on caribou to a seasonal shift in elevation by white-tailed deer and greater spatial overlap between cougars and caribou. Robinson et al. (2002) also found that summer selection for mule deer accounted for the greatest difference in cougar predation rates between white-tailed deer and mule deer. We concede that small sample sizes may have reduced our ability to detect selection in all cases (Type II errors).

The underlying reason for disproportionately higher prey selection and per capita predation on mule deer is presently unclear. For example, selection for mule deer may be habitat-based or behavioral-based. Cougars may forage more in certain habitat patches within their home range, where mule deer are more likely to be encountered. Alternatively, mule deer may simply be easier to kill than white-tailed deer. An analysis of species-specific attack success rates is needed to test these ideas.

Several other studies have also documented negative impacts of cougar predation on a secondary prey species. Cougars were found to be responsible for declining bighorn sheep (*Ovis canadensis*) populations in California, USA (Hayes et al. 2000), Arizona, USA (Kamler et al. 2002), Montana, USA (Jones and Worley 1994), Alberta, Canada (Ross et al. 1997), and Colorado, USA (Creeden and Graham 1997). In each case, bighorn sheep were the secondary prey species. Other declines include porcupines (*Erethizon dorsatum*; Sweitzer et al. 1997) and feral horses (*Equus caballus*; Turner and Morrison 2001). Katnik's (2002) investigation of cougar predation on endangered mountain caribou concluded that certain, but not all, cougars posed a threat. Only those that overlapped areas used by both white-tailed deer and caribou were problematic. Each of these studies suggested that declines in secondary prey species resulted from changes in prey availability and resulting changes in cougar predation in a multi-prey system.

## MANAGEMENT IMPLICATIONS

Many management jurisdictions are currently observing mule deer declines (Crete and Daigle 1999), of which predation is one hypothesized cause. Depending on whether predation is density-dependent or density-independent, predation can be stabilizing or destabilizing to a prey population. Our findings suggest that cougar predation on mule deer in Northeast Washington was density-independent during our study. As secondary prey, mule deer population recovery is unlikely in the absence of management changes.

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