PREY SELECTION AND KILL RATES OF COUGARS IN NORTHEASTERN WASHINGTON

By

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The members of the Committee appointed to examine the thesis of HILARY STUART CRUICKSHANK find it satisfactory and recommend that it be accepted.

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ABSTRACT

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We investigated prey selection and kill rates of cougars in northeastern Washington from 2002-2004, in a sympatric white-tailed deer and mule deer system. We tested two competing hypotheses of prey selection, “prey switching” and “apparent competition”. We developed a sightability model which corrected ground counts of white-tailed deer and mule deer using life-sized deer decoys to calculate relative prey availability. A logistic regression sightability model tested for effects of group size, distance, and habitat on deer sightability, then predicted relative numbers (availability) of both deer species on transects. To estimate use of prey by cougars, we examined 60 cougar kills. White-tailed deer comprised 60% of the kills (mule deer comprised 40%), a proportion larger than the study area’s prey population (70% white-tailed deer vs. 30% mule deer). Cougars selected for mule deer across the entire study area. We also detected strong seasonal changes in prey selection, with cougars strongly selecting for mule deer in summer, but not during winter. Mean annual kill rate was 6.68 days per deer killed. Kill rates did not differ between seasons or deer species. Habitat characteristics of kill sites did not differ significantly between white-tailed deer and mule deer kills. These findings are consistent with the apparent competition hypothesis and suggest that the current decline in mule deer numbers in northeastern Washington is caused by an abundant invading primary prey species (white-tailed deer) and a related increase in predation on the secondary prey species (mule deer) during summer months.

TABLE OF CONTENTS

Page

LIST OF TABLES

CHAPTER 1

ESTIMATING PREY AVAILABILITY IN HOME RANGES WITH A SIGHTABILITY MODEL

ABSTRACT

This study introduces an inexpensive, and convenient method to estimate ungulate sightability and relative numbers from ground counts using life-sized animal decoys. Logistic regression (LR) was used to test for effects of group size, distance, and habitat on deer sightability. The best-fit LR model was then applied to observations of free-ranging mule deer and white-tailed deer on transects to calculate their relative numbers. The model estimated relative populations in our northeastern Washington study area at 72% white-tailed deer and 28% mule deer. We compared this model to results obtained through an aerial count, and also tested for seasonal and geographic differences in relative prey availability. The corrected ground count and the aerial count yielded statistically equal proportions of deer. We detected significant seasonal and geographic variation in the ratio of deer species. When averaged across seasons, sub-areas, and surveys, relative prey availability was 70% white-tailed deer and 30% mule deer.

INTRODUCTION

Researchers must accurately determine animal numbers to meet wildlife management objectives. However, animal counts are often biased because seldom are all animals seen during surveys. When conducting surveys, observers count some unknown fraction of the total animals present. This fraction must be translated to estimates of population size. Sighting probability, or sightability, is the probability that an animal will be seen by an observer during a survey (Krebs 1999). Several methods are available to estimate sightability for animal counts including double sampling, marked sub-sample, line transects, quadrat counts, removal methods, capture-recapture, and plotless methods (Anderson 2003). Most of these methods are expensive (e.g., some require radio-collared animals), time consuming, and are often impractical. This study introduces an inexpensive and convenient method to estimate sightability for ungulate ground counts using life-sized animal decoys as "marked" animals.

To produce estimates that correlate with the actual population size, counts must relate to sightability. Many variables affect an animal's sightability such as observer effects (experience, interest, eyesight, fatigue), environmental variables (precipitation, habitat, time of day, vegetation type, temperature), and aspects of the species (color, behavior, group size) (Anderson 2001). These variables change depending on when, where, and what a researcher surveys, thus chances of observing an animal will also change with time, place, and target animal. Unless one can estimate the detection probability to relate count data (index data) to the size of the true population, one cannot assume it is representative of the population. The true population size is related to the index or count value (C) as N = C/p, where p is the detection probability of the animal being observed, or sightability (Anderson 2003).

Sightability models allow estimates of detection probabilities, thereby correcting for animals not seen during surveys. Sightability models establish detection probabilities by incorporating variation in detection among habitats, seasons, years, species, and distances (Williams et al. 2002). Once the detection probability ($\hat{p}$) is known, the parameter, $\hat{N} = c / \hat{p}$, can be calculated, and a confident population estimate made.

Logistic regression (LR) estimators are often used to develop sightability models because they can incorporate categorical and continuous, non-parametric, non-additive, and non-linear independent variables to predict a binomial dependent variable (sighted, not sighted) (Kleinbaum et al. 1982). LR models help eliminate problems associated with heterogeneous sightability among animals by correcting for each group of animals observed. Unlike mark-resight methods, marked animals are only needed during model development (Bartmann et al. 1987). Because of their flexibility and effectiveness, researchers have used LR models for aerial surveys of elk (*Cervus elaphus*) (Samuel et al. 1987, Otten et al. 1993), mule deer (*Odocoileus hemionus*) (Ackerman 1988), and moose (*Alces alces*) (Anderson 1996). While this method has proven successful for aerial surveys, researchers have not yet applied it to ground counts.

As part of an ongoing project studying cougar prey selection in northeastern Washington, we needed a simple, effective, and inexpensive way to assess differences in prey availability. While tracking cougars in the field, we conducted ground counts of white-tailed deer and mule deer during June 2002 – March 2004. Our goal was to develop and validate a technique that used ground counts to infer prey availability over space and time. To correct the ground counts for sighting biases, we developed a sightability model using LR and 6 deer decoys set in 48 combinations. We tested for differences in sightability between the two deer species in our study area. Although mule deer and white-tailed deer are similar in size and color, they use different habitats and display different behaviors, which could result in different sightabilities.

Specifically, our objectives were to 1) identify environmental variables that affect sightability of white-tailed deer and mule deer during year-round ground counts, 2) develop a sightability model to correct for biases in ground counts, 3) validate the model by comparing results with a winter helicopter survey, and 4) determine annual and seasonal relative abundances of white-tailed deer and mule deer for radio-collared cougars.

STUDY AREA

The study area covers approximately 3,800 km^2 in northeastern Washington. Boundaries extend from the Okanogan/Ferry County line west to the Columbia River, and from the Canadian/US border south to the Colville Indian Reservation. The study area lies entirely within the Okanogan Highlands physiographic province, composed of glacially subdued mountainous terrain, with elevations ranging from 400 m in the Columbia River valley to 2130 m at the top of the Kettle Crest. Forest overstory species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Inland maritime conditions characterize the climate, with mean temperatures ranging from –6 °C in January to 21 °C in July, and annual precipitation of 46 cm. Snowfall averages 136 cm during a 6-month period from mid-November to mid-April.

Field efforts were concentrated in two separate areas separated by the Kettle River. “The Wedge” study area lies to the east of the Kettle River, and the “Republic” area lies to the west of the River and the Kettle Crest Mountain Range. We conducted analyses on each replicate study area separately.

Robinson et al. (2002) found that white-tailed deer (*Odocoileus virginianus*) were the most abundant ungulate in a nearby study area, followed by mule deer (*Odocoileus hemionus*). Since climate and physiography create seasonally migratory deer populations, both white-tailed deer and mule deer congregate on winter ranges between December and April. Deer winter ranges are generally on south to west-facing gentle slopes in timber stands with higher canopy closure, providing wind and snow breaks

(Pauley et al. 1993, Armeleder et al. 1994). Across the study area, higher elevation winter ranges (i.e., 900-1200 m) are almost exclusively occupied by mule deer, whereas lower elevation ranges (i.e., ≤ 900 m) are predominantly used by white-tailed deer. During summer white-tailed deer move up in elevation and intermix with mule deer.

METHODS

Model Development

To determine detection probabilities for deer we conducted sightability trials, which standardized several controllable factors (e.g., number and experience of observers, driving speed), and measured biases of sightability caused by environmental factors (e.g., group size, distance, vegetation cover). Beginning in August 2003, 6 McKenzie HD30 deer decoys (McKenzie Targts, Granite Quarry, N.C.) were placed daily along secondary roads in the study area. Decoys were placed 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 to 130 m from transects. A second researcher drove the road later that day and recorded the decoys observed.

We used logistic regression (Proc Logistic, SAS Institute, Cary N.C.) to estimate the relative importance and parameter values of the independent variables (group size, distance to deer, and habitat type) on the dependent variable (individual deer sightings and non-sightings). We examined the influence of each variable on deer sightability by determining the effectiveness of the full model against models with a reduced number of parameters; in effect testing the null hypothesis that group size, perpendicular distance, and habitat type did not influence deer sightability (Ott and Longnecker 2001). We used the VIF (Variation Inflation Factor) diagnostic tool in SAS (SAS Institute, Cary, N.C.) to test for collinearity between independent variables.

To correct for individual sightability, we considered each decoy as an individual observation because decoys could be in groups ≥ 1. Steinhorst and Samuel (1989) suggested that if sightability is constant then success in observing an animal can be viewed as a simple binomial experiment (sightings and non-sightings). Given this, we coded the dependent variable, whether an animal was sighted or not, as 0 for sighted and 1 for not sighted. When a group of two or more decoys was placed in the forest, each decoy was assessed for individual sightability. For example, if only one of the decoys was observed, we categorized one as a success (coded as a 0), and one as a failure (coded as a 1). Although individuals in a group may seem to violate the assumption of independence between sampled units, our goal was to develop a correction factor for individual sightability with group size as an independent variable (Krebs 1999); so a violation of independence was not relevant in this case.

The LR model for sightability was:

$$\hat{p} = \frac{e^{\mu}}{1 + e^{\mu}},$$

where $\hat{p}$ is the detection probability, e is the natural log 2.718, and $\mu = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k$ is the set of variable parameters (β) multiplied by the independent variables (x_1, $x_{2,\ldots,} x_k$) (Unsworth et al. 1999). We corrected for each sighting of decoys based on the equation:

$$\hat{N} = C / \hat{p},$$

where C is the original count or index data, and $\hat{N}$ is the corrected population estimate.

Ground Surveys of Live Deer

To determine prey available to each radio-collared cougar within the study area, we did not establish static sampling transects, but instead adapted a dynamic sampling technique to follow the cougar's movements throughout their home ranges. From 2002-2004, researchers monitored radio-collared cougars' movements through daily, year-round ground telemetry. While conducting field work researchers documented all deer encountered in the cougars' home ranges on foot or in a vehicle. Because of the repetitious commute to our study area on a paved highway along the Columbia River, we omitted all deer observations on this highway for calculation of prey availability. On occasions when transects (roads, trails) were covered more than once per day, we recorded deer sightings only once per day. Because we were interested in relative numbers of available prey, rather than absolute availability, we avoided any biases of pseudo-replication that might occur by recording the same deer several days in a row.

At each observation, the date, time, Universal Transverse Mercator (UTM) coordinate, species, number of deer, habitat, and the straight-line distance from the transect were recorded. We classified deer as male or female, and adult or fawn. Habitat types were classified as open ponderosa pine, dense mixed forest, clear-cut, or agricultural.

Of these variables, we identified three that had the highest potential to affect the probability of detection for each deer species, and therefore the accuracy of our index: group size, habitat type, and perpendicular distance from the transect (road or trail) (Buckland et al. 2001). We examined whether sightability was the same for white-tailed deer and mule deer by testing for differences in independent variables between species.

We used the t-test (Proc Ttest, SAS Institute, Cary N.C.) to test for differences in group size and perpendicular distance among deer species. We conducted a chi-square test of homogeneity (Proc Freq/Chisq expected, SAS Institute, Cary N.C.) to test for a species/habitat association.

Helicopter Survey

As a second method of determining relative deer abundance, we conducted a helicopter survey on The Wedge portion of our study area. Because of funding restrictions we surveyed half of the study area for one year only. We identified 20 subunits with clear boundaries distinguishable from the air prior to conducting the survey. Size of subunits ranged from approximately 4 km^2 to 17 km^2 and each required < 1 hour to survey. We used ground count data, along with knowledge of the district biologists to define and stratify subunits as low or high quality white-tailed deer and mule deer habitat. We then selected 5 subunits for each of the 4 strata to survey according to methods described by Unsworth et al. (1999).

In February 2004, we surveyed all 20 subunits to determine relative white-tailed deer and mule deer availability. We flew each subunit via transects 200-500 m apart and at a consistent speed range of 65-80 km/h. Two researchers in the back seat observed from both sides of the helicopter while a third researcher recorded observations. When deer were spotted, the helicopter paused and circled the area to confirm the observation. We recorded group size, activity of the animal, canopy cover, habitat, and percent snow cover. The same primary observer and pilot were used throughout the survey, while secondary staff varied from day to day. Point estimates, variances, and confidence intervals were calculated based on formulas in the Mule Deer Spring model in program AERIAL SURVEY version 1.0 (Unsworth et al. 1999).

Model Comparisons

To validate the effectiveness of our ground survey, we compared the proportion 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 seasonal vs. annual proportions, and proportions of deer species in the entire study area vs. the two sub-areas (The Wedge, Republic). We used the chi square test of homogeneity for all comparisons.

RESULTS

Sightability Factors

From sightability trials using deer decoys, we were most successful at observing deer in open habitats, in larger group sizes, and at shorter distances. Success rates for individual deer sightings were 0.93 for agricultural areas, 0.80 in open ponderosa pine forest, 0.70 in clear cuts, and 0.23 in dense mixed forest. We observed 0.50 of deer in group sizes of 1 animal, 0.53 of deer in group sizes of 2 animals, and 0.76 of deer in group sizes of 3 + animals. We also observed 0.96 of deer at 0-50 m, 0.45 at 50-100 m, and 0.48 at 100 +m.

Sightability of decoys depended on habitat, group size, and distance. The VIF diagnostic showed little collinearity between independent variables (VIF < 1.01). The sightability models are given in Table 1.1, and parameter values for the best model are given in Table 1.2. No additional 2-way interaction models yielded significant chi-square improvements. The -2 Log Likelihood for the best model was 72.391 (d.f. = 5, p = 0.00) (Manly et al. 1993), and McFadden's Rho-Squared was very good at 0.476 (Hosmer and Lemeshow 1989) (Table 1.1).

Ground Count

We followed 15 radio-collared cougars from June 2002 through December 2003. Raw prey availability counts indicated that white- tailed deer were more abundant than mule deer, with more groups (317 vs. 150) and total individuals (843 vs. 355) observed during daily field work. The uncorrected relative deer population across the study area was 70% white-tailed deer and 30% mule deer.

We observed more white-tailed deer in open agricultural areas and at longer distances than mule deer; and observed mule deer more often in forested habitats closer to the observer (Table 1.3). We found a significant species by habitat association for individuals ($\chi^2 = 36.58$, d.f. = 3, $p < 0.001$) and groups of deer ($\chi^2 = 24.63$, d.f. = 3, $p < 0.001$). We also found a significant difference in distance between species ($t = 3.49$, d.f. = 370, $p < 0.001$), with mean distance and standard error for white-tailed deer at 23.6 ± 33 and 13.9 ± 25.4 for mule deer. We found no significant difference in group size ($t = 0.89$, d.f. = 392, $p = 0.37$). Mean group size and standard error for white-tailed deer was 2.66 ± 4.05 and 2.37 ± 2.91 for mule deer.

When applied to ground observations, the sightability model increased the estimated number of white-tailed deer 191% from 843 to 1612, and increased the mule deer estimate 180% from 355 to 639. Corrected relative availability across the entire study area was 72% white-tailed deer and 28% mule deer.

Helicopter Survey

The February 2004 aerial survey on the wedge indicated that white-tailed deer were more abundant than mule deer. The Spring Mule Deer model (Unsworth et al. 1999) estimated population size and 90% confidence intervals at 1,384 ± 221 (80%) for white-tailed deer and 354 ± 83 (20%) for mule deer. As expected, sightability variance accounted for nearly all of the total variance for both white-tailed deer (84.6%) and mule deer (89.5%).

Model Comparisons

The ground survey proved to be an effective method to measure relative abundances of white-tailed and mule deer populations. We found no difference ($\chi^2 = 0.0002$, d.f. = 1, p = .99) between the ground survey and helicopter survey on The Wedge during winter (Table 1.4). We detected significant differences in seasonal ($\chi^2 = 6.59$, d.f. = 1, p = 0.01) and spatial ($\chi^2 = 176.33$, d.f. = 1, p = 0.00) deer availability across the study area. White-tailed deer comprised 73% and mule deer 27% of prey during summer. White-tailed deer comprised 68% and mule deer 32% of prey during winter. Annual availability on The Wedge was 82% white-tailed deer and 18% mule deer, and availability in Republic was 56% white-tailed deer and 44% mule deer (Table 1.4). Mean annual prey availability for the entire study area was 70% white-tailed deer and 30% mule deer.

DISCUSSION

Sightability of deer was greater in open habitats (agricultural, open ponderosa pine, clear cuts) than in dense forested areas (mixed forest), and was greater with increasing group size, and at shorter distances. We often observed white-tailed deer in open habitats and at further distances, and observed mule deer in forested habitats closer to the observer. We expected these differences because white-tailed deer and mule deer typically use different habitats. Mule deer often prefer forested habitats, which is evident in a significantly lower sighting distance (perpendicular distance). White-tailed deer prefer open habitats, such as agricultural areas, and are thus often seen at greater distances from transects.

Results of the sightability model are consistent with results from the helicopter survey, suggesting that the corrected ground count is a valid measure of relative deer abundance. We saw significant variation in prey availability across geographic areas (The Wedge and Republic) and seasons. However, prey ratios consistently showed a dominant white-tailed deer population (Table 1.4) across the study area. We expected the large variations in prey population demographies in the two areas due to differences in landscape and habitat. Terrain on The Wedge, adjacent to the Columbia River, is characterized by large swaths of lower elevation agricultural fields, riparian areas, and deciduous/mixed forest. The Republic are landscape is generally higher in elevation and dominated by ponderosa pine and Douglas fir forests (Bio/West 1999). We also expected slight seasonal differences due to a seasonal shift in habitat use. Sightability variance accounted for nearly all of the total variance in the survey because we flew all subunits in the aerial survey and because we observed deer in different vegetation densities.

Prey availability is often determined by counts (Smith et al. 2004, Honer et al. 2002, Baker et al. 2001, Gil and Pleguezuelos 2000). However, because of the inherent variability a detection probability (correction factor) should always accompany animal counts. Of the studies using correction factors (e.g., distance sampling, sightability models) (Bagchi et al. 2003, Karanth and Sunquist 1995), most are designed such that transects and units are delineated and randomly chosen at the start of the study, and then surveyed at regular intervals throughout the study. While these types of static surveys may be useful to determine prey availability for animals with predictable, stable home ranges, cougars tend to shift daily movements, monthly home range use, and even entire home ranges in an unpredictable manner.

Of the 15 cougars that we followed, four of them spent significant time and occupied substantial area outside the physical boundaries of our 3800 km^2 study area. Additionally, very high annual mortality rates of cougars in our study (Lambert 2003) required us to frequently shift areas of field work. By surveying deer populations near daily telemetry locations of live cougars, we were able to determine prey availability in areas that cougars were actively using. This dynamic approach permitted us to deal more effectively with the irregular movements of cougars.

Without the flexibility to shift prey count transects so that they reflect cougar movements, much of the prey availability data collected would be irrelevant. For example, static surveys, designed within predetermined boundaries, would have omitted all prey availability in areas of use that fall outside the usual study area boundaries.

Conversely, static surveys would have included numerous white-tailed deer along the highway that were not actually available (within home ranges) to cougars. A dynamic survey is able to account for such areas, producing more accurate data when determining prey availability specific to animals.

Biologists are often confronted with two main problems when estimating population size: observability and sampling. Most animal survey methods do not result in counts or captures of all animals present in the area. Time and money are frequently limited, so a particular survey often cannot be applied to the entire area of interest. This sightability model addresses both of these problems by allowing valid inferences to be made about the population size from corrected ground counts.

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Table 1.1. Process of model selection for a logistic regression analysis of deer sightability in northeastern Washington, 2002-2004.

Univariate Results	**Log-likelihood χ^2**	**df**	**p-value**	**Improvement $\chi 2$**	**df**	**p-value**	**Rho-rsq**[b]
Habitat	35.215	4	0.000				0.231
Habitat, Distance	59.493	5	0.000	24.278	1	0.000	0.391
Habitat, Dist., Grp Size[a]	72.391	6	0.000	12.898	1	0.003	0.476

[a] Model with the best fit

[b] McFaddens' Rho-square

Table 1.2. Coefficients, standard errors, probabilitites of significance (t-ratio), and odds ratios for group size, distance and habitat parameters used in a logistic regression model for deer sightability in northeastern Washington during fall 2003.

Parameter	**β**	**SE**	**P**	**Odds Ratio**[a]
β_1 Group Size	0.682	0.222	0.002	0.505
β_2 Distance	-0.044	0.011	0.000	1.045
β_3 Habitat (Clear Cut)	0.463	0.526	0.379	0.629
β_3 Habitat (Forest)	-3.291	0.682	0.000	26.864
β_3 Habitat (Agricultural)	2.498	0.738	0.001	0.082
β_3 Habitat (P Pine)	0.330	0.500	0.510	0.719
Intercept	1.868	0.788	0.018	

[a] Odds ratio = Exp (β); the factor by which the odds that a deer will be sighted change for every unit increase in the independent variable.

Table 1.3. Raw (obs) and corrected (cor) numbers of deer observed in each of four habitat types from ground surveys in 2003 for northeastern WA.

	Habitat Types									
	Clear Cut		**Forest**		**Agricultural**		**Ponderosa Pine**		**Totals**	
Deer Species	**Obs**	**Cor**	**Obs**	**Cor**	**Obs**	**Cor**	**Obs**	**Cor**	**Obs**	**Cor**
Mule Deer										
Individual	17	18	155	431	152	159	31	31	355	639
Group	10	10	96	96	31	31	13	13	150	150
White-tailed Deer										
Individual	25	25	242	981	520	550	56	56	843	1612
Group	16	16	135	135	138	138	28	28	317	317
Total Deer										
Individual	42	43	397	1412	672	709	87	87	1198	2251
Group	26	26	231	231	169	169	41	41	467	467

Table 1.4. Estimated total (N) and relative (%) numbers of white-tailed deer and mule deer from corrected ground and aerial surveys in 2002-2004 in northeastern WA.

			White-tailed Deer		**Mule Deer**	
			N	%	N	%
Ground Survey	Annual	Study Area	1612	(71.6)	639	(28.4)
		Wedge	1130	(81.6)	255	(18.4)
		Republic	482	(55.7)	384	(44.3)
	Summer	Study Area	1139	(73.3)	416	(26.8)
		Wedge	783	(85.)	138	(15.)
		Republic	356	(56.1)	278	(43.9)
	Winter	Study Area	473	(68.)	223	(32.)
		Wedge	400	(77.8)	114	(22.2)
		Republic	73	(51.8)	109	(48.2)
Aerial Survey	Winter	Wedge	686	(77.8)	196	(22.2)

CHAPTER 2

PREY SELECTION AND KILL RATES OF COUGARS IN NORTHEASTERN WASHINGTON

ABSTRACT

We investigated prey selection of cougars in northeastern Washington during 2002-2004, where sympatric white-tailed deer and mule deer are the primary and secondary prey species, respectively. We tested two competing hypotheses of prey selection, the “prey switching” hypothesis, and the “apparent competition” hypothesis. . To estimate use of prey by cougars, we examined 60 cougar kills. White-tailed deer comprised 60% of the kills (mule deer comprised 40%), a proportion larger than the study area’s prey population (70% white-tailed deer vs. 30% mule deer). Cougars selected for mule deer across the entire study area. We also detected strong seasonal changes in prey selection, with cougars strongly selecting for mule deer in summer, but not during winter. Mean annual kill rate was 6.68 days per deer killed. Kill rates did not differ between seasons or deer species. Habitat characteristics of kill sites did not differ significantly between white-tailed deer and mule deer kills. These findings are consistent with the apparent competition hypothesis and suggest that the current decline in mule deer numbers in northeastern Washington is caused by an abundant invading primary prey species (white-tailed deer) and a related increase in predation on the secondary prey species (mule deer) during summer months.

INTRODUCTION

Within the last ten years, a major change in the population structure of deer in Western North America has taken place. Native mule deer (*Odocoileus hemionus)* populations have sharply declined, while non-native white-tailed deer (*Odocoileus virginianus)* populations have increased (Gill 1999). Recent work on sympatric deer in California (Bleich and Taylor, 1998) and south-central British Columbia (Robinson et al. 2002) showed that cougar predation was a major mortality factor for both deer species. Robinson et al. (2002) found that increasing sympatric white-tailed deer (primary prey) were more numerous than declining mule deer (secondary prey), but that intrinsic growth rates (birth rates) were not different between the two species. The study also found that per capita predation rates by cougars were greater for mule deer than for white-tailed deer, especially during summer, and that predation rates increased with increasing prey density for white-tailed deer, but increased with decreasing prey density for mule deer.

Two hypotheses could explain these differences in predation, including the "apparent competition" hypothesis, (Holt 1977), and the "prey switching" hypothesis (Holling 1961). The apparent competition hypothesis predicts that a primary prey species can increase predator numbers; thereby having a negative effect on a secondary prey through the commonly shared predator. The secondary prey can decline through, 1) lower reproductive rates if predation rates are proportionate to abundance, or 2) disproportionate predation rates (prey selection) if reproductive rates are similar. Prey switching occurs when the focus of a predator is switched from one prey type to another after the "alternate" prey species increases beyond some threshold density. The secondary prey can decline because of disproportionate predation caused by a shift in the predator's search image and/or habitat use.

If apparent competition is occurring in a predator-prey community, we would expect to see cougars following their primary prey and residing in its habitat (white-tailed deer), while killing (selecting) the secondary prey, mule deer, at a higher rate in the same habitats. Therefore, cougars would select for, or disproportionately kill, mule deer simply because they have greater success killing them than white-tailed deer. The kill rates should be equal to or higher than that of white-tailed deer despite greater body mass in mule deer. If prey switching is occurring, we would expect to see a shift in habitat use by the predator, as predators change their search image to seek out the more abundant secondary prey species. In this case, kill rate (days/kill) should also be lower when cougars prey on mule deer because of their greater body mass (Silva and Downing 1995). Seasonal abundance of mule deer should surpass white-tailed deer concurrent with the prey shift. Habitats at mule deer kill sites should be different than white-tailed deer kill sites; indicating that cougars purposefully shift to and select for mule deer in their associated habitats.

In this paper, we test Robinson's (2002) prediction that cougars select for mule deer over sympatric white-tailed deer. We also test the apparent competition and prey switching hypotheses, if such selection occurs. Specifically, our objectives were to 1) determine the relative proportions of white-tailed deer and mule deer available to cougars, 2) determine the relative proportions of cougar-killed white-tailed deer and mule deer, 3) determine the kill rate (kills/cougar/unit time) for white-tailed deer and mule deer, and 4) compare habitat characteristics at white-tailed deer and mule deer kill sites.

STUDY AREA

The study area covers approximately 3,800 km^2 in northeastern Washington. Boundaries extend from the Okanogan/Ferry County line west to the Columbia River, and from the Canadian/US border south to the Colville Indian Reservation. The study area lies entirely within the Okanogan Highlands physiographic province, composed of glacially subdued mountainous terrain, with elevations ranging from 400 m in the Columbia River valley to 2130 m at the top of the Kettle Crest. Forest overstory species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Inland maritime conditions characterize the climate, with mean temperatures ranging from –6 °C in January to 21 °C in July, and annual precipitation of 46 cm. Snowfall averages 136 cm during a 6-month period from mid-November to mid-April.

Field efforts were concentrated in two separate areas separated by the Kettle River. “The Wedge” study area lies to the east of the Kettle River, and the “Republic” area lies to the west of the River and the Kettle Crest Mountain Range. We conducted analyses on each replicate study area separately.

Robinson et al. (2002) found that white-tailed deer (*Odocoileus virginianus*) were the most abundant ungulate in a nearby study area, followed by mule deer (*Odocoileus hemionus*). Since climate and physiography create seasonally migratory deer populations, both white-tailed deer and mule deer congregate on winter ranges between December and April. Deer winter ranges are generally on south to west-facing gentle slopes in timber stands with higher canopy closure, providing wind and snow breaks

(Pauley et al. 1993, Armeleder et al. 1994). Across the study area, higher elevation winter ranges (i.e., 900-1200 m) are almost exclusively occupied by mule deer, whereas lower elevation ranges (i.e., ≤ 900 m) are predominantly used by white-tailed deer. During summer white-tailed deer move up in elevation and intermix with mule deer.

METHODS

Cougar Kills

We located cougars by observing cougar tracks from snowmobiles, trucks, and on foot. Trained hounds treed cougars, which were then immobilized with a 2ml mixture of Ketamine hydrochloride (3 mg/kg) and Medetomidine hydrochloride (.08 mg/kg) delivered via brown charged aluminum darts from a Cap Chur rifle (Cap-Chur, Inc., Powder Springs, GA). We used a drop net at the base of the tree to reduce any injuries from a fall. If a cougar remained in a tree, it was lowered to the ground using a rope secured around its chest or shoulder.

While immobilized, we classified each cougar into one of three age classes (kitten < 1yr, subadult 1-2 yrs, adult > 2yrs) based on gum regression (Shaw 1987). We fitted the cougar with two numbered ear tags and a mortality-sensitive VHF radio-collar. For details on capturing and collaring see Lambert (2003).

We located cougars approximately once per week using fixed wing aircraft. Two H antennas mounted underneath each wing allowed us to accurately determine cougar positions, which we marked with a Garmin (Garmin International, Inc., Olathe, KS) Global Positioning System (GPS) unit. We also kept track of cougar movements using ground telemetry and/or snow tracking several times per week on cougars throughout the study. Individual cougars were monitored over 21-day predation sequences (Murphy 1998, Nowak 1999). Daily locations were determined by plotting three or more converging bearings taken in the field. Error polygons were established in LOAS (Location of a Signal) telemetry triangulation software (Ecological Software Solutions, Sacramento, CA), and plotted on 1:24,000 United States Geological Survey topographic maps.

We discovered cougar kills by visiting sites that cougars occupied the previous day, and searched for a kill with the help of hounds. Searched locations were typically 100 m x 100 m (1 ha) in size. When a kill was located, we determined whether cougars were responsible based on the proximity to cougar locations and field sign (e.g., cougar bed site, cougar tracks or scat, and signs that the carcass had been covered or cached) (Shaw 1987). We determined deer species by examining the metatarsal gland on the outside of the lower hind leg. White-tailed deer have a relatively small, white metatarsal gland (30 mm long), whereas mule deer have a larger (50-150 mm long), darker metatarsal gland (Verts and Carraway 1998).

Time since the kill was calculated by recording the first day that the cougar was located at the site, and by noting the condition of blood and exposed muscle on the carcass, presence of maggots on the carcass, and knowledge of recent weather conditions that may affect the condition of the kill. We then assigned a kill date to the carcass, and calculated a predation sequence (interval, in days, between two consecutive kills) for each cougar.

Prey Availability

We determined relative prey availability for collared cougars using a dynamic sampling technique that followed cougar movements throughout their home ranges. While monitoring collared cougars, we recorded all live white-tailed deer and mule deer encountered on foot or in a vehicle. To ensure that deer were truly available to cougars, we included only those deer within the cougar home range. On occasions when transects (roads, trails) were covered more than once per day, we recorded deer sightings only one time per day.

Each time a group or a single deer was observed, the date, time, Universal Transverse Mercator (UTM) coordinate, species, number of animals, sex, age, habitat, and the straight-line distance from our position were recorded. We classified deer as male or female, and adult, yearling, or fawn. Habitat types were classified as open ponderosa pine, dense mixed forest, clear-cut, or agricultural. To incorporate an estimate of detection probability to our deer count, we developed a sightability model using life-sized deer decoys as "marked deer" (see chpt.1). We used logistic regression (LR) analyses (Proc Logistic, SAS Institute, Cary N.C.) to test for effects of group size, distance, and habitat on deer sightability, then used that LR model on deer sightability to calculate corrected relative numbers of live white-tailed deer and mule deer on survey transects.

We also conducted a late winter helicopter survey to estimate relative prey availability on one part of the study area (The Wedge) to compare against the ground count. Before the survey, we identified 20 subunits distinguishable from the air by roads, drainages, and topographic features. Size of subunits ranged from about 4 km^2 to 17 km^2 and each required less than one hour to survey. The data collected from our ground counts, along with knowledge of the district biologists helped us to define and stratify subunits as low or high white-tailed deer and mule deer density (Robinson et al. 2002).

In February 2004, we surveyed all 20 subunits following methods of Unworth et al (1999)to determine relative white-tailed deer and mule deer availability. The same primary observer and pilot were used throughout the survey, while secondary staff varied from day to day. Point estimates, variances, and confidence intervals were calculated based on formulas in the Mule Deer Spring model in program AERIAL SURVEY version 1.0 (Unsworth et al. 1999).

We compared the proportion 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 seasonal vs. annual proportions, and proportions of deer species in the entire study area vs. the two sub-areas (The Wedge, Republic). We used the chi square test of homogeneity for all comparisons.

Prey Selection and Kill Rates

Because of small sample sizes of kills for individual cougars, we tested if 2nd order landscape availabilities (The Wedge and Republic) were the same as 3rd order home range availabilities (Johnson 1980). Using 2nd order availabilities would allow us to include kills of animals with unspecified home ranges (< 32 radiolocations). We compared relative availability of white-tailed deer and mule deer within the 95% adaptive kernel home range for each cougar to relative availabilities on a broader, composite home range, landscape scale (The Wedge and Republic) using the t-test. If home range and landscape availabilities were not different, we used landscape availabilities and kills of all cougars to test for prey selection. We calculated a 95% adaptive kernel home range for each cougar with greater than 32 locations using the animal movement extension for ArcView (ESRI, Redlands, California, U.S.A.). Thirty-two locations were found to be adequate to describe home ranges by Logan and Sweanor (2001), additionally 30 locations is sufficient to approximate the standard normal distribution (Zar 1984). We experienced small sample sizes of kills for individual cougars because of very high cougar mortality across the study area; very few cougars lived for > 1 year (Lambert 2003).

We then tested for prey selection by comparing observed and expected numbers of white-tailed deer and mule deer kills for each individual cougar using the chi-square goodness of fit test. Expected kills were calculated by multiplying the total number of kills by the relative availability of each species in The Wedge and Republic. Because of small sample sizes of kills for each animal, we tested if kills could be pooled across cougars using the heterogeneity chi-square test (Zar 1984). If the heterogeneity chi-square test was not significant, we totaled all observed and expected values for deer in each study area (The Wedge and Republic) and performed a chi-square goodness of fit test on the totals. We performed this analysis on The Wedge and Republic separately. If pooling was justified for each area, we then performed the heterogeneity chi-square test on the study area as a whole. Once again, if differences were not significant, we pooled across both areas to increase sample sizes of kills.

To analyze seasonal selection, we used summer (May 1 through October 31) and winter (November 1 through April 30) observed and expected values. We used seasonal species-specific availabilities and deer kills from The Wedge and Republic to calculate expected values. A heterogeneity chi-square test was used to determine if seasonal selection could be pooled across cougars. If chi-square test of heterogeneity yielded no differences in selection of prey within the entire study area geographic area, we pooled seasonal selection across the entire study area.

For each of the preceding selection analyses, we calculated mean use/availability, or selection ratios (Manly et al. 1993), and tested for differences in mean selection ratios for mule deer and white-tailed deer with a t-test. We used a one-tailed test in selection ratio analyses because we hypothesized that cougars select for mule deer over white-tailed deer.

To estimate kill rate of cougars from predation sequences, we calculated the number of days between two consecutive deer kills (inter-kill interval). We pooled all inter-kill intervals for a mean annual and seasonal kill rate. Summer intervals occurred from 1 May through 31 October, and winter intervals occurred from 1 November through 30 April. To determine if kill rate differed between seasons, we used a t-test. We also used a t-test to compare kill rate following white-tailed deer kills to kill rate following mule deer kills.

Habitat Characteristics at Kill Sites

To determine whether mule and white-tailed deer were killed in different habitats, we recorded 9 habitat variables within a 25 m radius plot from the site center of each kill site. Variables included elevation, physiography (ridge crest, stream valley, cliff/rock bench, open slope, or forested slope), habitat type (mixed conifer, mixed forest, ponderosa pine, shrub steppe, riparian, clear-cut, or agricultural), tree species, slope, aspect, snow depth, canopy density (measured with a densitometer), shrub density (measured visually by estimating percent cover of 5.64 m radius circle surrounding kill). We used a chi-squared test of homogeneity to test for differences in categorical variables (physiography, habitat type, and aspect) between white-tailed deer kill sites and mule deer kill sites. A t-test was used to compare continuous variables (elevation, slope, snow depth, canopy density, and shrub density) between kill sites of mule deer and white-tailed deer. We tested for seasonal differences in kill sites (summer vs. winter) using identical techniques.

RESULTS

Cougar Kills

During 2002 through 2004, we monitored 14 (12 females and 2 males) of 19 collared cougars to determine prey selection and kill rate (5 cougars were inaccessible or died shortly after capture). We completed 27, 21-day monitoring sequences. Fourteen additional sequences were incomplete, as the animal moved into an inaccessible location, across the US/Canadian border, out of the study area.

From May 2002 to March 2004, we found 60 cougar-killed deer. Cougars killed more white-tailed deer during both winter ($\chi^2 = 5.14$, d.f. = 1, p = 0.02) and summer seasons ($\chi^2 = 3.5$, d.f. = 1, p = 0.06). We identified 35 white-tailed deer kills (58%), 23 mule deer kills (38%), but were unable to differentiate species of 2 kills (4%). During winter, white-tailed deer comprised 65% of kills and mule deer comprised 35% of kills. During summer, white-tailed deer comprised 57% of kills and mule deer comprised 38% of kills (5% of kills were unidentified).

Prey Availability

Raw counts of deer available to collared cougars indicated that white-tailed deer were more abundant than mule deer, with more groups (317 vs. 150) and total individuals (843 vs. 355). The uncorrected relative deer population across the entire study area (The Wedge and Republic) was 70% white-tailed deer and 30% mule deer. Our sightability model (see Chapter 1) increased the estimated number of white-tailed deer from 843 to 1612 (+ 191%), and mule deer from 355 to 639 (+ 180%). The corrected relative availability across the study area was 72% white-tailed deer and 28% mule deer. The February 2004 aerial survey on The Wedge also indicated that white-tailed deer comprised the bulk of the deer population ($\chi^2 = 2997$, d.f. = 1, $p < 0.001$), with an estimated population size of 1,384 ± 221 white-tailed deer (80%) and 354 ± 83 mule deer (20%).

We detected significant differences in seasonal ($\chi^2 = 6.59$, d.f. = 1, $0.01 < p < 0.025$) and spatial ($\chi^2 = 176.33$, d.f. = 1, $p < 0.001$) deer availability across the study area (see chpt.1). White-tailed deer comprised 68% and mule deer 32% in winter. White-tailed deer comprised 73% and mule deer comprised 27% in summer. Annual availability on The Wedge was 82% white-tailed deer and 18% mule deer, and availability in Republic was 56% white-tailed deer and 44% mule deer (Table 2.1). Chi square results yielded no difference ($\chi^2 = 0.0002$, d.f. = 1, $p > 0.10$) between the ground survey and helicopter survey on The Wedge during winter. Percentages of available deer appeared higher than the percentages of kills for white-tailed deer (70% available vs. 60% killed) and lower than the percentages of kills for mule deer (30% available vs. 40% killed). At no time or location did mule deer abundance equal or exceed white-tailed deer abundance.

Prey Selection and Kill Rates

Mean prey availability within home ranges was not different from landscape availabilities on The Wedge ($t = -0.34$, $p = 0.75$) and Republic ($t = 0.49$, $p = 0.67$), allowing landscape availabilities to be used to test for prey selection. Mean home range availabilities on The Wedge were 0.83 (± 0.09 SD) for white-tailed deer and 0.17 (± 0.09

SD) for mule deer compared to 0.82 and 0.18 for landscape availability across The Wedge. Mean home range availabilities in Republic were 0.58 (± 0.08 SD) for white-tailed deer and 0.42 (± 0.08 SD) for mule deer compared to 0.56 and 0.44 for landscape availability across Republic.

At the 3rd order (home range) of selection, only 3 of 13 individual cougars selected for mule deer (Table 2.1). However, chi-square tests of heterogeneity yielded no differences among selection, allowing cougars to be pooled within areas (Table 2.1). Pooled chi square goodness of fit values yielded significant 2nd order (landscape) selection for mule deer on The Wedge ($\chi^2 = 2.82$, d.f. = 1, $p = 0.09$), but not in Republic ($\chi^2 = 1.99$, d.f. = 1, $p = 0.16$) (Table 2.1). Mule deer selection ratios across the study area were not different from white-tailed deer ratios on The Wedge ($t = -1.37$, d.f. = 14, $p = 0.10$) and Republic ($t = -1.09$, d.f. = 10, $p = 0.15$) (Table 2.1). However, chi square tests of heterogeneity yielded no differences among The Wedge and Republic ($\chi^2 = 11.28$, d.f. = 13, $p = 0.59$), allowing cougars to be pooled across areas. Pooled chi square goodness of fit tests indicated that cougars selected for mule deer across the entire study area ($\chi^2 = 4.42$, d.f. = 1, $p = 0.04$). The mule deer selection ratio (1.53) for the entire study area was also higher than the white-tailed deer ratio (0.82) ($t = -1.75$, d.f. = 26, $p = 0.05$).

Cougars strongly selected for mule deer during summer ($\chi^2 = 4.28$, d.f. = 1, $p = 0.04$), but not during winter ($\chi^2 = 0.04$, d.f. = 1, $p = 0.84$) (Table 2.2). Selection ratios also showed significant selection for mule deer (1.441 vs. 0.829) over white-tailed deer, $t = -1.51$, d.f. = 22, $p = 0.07$) in summer, but not during winter (1.043 vs. 1.028) ($t = 0.04$, d.f. = 16, $p = 0.49$).

Mean annual kill rate of cougars was 6.68 days per deer kill (SD = 3.12; range = 2.0-14.0, n = 22 sequences). Kill rates did not differ between seasons (6.56 days/kill for summer and 7.0 days/kill for winter, t = -0.29, df = 20, p = 0.78) or deer species (7.00 days/kill for white-tailed deer and 6.14 days/kill for mule deer, t = 0.58, df = 19, p = 0.58).

Habitat Characteristics at Kill Sites

We assessed habitat variables at 55 kill sites (30 white-tailed deer and 25 mule deer) (Tables 2.3 & 2.4). All chi-square tests showed no difference (χ^2 = 0.18 – 0.85, d.f. = 1-3, p > 0.05) between white-tailed deer kill sites and mule deer kills sites. T-tests (t = 0.16 - 0.95, d.f. = 23-53, p > 0.05) also showed no differences in mule deer vs. white-tailed deer kill sites for the entire study area. We found a seasonal difference in habitat type (χ^2 = 6.63, d.f. = 2, p = 0.04) at kill sites, however no other habitat characteristics showed seasonal differences. When broken into geographic areas, mule deer kills were located in higher elevations than white-tailed deer kills in The Wedge during summer (t = 1.91, d.f. = 31, p = 0.07). Small sample sizes prevented me from analyzing kill sites in Republic.

DISCUSSION

Across the study area and within The Wedge, cougars selected for mule deer over white-tailed deer during the year. When examined seasonally, cougars strongly selected for mule deer during the summer but not during the winter, and in no season or location did they select for white-tailed deer. The annual kill rate of 7 days for cougars falls within the range of 7 to 11 days reported by other investigators (Hornocker 1970, Beier et al. 1995, and Murphy 1998). The interval may be at the low end because 15 of the 22 intervals were from female cougars with kittens, which typically show a higher kill rate than single adults (Murphy 1998). Only 2 intervals were from a male cougar (8 and 11 days). We found no differences in habitat characteristics between mule deer and white-tailed deer kill sites.

Our results indicate that cougars select for mule deer on a seasonal basis. White-tailed deer comprised the primary prey during both seasons, but disproportionate predation of mule deer occurred during the summer as cougars followed white-tailed deer into mule deer range during that season. Furthermore, our results on kill rate and habitat use are inconsistent with the "prey switching" hypothesis. Mule deer availability never equaled or exceeded white-tailed deer availability. Cougars showed no shift in habitat use at mule deer and white-tailed deer kill sites, and there were no differences in kill rates for white-tailed deer and mule deer; suggesting that cougars did not switch their search image to seek out more numerous, larger mule deer during the summer. These findings support the apparent competition hypothesis. Total numbers of cougar kills indicate that white-tailed deer are the primary prey of cougars (Tables 2.1 & 2.2). However, to fully understand predator-prey relationships, both use and availability must be taken into consideration (Johnson 1980). Cougars did not select for white-tailed deer, but selected for mule deer during the summer. It is evident that cougars, while primarily subsisting on white-tailed deer, are disproportionately affecting the mule deer population, as suggested by Robinson et al. (2002).

The similar kill rates between mule deer and white-tailed deer also suggest that cougars select for, or disproportionately kill, mule deer during the summer because they are easier to kill. The larger body mass of mule deer should result in a greater inter-kill interval, but this was not the case. Lingle (2002) suggested different anti-predator behaviors and escape mechanisms for white-tailed deer and mule deer as reasons for predator effectiveness. As a first line of defense, mule deer remain in high and rugged habitats as much as possible to minimize their exposure to predators and dissuade attacks. However, once encountered, mule deer are slower, and less able to avoid attack and capture. This appears to be the case in our study area.

From the seasonal selection that we found and the elevational shift of kill sites from lower to higher in summer, it is apparent that during winter, cougars occupy lower elevations and gentle slopes typical of white-tailed deer winter ranges (Pauley et al. 1993, Armeleder et al. 1994); and in the summer shift their home range use, following the elevational migration of white-tailed deer. When cougars move into higher terrain, they are more likely to overlap areas used by mule deer (rugged terrain, steep slopes, avg. summer elevation = 1800m) (Pauley et al. 1993, Armeleder et al. 1994). As a result, incidental encounters between mule deer and cougars increase. Katnick (2002) found similar relationships with cougar predation of white-tailed deer and mountain caribou.

His results showed annual landscape scale selection for white-tailed deer, and seasonal (summer) selection for caribou. He attributed this to a shift in elevation by deer, causing a high amount of spatial overlap between cougars and caribou during the summer months. Results of Robinson et al. (2002) also suggest this seasonal pattern of predation. In their area, the greatest difference in cougar predation rates between white-tailed deer and mule deer occurred during the summer.

Robinson et al. (2002) first suggested that the patterns of cougar predation on white-tailed deer and mule deer population growth rates fit the apparent competition theory. His observed mule deer decline, although directly attributed to cougars, was ultimately caused by an abundance of invading primary prey (white-tailed deer). As white-tailed deer numbers are increasing, mule deer have become secondary prey species, and are now at risk of depensatory predation. We urge other researchers to test for seasonal prey selection and apparent competition in systems with an invading, non-native primary prey and a declining secondary prey species.

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Table 2.1. Chi-square test results and selection ratios for 2^{nd} order cougar prey selection in northeastern Washington, during 2002-2004. Prey availability within study areas, observed deer kills, and expected deer kills are given for white-tailed deer (WT) and mule deer (MD). Omnibus statistics show results of pooling across areas and cougars.

		Availability		Observed		Expected				Selection Ratios	
	Cougar	**WT**	**MD**	**WT**	**MD**	**WT**	**MD**	**χ2**	**p**	**WT**	**MD**
Wedge	**102**	0.82	0.18	3	0	2.45	0.55	0.68	0.41	1.23	0.00
	223	0.82	0.18	5	3	6.53	1.47	1.94	0.16	0.77	2.04
	293	0.82	0.18	7	1	6.53	1.47	0.19	0.67	1.07	0.68
	402	0.82	0.18	0	1	0.82	0.18	4.56	0.03	0.00	5.56
	423	0.82	0.18	3	3	4.90	1.10	3.99	0.05	0.61	2.72
	662	0.82	0.18	5	2	5.71	1.29	0.48	0.49	0.88	1.55
	473	0.82	0.18	1	0	0.82	0.18	0.23	0.63	1.23	0.00
	683	0.82	0.18	3	1	3.26	0.74	0.12	0.73	0.92	1.36
Total χ2								12.17	0.14		
Pooled χ2				27	11	31.01	6.99	2.82	0.09	0.84	1.74
Heterogeneity χ2								9.35	0.23		
Republic	**145**	0.56	0.44	0	1	0.56	0.44	1.26	0.26	0.00	2.26
	154	0.56	0.44	1	6	3.90	3.10	4.85	0.03	0.26	1.93
	191	0.56	0.44	1	0	0.56	0.44	0.80	0.37	1.80	0.00
	261	0.56	0.44	4	2	3.34	2.66	0.29	0.59	1.20	0.75
	341	0.56	0.44	1	1	1.11	0.89	0.03	0.87	0.90	1.13
	593	0.56	0.44	1	2	1.67	1.33	0.61	0.44	0.60	1.50
Total χ2								6.58	0.36		
Pooled χ2				8	12	11.13	8.87	1.99	0.16	0.79	1.26
Heterogeneity χ2								4.59	0.47		
Omnibus χ2								13.99	0.45		
Pooled χ2				35	23	42.14	15.86	4.42	0.04	0.82	1.53
Heterogeneity χ2								11.28	0.59		

Table 2.2. Chi-square test results and selection ratios for seasonal 2^{nd} order cougar prey selection in northeastern Washington, during 2002-2004. Prey availability within cougar home ranges, observed deer kills, and expected deer kills are given for white-tailed deer and mule deer.

		Availability		Observed		Expected				Selection Ratios	
	Cougar	**WT**	**MD**	**WT**	**MD**	**WT**	**MD**	**χ2**	**p**	**WT**	**MD**
Summer											
Wedge	102	0.85	0.15	3	0	2.55	0.45	0.53	0.47	1.18	0.00
	223	0.85	0.15	3	2	4.25	0.75	2.46	0.12	0.71	2.67
	293	0.85	0.15	5	1	5.10	0.90	0.01	0.91	0.98	1.11
	423	0.85	0.15	2	2	3.40	0.60	3.85	0.05	0.59	3.34
	473	0.85	0.15	1	0	0.85	0.15	0.18	0.67	1.18	0.00
	662	0.85	0.15	1	1	1.70	0.30	1.93	0.17	0.59	3.34
	683	0.85	0.15	2	0	1.70	0.30	0.35	0.55	1.18	0.00
Republic	154	0.56	0.44	0	4	2.25	1.75	5.12	0.02	0.00	2.28
	191	0.56	0.44	1	0	0.56	0.44	0.78	0.38	1.78	0.00
	261	0.56	0.44	2	2	2.25	1.75	0.06	0.80	0.89	1.14
	341	0.56	0.44	1	1	1.12	0.88	0.03	0.86	0.89	1.14
	593	0.56	0.44	0	1	0.56	0.44	1.28	0.26	0.00	2.28
Total χ2								16.58	0.17		
Pooled χ2				21	14	26.29	8.71	4.28	0.04	0.829	1.441
Heterogeneity χ2								12.30	0.34		
Winter											
Wedge	223	0.78	0.22	2	0	1.56	0.44	0.57	0.45	1.29	0.00
	293	0.78	0.22	2	0	1.56	0.44	0.57	0.45	1.29	0.00
	423	0.78	0.22	1	1	1.56	0.44	0.90	0.34	0.64	2.25
	662	0.78	0.22	3	1	3.11	0.89	0.02	0.89	0.96	1.13
	683	0.78	0.22	1	1	1.56	0.44	0.90	0.34	0.64	2.25
Republic	145	0.60	0.40	0	1	0.60	0.40	1.50	0.22	0.00	2.50
	154	0.60	0.40	1	2	1.80	1.20	0.89	0.35	0.56	1.67
	261	0.60	0.40	2	0	1.20	0.80	1.33	0.25	1.67	0.00
	593	0.60	0.40	1	1	1.20	0.80	0.08	0.77	0.83	1.25
Total χ2								6.76	0.66		
Pooled χ2				13	7	12.55	7.45	0.04	0.84	0.875	1.228
Heterogeneity χ2								6.71	0.57		

Table 2.3. Continuous variables from habitat characteristics at kill sites of white-tailed deer and mule deer investigated during 2002-2004 in northeastern Washington.

	White-Tailed Deer		Mule Deer	
Feature	**n**	**Mean (SD)**	**n**	**Mean (SD)**
Mean Slope (degrees)	29	6.6 (4.9)	24	7.8 (4.6)
Mean Snow Depth (cm)	15	8.13 (11.3)	10	9 (14.7)
Mean Canopy Density (%)	30	80 (35.8)	25	77.3 (29.3)
Mean Shrub Density (%)	30	38.8 (37.2)	25	34.7 (31.3)

Table 2.4. Categorical variables from habitat characteristics at kill sites of white-tailed deer and mule deer investigated during 2002-2004 in northeastern Washington.

		White-Tailed Deer	**Mule Deer**
	Feature	**n**	**n**
Landform Class	Forested Slope	21	15
	Open Slope	2	2
	Stream Valley	5	4
	Ridge Crest	2	2
Habitat Class	Mixed Conifer	19	11
	Mixed Forest	8	11
	Other	3	2
Aspect	North & East	11	9
	South & West	19	12