

Assessing differential prey selection patterns between two sympatric large carnivores

Jason S. Husseman, Dennis L. Murray, Gary Power, Curt Mack, C. R. Wenger and Howard Quigley

Husseman, J. S., Murray, D. L., Power, G., Mack, C., Wenger, C. R. and Quigley, H. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. – *Oikos* 101: 591–601.

Several conceptual models describing patterns of prey selection by predators have been proposed, but such models rarely have been tested empirically, particularly with terrestrial carnivores. We examined patterns of prey selection by sympatric wolves (*Canis lupus*) and cougars (*Puma concolor*) to determine i) if both predators selected disadvantaged prey disproportionately from the prey population, and ii) if the specific nature and intensity of prey selection differed according to disparity in hunting behavior between predator species. We documented prey characteristics and kill site attributes of predator kills during winters 1999–2001 in Idaho, and located 120 wolf-killed and 98 cougar-killed ungulates on our study site. Elk (*Cervus elephus*) were the primary prey for both predators, followed by mule deer (*Odocoileus hemionus*). Both predators preyed disproportionately on elk calves and old individuals; among mule deer, wolves appeared to select for fawns, whereas cougars killed primarily adults. Nutritional status of prey, as determined by percent femur marrow fat, was consistently poorer in wolf-killed prey. We found that wolf kills occurred in habitat that was more reflective of the entire study area than cougar kills, suggesting that the coursing hunting behavior of wolves likely operated on a larger spatial scale than did the ambush hunting strategy of cougars. We concluded that the disparity in prey selection and hunting habitat between predators probably was a function of predator-specific hunting behavior and capture success, where the longer prey chases and lower capture success of wolf packs mandated a stronger selection for disadvantaged prey. For cougars, prey selection seemed to be limited primarily by prey size, which could be a function of the solitary hunting behavior of this species and the risks associated with capturing prime-aged prey.

J. S. Husseman and D. L. Murray, Dept of Fish and Wildlife Resources, Univ. of Idaho, Moscow, ID 83844-1136, USA (jason_husseman@hotmail.com). Present address of DLM: Depts of Biology and Environmental and Resource Studies, Trent Univ., Peterborough, ON, K9J 7B8 Canada. – G. Power, Lemhi County Winter Predator Study, Salmon, ID 83467, USA. – C. M. Mack, Nez Perce Tribe, PO Box 365, Lapwai, ID 83501, USA. – C. R. Wenger, USDA Forest Service, Salmon-Challis National Forest, Salmon, ID 83467, USA. – H. Quigley, Hornocker Wildlife Institute, Bozeman, MT 59718, USA.

The patterns of prey selection exhibited by various predator species tend to be shaped by a suite of factors, including predator and prey behavior, morphology, and habitat requirements related to hunting or escape (Bakker 1983, Kruuk 1986). In general, such factors interact to affect predator-prey encounter and capture probabilities, and thus ultimately determine prey selec-

tion patterns occurring within a particular predator-prey system (Pastorok 1981, Sih and Moore 1990, Litvak and Leggett 1992). Yet, even within a given prey species the attributes of depredated individuals may vary spatially, temporally, or between predator species, implying that patterns of differential prey vulnerability to predation need not always follow a standard model.

Accepted 17 October 2002

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ISSN 0030-1299

Indeed, while the notion that predators select disadvantaged individuals disproportionately from the prey population has received widespread empirical support (Errington 1946, Curio 1976, Keith et al. 1984, Murray 2002), many studies have failed to detect such patterns (Koivunen et al. 1996, Rohner and Krebs 1996, Wirsing et al. 2002). However, the specific reasons for such disparity remain to be fully elucidated for the majority of predator and prey species.

While several hypotheses attempting to explain prey selection patterns have been presented in the literature, their specific relevance may vary across predator-prey systems. For instance, among some invertebrates, ambush predators may be more likely to prey upon older and larger individuals due to their higher visibility, whereas cruising predators should kill prey randomly from the population (Gerritsen and Strickler 1977, Greene 1986). Also, among aquatic invertebrates and piscivores, predators often are gape-limited, and this morphological constraint can elicit size-selective prey selection (Murtaugh 1981, Unger and Lewis 1983, Newman and Waters 1984). For some predator species, group-hunting can serve to reduce morphological disadvantages such that larger prey can be killed when hunted communally (Rosenzweig 1966, Gittleman 1989), while in other predators hunting success rate may determine prey selection patterns through selection for disadvantaged individuals only where prey species are difficult to capture (Temple 1987). For this latter scenario, it follows that differential hunting strategies and hunting success rates between predators may account for variability in prey selection patterns, even within a given prey species. However, it is important to note that few empirical comparisons of the above hypotheses currently exist, particularly for terrestrial vertebrates where both the dynamic nature of predator-prey relationships, as well as the difficulty in observing chase sequences and prey selection, render any such research particularly difficult.

Canids are coursing predators, and thus typically exhibit prolonged pursuit of prey through relatively open terrain (Estes and Goddard 1967, Kruuk 1972, Schaller 1972). Because canids usually chase swift prey, capture success tends to be low and depredated individuals typically are disadvantaged in some way (Pimlott 1967, Schaller 1972, Ewer 1973, Kunkel et al. 1999). In contrast, felids generally stalk prey and rely more upon cover to remain concealed prior to a chase; the absence of a prolonged pursuit in felids should favor random choice of individuals from a prey population (Rosenzweig 1966, Estes and Goddard 1967, Kleiman and Eisenberg 1973, Caro and Fitzgibbon 1992). These patterns imply that when canids and felids are sympatric and thus rely upon the same food base, both predators should select prey having different demographic or physical attributes.

Gray wolves (*Canis lupus*) are group hunting, coursing predators preying nearly entirely upon ungulates in winter (Mech 1970, Mech and Frenzel 1971, Carbyn 1983, Huggard 1993). Because wolves are reliant upon pursuit for prey capture, the location where they kill prey probably is influenced more by specific prey attributes rather than habitat characteristics, with kills likely occurring when prey become exhausted or exhibit discernible disadvantage. Cougars (*Puma concolor*) are solitary stalking predators that also depend heavily upon ungulate prey in winter (Hornocker 1970, Murphy 1998, Kunkel et al. 1999). The stalking approach and short pursuits exhibited by cougars favors kills occurring in habitats providing sufficient concealment in the form of structural cover, and thus kills should be located in habitat types conducive to prey encounter and capture.

The objectives of this paper were to compare patterns of prey selection and hunting habitat between two sympatric large carnivores exhibiting differing hunting behavior patterns. We sought to test the hypothesis that disparity in hunting behavior between coursing/group hunting versus ambush/solitary predators leads to differential selection of prey and kill site attributes. Specifically, we predicted that i) wolves would kill a greater proportion of young, old, and nutritionally compromised prey relative to cougars. Furthermore, we speculated that ii) wolves would kill prey in areas of less cover than cougars. The difference in hunting behavior between both predator species also should lead to iii) wolf kills occurring in habitat that is more representative of the study area, when examined at a broader spatial scale.

Methods

Study area

The study was conducted in the Salmon River Mountains west of Salmon, Idaho (46°N, 114°W), during January–early April of 1999–2001. The area is characterized by rugged mountain peaks and ridges interspersed with deep drainages. Snow begins to accumulate in October with peak snow depths occurring in February; snow generally persists in valleys and north-facing slopes into early April, with upper elevations retaining snow into May–June. The study area is largely forested, with Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) occurring along slopes and higher elevations; valley bottoms and riparian areas are characterized by ponderosa pine (*P. ponderosa*) and deciduous tree species (*Populus tremuloides*, *P. trichocarpa*, *Salix* sp., *Alnus* sp.), with an understory of shrubs and grasses. The prey complement available within the study area consisted predominantly of elk (*Cervus elaphus*), followed by mule deer (*Odo-*

coileus hemionus); a small number of bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americana*) also resided in the area.

Prey availability

Aerial elk population surveys conducted by Idaho Dept of Fish and Game (1999 and 2001) provided estimates of elk population size and age/sex structure for comparison with the composition of our sample of predator-killed animals (Idaho Department of Fish and Game, unpubl.). These data were collected systematically, with the entire game management unit (GMU) enveloping the study area being divided into sub-units; sub-units were then classified as low, medium, or high density, based on historical trends of elk numbers within each sub-unit. Total flying time spent performing a complete survey of the GMU (approximately 65 hours) was distributed among a sample of sub-units; samples were intentionally skewed towards medium and high density sub-units in order to maximize the number of elk observed. Elk were located by helicopter and classified by age and sex. During 2000, surveys were limited to assessing elk sex- and age-ratios only because the number of sub-units that were surveyed was reduced. Although modest changes in calf/cow and bull/cow ratios occurred between years, these changes were not significant ($P > 0.20$), thus allowing us to pool the three age/sex classes (cows, calves, bulls) over the three years.

Two wolf packs were monitored via aerial and ground-based telemetry. Wolf pack sizes ranged from 7–11 animals, with the exception of the winter of 2000, when one of the two packs was reduced to two individuals. During 2001, in addition to the resident wolf packs, we monitored 2 groups of dispersing wolves consisting of 1–2 animals from nearby and resident packs. Nine cougars were captured and radio-collared over the course of the three-year study, with a maximum of six transmitting individuals on air during any one year of study. An unknown number of uncollared cougars residing in the study area were snow-tracked periodically to supplement our sample of cougar kills.

Carcass recovery and examination

Predator-killed carcasses were located during aerial flights and ground searches within wolf and cougar home ranges. We attempted to maintain daily locations of predators to locate their kills, often by initial aerial observation. When the wolves were accessible by foot, we searched intensively for kills in areas near radio-locations, while the majority of our sample of cougar kills consisted of carcasses from both collared and uncollared individuals that were tracked in snow.

Upon discovery of a carcass, cause of death (predation, starvation, etc.) was determined, followed by identification of predator species responsible for the mortality, as determined by predator-specific injury patterns and other evidence found at the site, such as tracks, scat, and carcass location (O' Gara 1978, Kunkel et al. 1999). Kills were characterized by a definite chase trail, carcass hemorrhaging, or other evidence suggesting a predatory event.

We examined kills for abnormalities, and femur, metatarsus, and mandible bones were collected for marrow fat analysis; because marrow fat analysis provides pre-starvation condition measurements (Mech and Del-Giudice 1985), the method can be used to detect 'doomed surplus' individuals (sensu Errington 1946, Cheatum 1949). The procedure involved removing a 2–3 inch segment of marrow from the central portion of the bone which was then weighed, oven-dried at 60° for 48 hours, and then reweighed to calculate percent dry-to-wet mass of fat (Neiland 1970). A strong correlation between fat content for the various bones (Femur-metatarsus: $r^2 = 0.93$, root mean square error, RMSE = 61.87, $n = 109$; Femur-mandible: $r^2 = 0.75$, RMSE = 187.79, $n = 94$) allowed us to adjust metatarsus and mandible fat values to femur equivalents for carcasses where a femur could not be recovered. We found no effect of prey species on either the femur-metatarsus ($P = 0.22$) or femur-mandible ($P = 0.14$) fat relationship, and thus pooled fat samples between species (Husseman et al., in press). Using simple linear regression, femur equivalents were calculated via:

$$\text{Femur-equivalent} = 5.44 + 0.91(\text{metatarsus fat}) \quad (1)$$

$$\text{Femur-equivalent} = -14.44 + 1.32(\text{mandible fat}) \quad (2)$$

where the independent variable is expressed as a proportion. When both jaw and metatarsus measurements were available as replacements for missing femur measurements, we used the metatarsus value due to the stronger correlation between the two bones.

Age

Prey age was determined by visual assessment of tooth eruption and wear (Robbinette et al. 1957, Quimby and Gaab 1957). Jaws were aged and assigned to one of three qualitative categories: young (1–3), prime-age (4–8), and old (9+). For the 2001 sample, we validated our assessment with cementum annuli analysis (Matson's Laboratory, Milltown, MT, USA). Our blind validation study revealed that of 24 jaws aged using both methods, 88% were correctly categorized, while for the remaining 12%, our visual assessment differed from annuli counts by 1–3 years; therefore, we felt confident in using our ocular estimates of age for

determining patterns of prey selection. During the 2000 fall elk hunt, we also obtained a sample ($n = 31$) of cow elk jaws killed by hunters for use as a reference sample.

Habitat assessment

In order to assess the prediction that hunting behavior influences the habitat where prey are killed, we measured vegetation/topographic cover at documented wolf and cougar kill sites. Vegetative/topographic cover was estimated using a canvas coverboard (Nudds 1977) and expressed as the mean of four measurements taken from the cardinal directions at 25 meters. Also, we established a comparison plot 200 meters in a randomly chosen direction from the kill location, where cover measurements were repeated; this allowed us to determine whether kills occurred randomly with respect to local cover conditions.

Statistical analyses

We used Pearson chi-square analysis to test for differences between elk age/sex class selection and population availability by wolves and cougars, as well as for assessing differences in proportions of age-classes between the two predator species, where aged jaws were categorized as either young, prime age, or old. Differences in percent femur fat were tested using ANOVA, blocking for month of kill (Jan.–March) and prey age (juvenile vs adult elk); bull elk were excluded from the marrow fat analysis due to small sample sizes. All significant parameters were tested for interaction. Prior to analysis, percentage distributions were normalized via arcsine of the square root transformation (Krebs 1999).

We used logistic regression to identify factors characterizing prey selected by wolves versus cougars (Hosmer and Lemeshow 2000). Parameters were evaluated and retained in a forward stepwise manner, and included prey species, sex, age, percent femur fat, year, and month of kill. We also represented femur fat percentages as a discrete measure using < 20 , < 25 , and $< 30\%$ fat content separately as thresholds of severe malnutrition (Keith et al. 1984, but see Mech et al. 1995). Separate analyses were performed using two datasets: i) all prey species, and ii) elk only, which were the predominant prey of both predators. However, we found that results obtained from the analysis of elk only were qualitatively similar to models including all prey. Additionally, because prey species was not a significant variable in predicting predator species responsible for the mortality event, we pooled our sample of kills and limited the analysis to two statistical models: i) an overall model considering all prey samples, and ii) a model excluding adult males to eliminate the potential effect of sex bias on parameter estimation. We

used Akaike Information Criteria with a small sample size correction factor (AIC_c), to determine which parameters were to be retained in the regression model, and differences in model AIC_c 's that exceeded 2.0 were considered to be significant (Burnham and Anderson 1998).

To examine if predator species differed with respect to kill site attributes, we used logistic regression to evaluate habitat differences measured at kill sites, where predator species was the dependent variable. Wolf and cougar kill locations were compared using data collected at the kill site, including percent slope, elevation, aspect (north or south-facing slope) and physiography (slope or bottom/riparian); additionally, we used a Geographic Information System (GIS) data layer describing the major vegetation types within the study area to determine the vegetation classification for a kill location, which we further reclassified into one of four general categories (open terrain, open/ponderosa, dense/fir, deciduous; Salmon National Forest GIS data). Logistic regression also was used to test whether wolves and cougars killed prey in random locations or else were selective with respect to habitat type. Using Arc View (ESRI, Redlands, CA, USA), one- and two-kilometer diameter buffers were plotted around each kill location and a random point selected within each buffer. We determined the attributes at each random point using GIS layers describing slope, aspect, physiography, vegetation type, and elevation (Salmon National Forest GIS data). Kill site attributes were regressed against their corresponding randomly-generated points using logistic regression. This approach enabled us to determine the scale of habitat selection patterns operating for both predator species.

For the previously mentioned logistic regression analyses, all continuous variables retained in the models were checked for conformity to linearity using the quartile method (Hosmer and Lemeshow 2000). Additionally, final models were tested with the Hosmer and Lemeshow goodness-of-fit test statistic (H-L Stat) to ensure model fit (Hosmer and Lemeshow 2000).

We tested for differences in kill site horizontal cover between predators using ANOVA, blocking for elevation, month, year, and study area region. We blocked for canopy closure (the only variable found to affect horizontal cover significantly) when testing for differences between horizontal cover at kill sites. Differences in cover at the kill location and the 200-m comparison plot were analyzed using a paired t-test.

Results

We documented 120 wolf and 98 cougar-killed ungulates during the study. We found little difference in the overall spatial distribution of wolf and cougar kills,

suggesting that both predators were utilizing the same prey base in the same general habitat within the study area (Fig. 1). Elk were the primary prey species found in our sample of kills for both wolves (77%) and cougars (73%), while the remaining prey consisted of mule deer (23%) for wolves, and mule deer (25%), bighorn sheep (1%), and mountain goat (1%), for cougars. The proportion of elk kills differed between years for cougars ($\chi^2 = 6.60$, d.f. = 2, $P = 0.04$), with a greater proportion of deer killed in 2001 than in 1999–2000 (39% deer in 2001 vs 14% and 21% for 1999 and 2000, respectively). The proportion of wolf-killed deer and elk in our sample differed marginally between years ($\chi^2 = 5.97$, d.f. = 2, $P = 0.051$), with deer kills increasing from 10% in 1999 to 30% in both 2000 and 2001.

Prey availability and selection patterns

Overall, aerial surveys of elk in the study area indicated that cows comprised the bulk of the population, followed by calves and bulls; these proportions were largely consistent between years (Fig. 2). We found no annual differences in selection of juvenile (i.e. < 1 yr) versus adult elk by either wolves ($\chi^2 = 1.12$, d.f. = 2, $P = 0.57$) or cougars ($\chi^2 = 2.97$, d.f. = 2, $P = 0.23$), allowing us to pool kill samples from different years for each predator species.

The proportion of elk age/sex classes killed by wolves differed from their availability in the live population ($\chi^2 = 37.72$, d.f. = 2, $P < 0.001$; Fig. 3). Wolves preyed predominantly upon juvenile elk (60%), followed by cow elk (32%) and bulls (8%). Cougar predation on elk age/sex classes also differed from estimates of availabil-

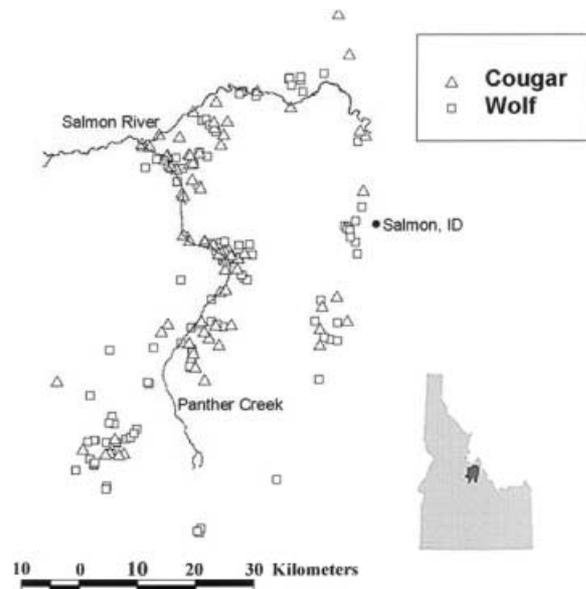


Fig. 1. Distribution of wolf- and cougar-killed elk and deer in east-central Idaho, 1999–2001.

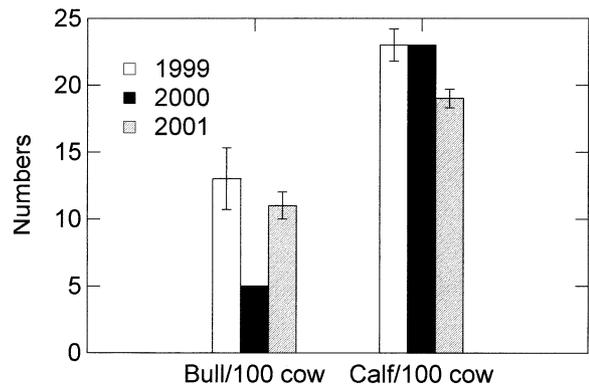


Fig. 2. Estimated ratios (+/- 90% C.I.) for elk bulls and calves relative to cows, in game management unit 28, in east-central Idaho. Confidence bars were not included with 2000 data because too few subunits were flown within the unit.

ity in the population ($\chi^2 = 17.65$, d.f. = 1, $P < 0.001$; Fig. 3); like wolves, cougars killed primarily juvenile elk (51%), followed by cows (46%) and bulls (3%). We found no difference in the proportions of juvenile versus adult elk (cows and bulls) killed by wolves and cougars ($\chi^2 = 1.205$, d.f. = 1, $P = 0.27$).

We were able to classify 82% of wolf-killed ($n = 28$), and 100% of cougar-killed mule deer ($n = 24$) according to age class (fawn versus adult). Wolves killed more juvenile mule deer compared to cougars (wolf-killed fawns: 65%; cougar-killed fawns: 21%; $\chi^2 = 8.85$, d.f. = 1, $P = 0.003$). While we did not have availability estimates for age classes of mule deer, we strongly suspect that wolves, rather than cougars, were primarily responsible for selecting prey in that species, given the unlikelihood that juveniles outnumber adults in the population.

Prey age

We estimated the age of 56 elk aged greater than 1 yr. We found no difference in the age distribution of elk

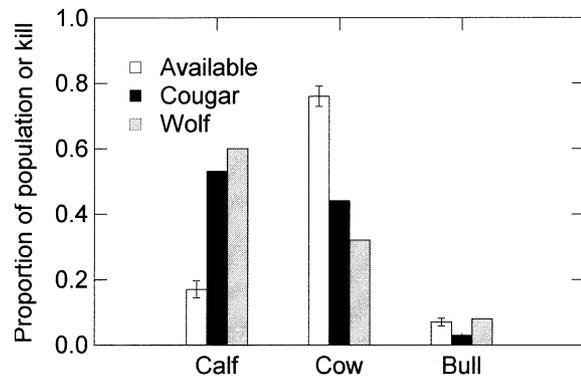


Fig. 3. Age/sex of wolf and cougar-killed elk vs estimated availability in east-central Idaho, 1999–2001. Bars represent the standard error of the availability estimate.

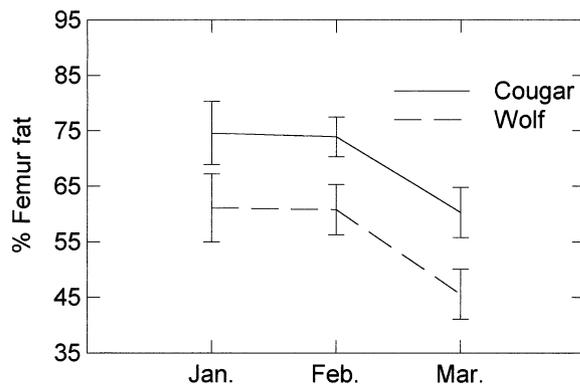


Fig. 4. Percent femur fat by month – excluding bulls – of elk killed by wolves and cougars in east-central Idaho, 1999–2001. Bars represent the standard error of the estimate.

(young, prime-age, old) killed by wolves versus cougars ($\chi^2 = 1.24$, d.f. = 2, $P = 0.54$). Using our ocular categorization of elk teeth, the age distribution of wolf-killed ($\chi^2 = 0.80$, d.f. = 2, $P = 0.67$) and cougar-killed ($\chi^2 = 0.07$, d.f. = 2, $P = 0.96$) elk did not differ significantly from a hunter-killed sample of 32 cow elk. However, for our sub-sample of teeth aged by cementum annuli, we found that the mean age of adult elk killed by wolves ($\bar{x} = 12.6 \pm 1.6$ years, $n = 9$) and cougars ($\bar{x} = 11.6 \pm 1.3$ years, $n = 8$) was significantly older than those killed by hunters ($\bar{x} = 7.3 \pm 0.7$ years, $n = 31$; $F_{2,45} = 7.99$, $P < 0.01$).

Nutritional condition

After blocking for month-of-kill and age class, we found that percent femur marrow fat was significantly less in wolf-killed than cougar-killed elk (wolf: $\bar{x} = 53.9 \pm 2.9\%$, $n = 79$; cougar: $\bar{x} = 68.3 \pm 2.8\%$, $n = 64$; $F_{1,136} = 10.97$, $P = 0.001$). Marrow fat of all age/sex

classes of elk declined dramatically in March; however, selection according to nutritional status remained remarkably consistent between predators (Fig. 4). After blocking for month of kill and age class, we found that mean marrow fat values for wolf-killed mule deer ($\bar{x} = 60.9 \pm 5.6\%$, $n = 18$) were lower than those for cougar-killed mule deer ($\bar{x} = 78.3 \pm 4.6\%$, $n = 18$; $F_{1,29} = 6.25$, $P = 0.02$). Thus, wolves consistently selected prey that were in poorer condition than those killed by cougars.

Logistic regression further revealed that predators selected prey differentially. Results from the full model, with all prey included, indicated that sex (adult), and then percent femur fat, were the most important factors distinguishing prey killed by wolves versus cougars (Table 1). The odds-ratio for the model (1.91; 95% C.I. 0.65–5.7) indicated that wolves were nearly twice as likely to prey upon males than were cougars. Prey condition also was a significant predictor of the predator responsible for the kill, where probability of a kill being made by a wolf rather than a cougar increased as percent femur fat decreased (Fig. 5). When adult males were excluded from the analysis, prey condition became the most significant variable in predicting predator species, indicating that differential predation for males between the two predators occurred primarily among the adult cohort. As indicated by the odds-ratio of 0.98 (95% C.I. 0.96–0.99), probability of a kill being made by a wolf increased with a decline in percent fat. Age class was the second-most significant predictor variable in the males-excluded model, with wolves exhibiting a greater tendency to kill juvenile prey (Table 1). Femur fat coefficients changed minimally between models with versus without males, indicating a robust relationship between prey condition and predator species. Both models met linearity assumptions and held up to additional model fit tests (All prey: H-L stat = 7.96, d.f. = 8, $P = 0.438$; All prey, no adult males: H-L stat = 12.99, d.f. = 8, $P = 0.12$).

Table 1. Logistic regression models of variables found to be significant in predicting the likelihood of kills being made by wolves vs cougars, where cougars are the reference cell. Variable significance is expressed as the change in the AICc value ($\Delta AICc$) from the reduced to the more complete model. Odds ratios and corresponding 95% confidence intervals for retained variables are given, and model significance was determined via the likelihood ratio test.

Model	Equation	O.R. ₁	O.R. ₂	C.I. ₁	C.I. ₂	AICc	$\Delta AICc$	Model P-value
All prey								
Constant	$g(x) = 0.223$	–	–	–	–	300.8	–	0.103
Constant + sex ^a	$g(x) = -0.022 + 1.003(x_1)$	2.73	–	0.98–7.59	–	158.1	142.7	0.045
Constant + sex ^a + fat	$g(x) = 1.96 + 0.63(x_1) - 0.035(x_2)$	1.88	0.97	0.64–5.6	0.94–0.99	138.0	162.8	0.003
All prey, no adult males								
Constant	$g(x) = 0.18$	–	–	–	–	285.3	–	0.208
Constant + fat ^c	$g(x) = 2.35 - 0.041(x_1)$	0.96	–	0.94–0.98	–	232.7	52.6	0.065
Constant + fat ^c + age ^b	$g(x) = 1.91 - 0.039(x_1) + 0.55(x_2)$	0.96	1.73	0.94–0.98	0.91–3.32	226.9	58.4	0.000

^a Design coded with females as reference (i.e. – males 1.88 times more likely than females to be killed by wolves).

^b Design coded with adults as reference (i.e. – juveniles 1.73 times as likely than adults to be killed by wolves).

^c Coefficient represent arcsine-square-root transformed data.

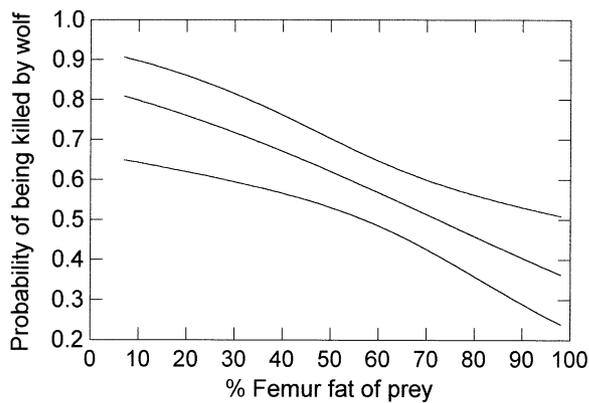


Fig. 5. Probability of a kill being made by wolves versus percent marrow fat of the prey in, east-central Idaho, 1999–2001. Figure includes 95% upper and lower confidence intervals.

Kill site attributes

Our examination of the distribution of wolf kills within the study area suggested that these kills did not occur at random with respect to habitat. Both physiography and aspect were significant predictors of the site attributes where wolf kills occurred; the resulting odds-ratios indicated that wolf kills were more likely to occur in bottom/riparian areas along south facing aspects when compared to a selection of random points (Table 2). Scale of analysis (1 km vs 2 km buffers) had no qualitative effect on either of the resulting model outcomes (Table 2), implying that wolf selection of general hunting habitat operated at a relatively large spatial scale. Both models performed well in additional model fit tests (1 km: H-L stat = 0.589, d.f. = 2, $P = 0.75$; 2 km: H-L stat = 0.007, d.f. = 2, $P = 0.997$).

Cougar kill site attributes also deviated from the 1 km random point sample, where physiography was found to be a significant predictor in cougar kill locations (Table 2). At the 2 km buffer scale, while physiography was again retained, vegetative structure also was significant, with cougar kills being approximately one-fourth as likely to occur in dense conifer stands associated with higher-elevations than in open shrub habitat (odds-ratio = 0.23; 95% C.I. 0.1–0.52). The differences between models indicates that scale is an important factor in predicting cougar kill locations, suggesting that cougars confine their hunting within specific microhabitats. While there were an insufficient number of retained variables to determine the H-L stat for our 1 km model, the 2 km model performed well (H-L stat = 4.56, d.f. = 2, $P = 0.34$).

The analysis comparing wolf versus cougar kill sites revealed that there were significant differences in kill site habitat attributes between the two predators (Table

2). Physiography was the first variable to be retained in the model; the resulting odds-ratio indicated that wolf kills were 3.3 times as likely to occur in bottom/riparian areas than cougar kills (Table 2). Slope, followed by elevation, were the final variables that were retained, with wolf kills occurring on lesser slopes and at higher elevation relative to cougars (Table 3). Again, our model performed well under additional fit testing (H-L stat = 4.804, d.f. = 8, $P = 0.78$), and met the assumption of linearity.

Horizontal vegetation cover, as measured by the number of cover board quadrats obstructed from view, was marginally greater at wolf kill sites than at the comparison plot ($t_{57} = 1.53$, $P = 0.06$; Table 3). Percent cover was greater at cougar kill/cache locations than at the comparison plot ($t_{30} = 3.42$, $P = 0.002$; Table 3). There was no difference in horizontal cover at wolf versus cougar kill sites ($F_{1,112} = 0.717$, $P = 0.40$). Thus, horizontal cover at both wolf and cougar kills was greater than expected when compared to random points, but did not differ between the two predator species.

Discussion

Prey selection patterns

Our results indicate that while both wolves and cougars selected disadvantaged prey, notable differences exist in actual selection patterns observed for each predator species. Wolves exhibited a greater overall tendency to select juveniles and malnourished individuals among both deer and elk prey, than did cougars. While cougars also demonstrated selection for juvenile elk, this pattern was qualitatively less pronounced for elk and not apparent for deer. For both wolves (Huggard 1993, Carbyn 1983) and cougars (Hornocker 1970, Murphy 1998), patterns of prey selection generally were consistent with other studies where elk served as the primary prey species. However, the observed disparity between predators in terms of specific prey selection patterns doubtless highlights the importance of other factors associated with the predator-prey interaction, such as predator hunting behavior and capture success, on prey vulnerability to predation.

While distinct prey selection patterns emerged when we compared prey attributes for the two predator species, our results did not clearly follow predictions related to standard prey selection models. For example, prey selection patterns for both predator species fail to support the hypothesis that coursing predators select prey randomly while ambush predators select larger prey (Gerritsen and Strickler 1977, Greene 1986). Intuitively, such a hypothesis seems rather simplistic for explaining complex predator-prey interactions between vertebrate predators and their prey.

Table 2. Logistic regression models of the variables found to be significant in predicting habitat variables at wolf vs cougar kill locations (model 5; cougars are the reference cell) or the variables that differed significantly from habitat attributes at random locations (models 1–4). Variable significance is expressed as the change in the AICc value (Δ AICc) from the reduced to the more complete model. Odds ratios and corresponding 95% confidence intervals for retained variables are given, and model significance was determined via the likelihood ratio test.

Model	Equation	O.R. ₁	O.R. ₂	O.R. ₃	O.R. ₄	C.I. ₁	C.I. ₂	C.I. ₃	C.I. ₄	AICc	Δ AICc	Model P-value
Wolf vs 1km.												
Constant	$g(x) = 0.00$	–	–	–	–	–	–	–	–	311.8	–	1.0
C + phys.	$g(x) = -0.81 + 2.03(x_1)$	7.61	–	–	–	4.1–14	–	–	–	265.4	46.4	0.000
C + phys. ^a + aspct. ^b	$g(x) = -0.49 + 1.97(x_1) - 0.63(x_2)$	7.15	0.53	–	–	3.8–13.3	0.29–0.97	–	–	263.2	48.6	0.000
Wolf vs 2km.												
Constant	$g(x) = 0.00$	–	–	–	–	–	–	–	–	311.8	–	1.0
C + phys.	$g(x) = -0.81 + 2.03(x_1)$	14.64	–	–	–	7.2–29.9	–	–	–	241.5	70.3	0.000
C + phys. ^a + aspct. ^b	$g(x) = -0.59 + 2.65(x_1) - 0.65(x_2)$	14.13	0.52	–	–	6.9–29	0.28–0.99	–	–	239.5	72.3	0.000
Cougar vs 1km.												
Constant	$g(x) = 0.00$	–	–	–	–	–	–	–	–	227.2	–	1.0
C + phys. ^a	$g(x) = -0.4 + 1.5(x_1)$	4.47	–	–	–	2.1–9.7	–	–	–	213.3	13.9	0.000
Cougar vs 2km.												
Constant	$g(x) = 0.00$	–	–	–	–	–	–	–	–	227.2	–	1.0
C + phys.	$g(x) = -0.44 + 1.86(x_1)$	6.41	–	–	–	2.7–15.1	–	–	–	207.3	19.9	0.000
C + phys. ^a + veg. ^c	$g(x) = 0.15 + 2.09(x_1) - 0.44(x_2) - 1.46(x_3) - 0.28(x_4)$	8.11	0.64	0.23	0.76	3.2–20.5	0.05–8.7	0.1–0.52	0.28–2.03	198.9	28.3	0.000
Wolf vs cougar												
Constant	$g(x) = 0.33$	–	–	–	–	–	–	–	–	263.8	–	0.03
C + phys.	$g(x) = -0.16 + 0.93(x_1)$	2.53	–	–	–	1.4–4.6	–	–	–	256.1	7.7	0.002
C + phys. + slope	$g(x) = 0.89 + 1.0(x_1) - 0.05(x_2)$	2.71	0.96	–	–	1.5–5.0	0.93–0.99	–	–	249.0	14.8	0.000
C + phys. ^a + slope + elev.	$g(x) = -1.54 + 1.18(x_1) - 0.05(x_2) + 0.001(x_3)$	3.26	0.95	1.001	–	1.7–6.2	0.93–0.98	1.0–1.003	–	244.5	19.3	0.000

^a Design coded with slope as reference (categorical variable includes bottom/riparian, slope).

^b Design coded with southern exposure as reference (categorical variable includes southern, northern exposure).

^c Design coded with open-shrub as reference (categorical variable includes deciduous tree sp.(x_2), dense conifer(x_3), open conifer(x_4)).

Table 3. Habitat measurements taken at wolf, cougar kill sites and comparison plots located 200 meters away in a random direction, east central Idaho, 1999–2001.

	Wolf			Cougar		
	mean	SE	<i>n</i>	mean	SE	<i>n</i>
Kill site						
Snow depth (cm)	31	2.1	100	14	2.1	34
% vegetative cover	41	3.6	75	48	4.3	40
degrees slope	21	1	111	26	1.1	80
Elevation (m)	1688	27	111	1606	34	80
Comparison plot						
Snow depth (cm)	24	2.4	57	13	2.3	27
% vegetative cover	32	3.6	59	24	3.7	32

Considering the predictions for the remaining hypotheses (i.e. predator morphology/group hunting favoring size-selective predation: Rosenzweig 1966, Gittleman 1989; low predator capture success favoring selection for disadvantaged individuals: Temple 1987), our results were variable according to predator species. For example, group hunting did not appear to bias wolf predation towards large-sized prey; rather, wolves preyed disproportionately upon juveniles (for both elk and deer). While this result goes counter to the group-hunting hypothesis, and such behavior clearly fails to maximize absolute energy gain for wolves during a given predatory encounter, it seems likely that it is the direct result of the easier capture of the younger or older age classes following an extended predatory chase. In contrast, the disparity in selection for juvenile prey by cougars (i.e. selection for juvenile elk but not juvenile deer) suggests that the vulnerability of this age cohort was not determined primarily by younger age or smaller structural size of juveniles, per se. Rather, the higher frequency of selection for moderately-sized prey (i.e. elk calves and adult deer) supports the contention that solitary hunting imposes limits on the size of prey captured by these predators, and that within each prey species cougars maximized the size of individual prey that could effectively be captured (Sunquist and Sunquist 1989, Murphy 1998). Indeed, the imposing size of adult elk likely biased cougar prey selection patterns towards smaller juveniles, whereas adult deer may have been less difficult to capture successfully. Yet, the observed selection for old-aged elk may be indicative of limited selection of substandard prey by cougars, as determined by possible differential predator avoidance or escape ability of older animals.

Under the assumption that wolf capture success is lower than cougar success (Hornocker 1970, Mech 1970, Mech et al. 2001), our results generally support Temple's (1987) hypothesis regarding selection for disadvantaged individuals. As per Temple's hypothesis, differential predation on substandard prey appears to be a direct result of the likely disparity in capture success between the two predator species. Although capture success is likely to vary with prey species,

studies indicate that wolf success generally is low (7–25%), and wolves must search extensively to encounter sufficient numbers of prey to test for their vulnerability to predation (Mech 1966, Shelton 1966, Mech 1970, Mech et al. 2001). In contrast, cougars may exhibit success rates surpassing 80% when hunting deer and elk (Hornocker 1970). Results from other studies have further substantiated the argument that stalking is generally a more effective means of prey capture than is coursing (Saunders 1963, Haglund 1966, Nellis and Keith 1968, Schaller 1972), and in instances where prey selection and/or success rate differed little between sympatric canids and felids, predatory behavior by canids was thought to be influenced by dense vegetation such that they approached and killed prey in a felid-like manner (Murray et al. 1995, Kunkel and Pletscher 2001).

The assertion that hunting success rates influence prey selection patterns is supported strongly by the fact that primary differences in prey selection between wolves and cougars in our study was manifested in terms of prey condition and age class. The greater proportion of wolf-killed prey approaching starvation levels suggested by others (Greer 1968, Mech et al. 1995) illustrates the partially compensatory nature of wolf predation. Furthermore, while several studies indicate that prey killed by wolves were debilitated or in poor condition (Mech 1970, Huggard 1993, Mech et al. 1995), few, if any, have detected the tendency for cougars to kill undernourished prey (Pence et al. 1988, Spreadbury 1988, O' Gara and Harris 1988, Kunkel et al. 1999).

Kill site attributes

As predicted, spatial scale of analysis affected our interpretation of cougar kill site attributes, while no such pattern was observed for wolves. The fact that wolf kill site parameters did not change with scale of analysis, despite clear changes in proportional distribution of vegetation types at the 1 and 2 km level, indicates that wolf kills were not habitat-specific. As

would be expected from a coursing predator that may chase prey over extended distances, the occurrence of kill sites appeared to be dictated more by characteristics of the prey; ungulates were killed primarily in bottom/riparian zones where flight ability may have been inhibited, particularly where deeper snow associated with such lowlands could offer a distinct locomotory advantage to the predator (Telfer and Kelsall 1984). Yet, in accordance with our prediction, models describing cougar kill locations were scale-dependent. The high proportion of kills occurring in the lower elevation open-shrub areas likely reflect the preferential use and increased prey capture success afforded to a stalking predator that is dependent upon cover to approach prey (Hornocker 1970). While it could be argued that the distribution of both cougars and their kill sites simply reflects prey distribution (Pierce et al. 2000), this assertion can be countered for our study by the fact that wolves consistently killed prey at higher elevations and in different vegetation zones, suggesting that prey were not limited to the low-elevation open shrub habitat types where most cougar kills occurred. Rather, cougars appeared to focus their hunting in smaller patches that facilitated stalking of prey, whereas wolves searched for and pursued prey at a broader spatial scale irrespective of specific habitat type.

The distinct differences in the method coursers versus stalkers approach and subdue prey ostensibly should lead to cougar kills occurring in areas of greater structural cover relative to wolves, yet our data failed to support this prediction. The high cover we recorded at wolf kills likely reflects the fact that their relatively long chases simply ended in areas where vegetation was denser. While cougars probably do seek out and kill prey in areas with sufficient cover for stalking, our results may not reflect the specific habitat in which wolves encountered prey and initiated a pursuit.

To our knowledge, the results presented herein are the first demonstrating strong evidence for differential prey selection due to hunting behavior among terrestrial carnivores. Our findings suggest that the specific attributes of depredated prey likely are a result of predator hunting behavior and capture success. Such capture success also is shaped to a lesser extent by prey size limitations imposed upon solitary predators. While these results are largely consistent with the framework of Temple's (1987) hypothesis, additional efforts are needed to further evaluate how various predator hunting behaviors affect prey species differentially, and how disparate prey selection patterns affect prey population demography and prey behavioral responses. Understanding the difficulties associated with collecting these types of data from model species and making cross-taxa generalizations, such studies should be initiated across a broad range of predator-prey systems before researchers should attempt to generalize upon the factors affecting prey vulnerability to predation.

Acknowledgements – We are grateful to the Hornocker Wildlife Institute, Idaho Department of Fish and Game, Lemhi County, the Nez Perce Tribe, Global Carnivore Project, Rocky Mountain Elk Foundation, Salmon/Challis National Forest, Bureau of Land Management (Salmon office), the University of Idaho, U.S. Fish and Wildlife Service, Wildlife Conservation Society, and the Wolf Education and Research Center, all of whom contributed equipment and/or financial assistance to conduct the research from which this paper is based. I. Babcock, A. Gall, C. Gardner, J. Holyan, K. Laudon, R. Long, J. Muir, A. Ohl, and D. Wenger worked long hours under difficult conditions to collect samples. We thank C.W. Hunt for constructive comments on an earlier draft. D.L.M. wishes to acknowledge the Canada Research Chairs program and Trent University for support during the writeup of this paper.

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