COUGAR FOOD HABITS IN SOUTHERN UTAH

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Abstract: Diets of cougars (Felis concolor) were studied from December 1978 to August 1981, on a 4,500-km² study area near Escalante, Utah. Prey eaten by cougars was estimated from analysis of 112 animals consumed as prey and from 239 cougar scats. Composition of diet was corrected based on feeding trials using captive cougars. Mule deer (Odocoileus hemionus) were to be the major prey item, 81% of biomass consumed. Lagomorphs, large rodents, and smaller predators were also important components of the diet. Cattle comprised less than 1% of the diet, although they were abundant on the cougars’ summer range. Age structure of deer killed by cougars indicated that older (>7 years) deer were killed more often than expected (P < 0.005).

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Cougar dietary habits have been studied in Utah (Connolly 1949, Robinette et al. 1959), Idaho (Hornocker 1970), Arizona (Shaw 1977, 1982), Oregon (Toowell and Meslow 1977), British Columbia (Spalding and Lesowski 1971), and the West in general (Young and Goldman 1946). Food habits were generally similar, the diet consisting predominantly of wild and domestic ruminants, with lesser amounts of rodents, rabbits, and other predators. Results of the more intensive studies in Utah, Idaho, and Arizona differed, however, in the relative proportions of mule deer, elk (Cervus elaphus), and cattle in the diet. During years of peak snowshoe hare (Lepus americanus) abundance in British Columbia, 27% of the cougars’ diet was composed of hares, indicating that cougars take advantage of numerically abundant prey.

Because inferences are frequently drawn from food-habits studies of predators to predict their influence on the dynamics of prey populations, it is important that results from such studies accurately describe the diet. Floyd et al. (1978) determined that the number of “field-collectible” scats produced by gray wolves (Canis lupus) was inversely related to prey size. Selective feeding on flesh alone resulted in loose, liquid scats that would seldom be found in the field. Consumption of smaller prey, on the other hand, would generally include more indigestible material and would result in more persistent scats. In addition, Johnson and Aldred (1982) and Weaver and Hoffman (1979) have documented differential digestibility of smaller mammals and the problems of enumerating small mammals in scats.

The method employed to collect food-habits data may further reduce general applicability. Dietary samples from cougars killed by sport hunters or damage-control personnel may be biased toward specific groups of cougars or may be restricted to specific seasons of the year (Young and Goldman 1946, Robinette et al. 1959, Spalding and Lesowski 1971, Toowell and Meslow 1977). Only Robinette et al. (1959) and Shaw (1982) reported summer food habits. Several authors have indicated that vulnerability of mule deer to cougar predation is influ-

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enced by sex of the deer and season of the year (Robinette et al. 1959, Hornocker 1970, Shaw 1977) and by age of the deer (Hornocker 1970, Spalding and Lesowski 1971).

This paper reports on an intensive effort to determine the year-round diet of cougars and relative vulnerability of the various age-classes of mule deer to cougar predation between December 1978 and August 1981.

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STUDY AREA

The 4,500-km² study area is located in Garfield and Kane counties in south-central Utah. The Boulder–Escalante mountains and adjacent canyonlands dominate the area topographically. More than 95% of the area is public land. Climate is characterized by moderate accumulations of snow in winter, hot dry summers, and late summer rainfall.

At the lowest elevations (1,350–1,800 m), vegetation types include desert shrub and big sagebrush (Artemisia tridentata)–grass types and riparian vegetation. Pinyon pine (Pinus edulis)–juniper (Juniperus osteosperma) woodlands, ponderosa pine (P. ponderosa) forests, and oak brush (Quercus gambelii) dominate mid-elevations (1,800–2,700 m). Quaking aspen (Populus tremuloides), Engelmann spruce (Picea engelmannii), and white fir (Abies concolor) forests, and subalpine meadows occur on the higher mountain slopes (2,700–3,355 m). The drainage of the Escalante River, which traverses the center of the study area, is characterized by extremely rough terrain. Deep, rocky, vertical-walled canyons on many of the tributaries impede overland travel. The southern deserts include extensive areas of bare sandstone and are marginal range for both mule deer and cattle. Three areas over 190 km² are roadless.

Mule deer were the most common wild ruminant on the area. Number of deer on the winter range was estimated to be 4,800 (Ackerman 1982). Elk were introduced during the winter of 1976–77 and numbered about 200 during the study. Other potential prey items included black-tailed jack rabbit (Lepus californicus), snowshoe hare, Nuttall’s (Sylvilagus nuttalli) and desert (S. audubonii) cottontail, and a variety of rodents. Sciurids present on the area included yellow-bellied marmot (Marmota flaviventris), rock squirrel (Spermophilus variegatus), golden-mantled ground squirrel (S. laterialis), white-tailed antelope squirrel (Ammospermophilus leucurus), and chipmunks (Tamias spp.). Beaver (Castor canadensis) were common only along the Escalante River. Porcupine (Erethizon dorsatum), once apparently common, were rare on the area. Smaller predators included coyote (Canis latrans), gray fox (Urocyon cinereoargenteus), bobcat (Felis rufus), and badger (Taxidea taxus). Based on grazing permits, about 6,200 cattle (including calves) were present on the study
area between mid-June and the end of September. Domestic sheep were not present on the study area. Livestock depredation has been infrequent on the study area in recent years (Utah Div. Wildl. Resour. 1981a). The area was closed to cougar hunting in April 1979 to facilitate the research.

**METHODS**

Trained hounds were used to capture cougars after fresh tracks were located (Hemker 1982). Each captured cougar was weighed, measured, and fitted with an activity-type motion-sensitive radio collar. Relocations were made from the ground with directional antennas and from fixed-wing aircraft using paired, underwing, two-element Yagi antennas.

**Analysis of Kills**

Kills made by cougars (Shaw 1979) were found while following tracks of unmarked and radio-collared cougars. Additionally, we intensively searched for kills in areas where cougars had been located several days in succession. Estimated date the kill was made (if fresh), species, age, and sex of prey, location, and elevation were recorded for each kill.

Sex and age were determined for all other deer carcasses we found, as well, if the deer had died no more than 4 years before the study began. We made the decision of time of death of kills and other carcasses by comparing them to deer carcasses for which we knew the time of death. Age of deer at the time of death was determined from tooth replacement and wear (Robinette et al. 1957, 1977) and sex from characteristics of the skull and pelvis (Taber 1956). Although both sexes of dead deer were visible because of their bleached and usually scattered bones, carcasses of males with antlers may have been more easily seen.

**Analysis of Scats**

Cougar scats (feces) were collected whenever found, but generally not at sites of kills we located using telemetry (Shaw 1977). Cougar scats were identified on the basis of size, color, and location and by comparison with scats from captive cougars fed various diets. Searching for scats in the vicinity of other kills was generally proportional to the intensity of normal search efforts. Each scat was airdried, soaked in soapy water, and washed through 1- and 3-mm sieves. Skeletal material recovered from scats was identified by comparison with specimens of taxa known to occur on the area. Hair was identified using macro- and microscopic characters (Stains 1958).

Contents of scats are presented both as frequency of occurrence (percentage of total scats in which an item was found) and percent occurrence (number of times a specific item was found as percentage of all items found). Although frequency of occurrence indicates how common an item is in the diet, percent occurrence provides a better indication of the relative frequency with which each item is consumed because it accounts for more than one of a given item being found in a scat.

Remains of all lagomorphs were grouped as rabbits; sciurids smaller than marmots as ground squirrels; and cricula, microtine, and heteromyid rodents as small rodents. Although some overlap of summer and winter ranges of the cougars occurred (Hemker 1982), an elevation of 2,600 m was used to separate those deposited in winter from those deposited in summer.

Because predator deposition of scats that would normally be found in the field ("collectible," those including hair and skeletal material) may be related to the weight of the prey (Floyd et al. 1978), we
conducted 14 feeding trials with three captive cougars to determine the relationship between prey size and scats produced. Cougars were confined singly or in pairs in either a 1.3 × 1.3 × 4.0-m cage or a larger (13 × 6 × 3-m) pen. They were starved for 1–2 days before 12 trials and for less than 1 day for the other 2. No food was provided after the initial food was offered until scat production ceased. Scats were collected daily. Food items used in the trials were whole mule deer (adult and fawn), eviscerated jack rabbits, and Uinta ground squirrels (Spermophilus armatus).

Prey biomass consumed per scat produced was regressed against live body weight of the prey animals to determine the relationship between body weight of prey and collectible scats produced. The resulting linear relationship was then applied in the form of a correction factor to convert frequency-of-occurrence values for each taxon to a relative estimate of biomass of each consumed (Floyd et al. 1978).

Because the smaller the prey animal is, the less likely it is to comprise a total scat, species less than 2 kg were not corrected for digestibility. Each occurrence was assumed to be an individual and was simply multiplied by live weight of the taxon to estimate biomass consumed. Analyses of cougar stomach contents by Robinette et al. (1959) indicated that one stomach seldom contained more than one animal of a species, reducing the probability of an occurrence representing more than one of a species.

Age distributions of deer killed by cougars and deer dying of all causes were used to test the null hypothesis that cougars sampled randomly from the live deer population. Because the actual age distribution of the deer population was not known, we estimated it from an $l_{x}$ distribution (survivorship) constructed from the samples of deer killed by cougars, human hunters, and dying of other causes ($d_{x}$, Caughley 1977). We assumed the $d_{x}$ sample proportionately represented those major causes of death and that, with the exception of fawns (<1 year), deer of various age-classes were found with equal likelihood. If cougar kills were overrepresented in the $d_{x}$ sample because of the methods we used to find them, rejection of the null hypothesis would be made more difficult, resulting in conservative conclusions.

Construction of the $l_{x}$ distribution involved meeting several basic assumptions about the population. The deer population decreased substantially in the early 1970's, but had apparently remained relatively stationary since that time (Utah Div. Wildl. Resour. 1981b). If the age structure of the population had changed over this period, cougar predation and other causes were presumably at least sampling from the same live population.

RESULTS

Twenty-two cougars (1 adult male, 9 adult females, and 12 cubs in seven litters) were captured and radiocollared. Ten others (including seven cubs in the observed litters) were known to be in the area, but were not captured (Hemker 1982).

We examined 112 kills between December 1978 and August 1981, 66 within 1 month of death. Stomach contents of a cub that died of natural causes during the study were included in analysis of the sample of kills.

Seven species were represented in the kill sample (Table 1). Mule deer accounted for 88% of the kills examined and elk 4%. One of the elk was a young male, two were adult females, and the fourth was an adult male. One domestic cow, a calf es-
Table 1. Composition (%) of cougar diet on Boulder-Escalante study area, Utah, December 1978–August 1981.

<table>
<thead>
<tr>
<th>Prey</th>
<th>Kills (N = 112)</th>
<th>Entire year items occur a</th>
<th>Scats (N = 316) items occur b</th>
<th>Winter c items occur c</th>
<th>Summer d items occur</th>
<th>Summer e items occur f</th>
<th>Scats (N = 239) items occur g</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mule deer</td>
<td>87.5</td>
<td>61.0</td>
<td>80.3</td>
<td>60.1</td>
<td>67.3</td>
<td></td>
<td></td>
<td>100.1</td>
</tr>
<tr>
<td>Elk</td>
<td>3.6</td>
<td>0.3</td>
<td>0.4</td>
<td>0.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cattle</td>
<td>0.9</td>
<td>0.3</td>
<td>0.4</td>
<td>0.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rabbit</td>
<td>2.7</td>
<td>15.7</td>
<td>17.2</td>
<td>15.5</td>
<td>7.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground squirrel</td>
<td></td>
<td>7.6</td>
<td>8.8</td>
<td>6.0</td>
<td>9.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small rodent</td>
<td></td>
<td>2.5</td>
<td>3.3</td>
<td>1.2</td>
<td>1.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marmot</td>
<td></td>
<td>1.3</td>
<td>1.7</td>
<td>0.6</td>
<td>1.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beaver</td>
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<td>1.8</td>
<td>1.7</td>
<td>0.6</td>
<td>2.7</td>
<td></td>
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<tr>
<td>Porcupine</td>
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<td>0.6</td>
<td>0.8</td>
<td>0.6</td>
<td>1.8</td>
<td></td>
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<tr>
<td>Coyote</td>
<td></td>
<td></td>
<td>0.3</td>
<td>0.4</td>
<td>0.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gray fox</td>
<td></td>
<td></td>
<td>1.6</td>
<td>2.1</td>
<td>3.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bobcat</td>
<td></td>
<td></td>
<td>1.3</td>
<td>1.7</td>
<td>2.4</td>
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<tr>
<td>Cougar</td>
<td>0.9</td>
<td></td>
<td>0.3</td>
<td>0.4</td>
<td>0.6</td>
<td></td>
<td></td>
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<tr>
<td>Badger</td>
<td>0.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Bird</td>
<td></td>
<td></td>
<td>1.0</td>
<td>1.3</td>
<td>1.2</td>
<td>0.9</td>
<td></td>
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<td>Carrion</td>
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<td></td>
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<td></td>
</tr>
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<td>Unknown animal</td>
<td></td>
<td>2.5</td>
<td>3.8</td>
<td>3.0</td>
<td>3.5</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Grass and</td>
<td></td>
<td>4.4</td>
<td>5.9</td>
<td>4.2</td>
<td>3.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>vegetation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

125 scats, containing 168 food items.
89 scats, containing 113 food items. 25 additional scats containing 35 food items could not be classified by season.
Includes stomach contents of a radio-collared cub that died.
230 scats, containing 316 food items (1.32 items/scat).
Four scats contained two or more items in same taxon.
Consumed as carrion, see text.
Two additional cougars consumed but not included because carcasses were located with use of radio transmitter.

Estimated to weigh 80 kg, was known to have been killed by a cougar during the study. Two other cows were consumed by cougars after having died of other causes. In addition, we observed a mule deer that was scavenged by a cougar. Kills of two coyotes and three jack rabbits were also found. Badger remains were found in the stomach of the cub.

Three instances of cannibalism were observed. A yearling cougar was killed, eaten, and buried by another cougar, believed to be an adult male. In two other instances, cubs of radio-tagged females were eaten by other cougars. An unidentified adult consumed one of these cubs, and the remaining members of the family consumed the second.

Scats
We examined 239 scats and detected 316 prey items (Table 1). A wider array of prey items (15 taxa vs. 7) was found in the scats than among the kills. Only minor seasonal differences were detected. Mule deer comprised only 61% of items detected, but occurred in 80% of all scats. Rabbits comprised 14% of all items and small rodents 3%. Ground squirrels (primarily rock squirrels) comprised 8%. Larger rodents, yellow-bellied marmots, beaver, and porcupine together comprised 3%. Do-
mestic cattle and elk remains were each detected once.

Bobcat remains were found four times, gray fox and badger once each, and small birds three times. Grass and other vegetation occurred commonly in scats.

Cougar remains were found in four scats. Two of these were found near the site where a cub was consumed by members of its family. The other two, however, were found some distance from each other and were not closely associated with sites where other cougars were known to have been eaten. These scats, along with observations of deaths of other cougars, represent a minimum of three, and perhaps five, instances of cannibalism. Balls of cougar hair, likely the result of grooming, were found in 22 scats. The scat containing cattle remains was found in an area where a solitary female fed on a cow that had died of a cause other than predation.

Feeding Trials

Regression of biomass consumed per scat produced against prey weight resulted in the linear relationship

\[ \hat{Y} = 1.98 + 0.035X, \]

\[ r = 0.77 \ (P < 0.05) \]

where \( \hat{Y} \) is weight of prey consumed per scat and \( X \) is prey body weight (kg) (Fig. 1). Proportionately more collectible scats were produced when cougars consumed smaller prey. Wolves produced 4.3 times more scats (Floyd et al. 1978) per weight eaten than did cougars, but cougar scats (wet weight) were heavier (\( \bar{x} = 203 \) g, \( N = 45 \)) than the average scat produced by wolves (\( \bar{x} = 64 \) g, \( N = 196 \)). Relative biomass and prey numbers consumed were calculated using this correction factor (Table 2).

Deer that could not be aged and fawns were removed from samples, and age structure of cougar-killed deer (\( N = 50 \)) was then compared to age structure of the population (\( l \) curve) in 2-year intervals (Fig. 2). The two distributions differed significantly (\( P < 0.005, \chi^2 \) test). Cougars killed more older (>7 years) and fewer younger adults than expected. Because of small sample sizes, male and female deer were not treated separately.

Adult females (>1 year) were more frequently consumed by cougars than were other cohorts of mule deer during both spring and summer (Table 3). Adult males and fawns were consumed most frequently during winter.

DISCUSSION

Mule deer dominated the cougars’ diets in southern Utah as they do elsewhere in the western United States. Most prey species that were common on the study area, both nocturnal and diurnal, were represented in the diet. Red squirrels (Tamiasciurus hudsonicus) and woodrats (Neotoma spp.) were conspicuously absent, however. Jack rabbits were twice as common in the winter sample as they were in the summer sample, and smaller car-
Table 2. Calculation of relative biomass and relative number of prey individuals consumed by cougar population, based on 239 scats collected on Boulder-Escalante study area, Utah, 1976-81.

<table>
<thead>
<tr>
<th>Prey</th>
<th>(A) Freq. occur [%]</th>
<th>(B) Est. weight (kg)</th>
<th>(C) Correction factor (kg/scat)</th>
<th>(D) Relative biomass consumed (%)</th>
<th>(E) Relative number of individuals consumed (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elk</td>
<td>0.4</td>
<td>250</td>
<td>10.73</td>
<td>1.2</td>
<td>0.05</td>
</tr>
<tr>
<td>Cattle</td>
<td>0.4</td>
<td>100</td>
<td>5.48</td>
<td>0.6</td>
<td>0.05</td>
</tr>
<tr>
<td>Mule deer</td>
<td>80.3</td>
<td>50</td>
<td>3.73</td>
<td>81.1</td>
<td>15.1</td>
</tr>
<tr>
<td>Cougar</td>
<td>1.7</td>
<td>27</td>
<td>2.92</td>
<td>1.4</td>
<td>0.5</td>
</tr>
<tr>
<td>Beaver</td>
<td>1.7</td>
<td>18</td>
<td>2.61</td>
<td>1.2</td>
<td>0.6</td>
</tr>
<tr>
<td>Bobcat</td>
<td>2.1</td>
<td>11</td>
<td>2.36</td>
<td>1.4</td>
<td>1.1</td>
</tr>
<tr>
<td>Badger</td>
<td>0.4</td>
<td>9</td>
<td>2.29</td>
<td>0.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Porcupine</td>
<td>0.8</td>
<td>7</td>
<td>2.22</td>
<td>0.5</td>
<td>0.6</td>
</tr>
<tr>
<td>Gray fox</td>
<td>0.4</td>
<td>5</td>
<td>2.15</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Marmot</td>
<td>1.7</td>
<td>3</td>
<td>2.08</td>
<td>0.9</td>
<td>3.0</td>
</tr>
<tr>
<td>Rabbit</td>
<td>17.2</td>
<td>2</td>
<td>2.05</td>
<td>9.5</td>
<td>44.4</td>
</tr>
<tr>
<td>Ground squirrel</td>
<td>8.8</td>
<td>0.7</td>
<td>0.70</td>
<td>1.7</td>
<td>22.2</td>
</tr>
<tr>
<td>Bird</td>
<td>1.3</td>
<td>0.06</td>
<td>0.06</td>
<td>0.02</td>
<td>3.3</td>
</tr>
<tr>
<td>Small rodent</td>
<td>3.3</td>
<td>0.03</td>
<td>0.03</td>
<td>0.03</td>
<td>8.3</td>
</tr>
</tbody>
</table>

* From Table 1.
* Estimated mean live weight (kg) of individuals consumed, Burt and Grossenheider (1964).
* Estimated weight of prey consumed per collectible scat produced, when such prey is the only item in a scat (C = 1.98 + 0.035B).
* \( D = (A + C)/2(A + C) \).
* \( E = (D + B)/2(D + B) \).
* No correction factor, see text.

Ninivores were represented only in the winter sample. Small rodents, ground squirrels, and marmots were most common in summer samples, presumably because of lengthy periods of winter inactivity. Seidensticker et al. (1973) concluded that cougars were feeding more on small, diurnal prey during summer, because they found fewer kills of large mammals during this period, when cougars were more active diurnally.

The low incidence of predation on cattle on the study area may be explained by husbandry practices. Calves were generally born on low-elevation ranges or in fenced pastures during the spring and not trailed onto the higher ranges occupied by cougars until several months old. In contrast, in central Arizona (Shaw 1977), where losses of cattle to cougars are high, calves are born year-round on ranges occupied by cougars. Most (87%) cattle killed were small calves.

Although composition of the kill sample was generally similar to estimates of biomass consumed of the various taxa, the kill sample was biased toward larger animals. Cougars would generally remain in an area for a number of days when feeding on a large animal, thus increasing our chances of locating the kill. Small prey was generally quickly consumed, leaving little evidence, whereas bones, hair, drag marks, and piles of debris were common at sites of a large animal kill.

A better estimate of the numerical importance of the various taxa in the diet was provided by correcting for number of collectible scats produced per animal consumed. Mule deer were only 15% of the animals eaten, and small animals became a more important part of the diet than...
suggested by the uncorrected sample. Apparently, four or five rabbits or squirrels were eaten for every deer consumed, rather than one for every three deer as might be inferred from percent-occurrence or frequency-of-occurrence analyses alone.

Older deer, both males and females, appeared more vulnerable to cougar predation than did younger adults. Increased vulnerability of older deer was also noted by Hornocker (1970) and Spalding and Lesowski (1971). Similarly, others (Robinette et al. 1959, Shaw 1977) have noted the increased vulnerability of bucks during the winter. Deer that most frequently die on winter ranges (older deer, bucks, fawns) are those that predominate in the cougars' winter diets. Cougars will scavenge (Robinette et al. 1959, Spalding and Lesowski 1971), and it seems prudent behavior to consume dead animals preserved by cool weather to meet energetic needs while reducing the risk of harm involved in prey capture (Gashwiler and Robinette 1957).

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