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Author(s): Jeffrey T. Villepique, Becky M. Pierce, Vernon C. Bleich, and R. Terry Bowyer

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DIET OF COUGARS (*PUMA CONCOLOR*) FOLLOWING A DECLINE IN A POPULATION OF MULE DEER (*ODOCOILEUS HEMIONUS*): LACK OF EVIDENCE FOR SWITCHING PREY

JEFFREY T. VILLEPIQUE,* BECKY M. PIERCE, VERNON C. BLEICH, AND R. TERRY BOWYER

Department of Biological Sciences, 921 South 8th Avenue, Stop 8007, Idaho State University, Pocatello, ID 83202 (JTV, RTB)
Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game, 407 West Line Street, Bishop, CA 93514 (BMP, VCB)
Present address of JTV: California Department of Fish and Game, P.O. Box 3222, Big Bear City, CA 92314
Present address of VCB: Department of Biological Sciences, 921 South 8th Avenue, Stop 8007, Idaho State University, Pocatello, ID 83202
**Correspondent: jvillepique@dfg.ca.gov*

ABSTRACT—We investigated diet of cougars (*Puma concolor*) in the eastern Sierra Nevada, California, following a decline in the population of mule deer (*Odocoileus hemionus*). Mule deer declined 84% from 1985 to 1991, a period concurrent with declines in bighorn sheep (*Ovis canadensis sierrae*; an endangered taxon). An index to numbers of cougars lagged behind those declines, with a reduction of ca. 50% during 1992–1996. We determined diet of cougars by analysis of fecal samples collected during 1991–1995, when the population of mule deer was <25% of its former size. Mule deer was in 79% of 178 feces in winter and 58% of 74 feces in summer. Although most (69%) fecal samples in winter were <5 km from, or within (25%) winter range of bighorn sheep, none contained evidence of bighorn sheep. One fecal sample in summer contained remains of bighorn sheep, indicating that those ungulates were not an important component of the diet during our investigation.

RESUMEN—Investigamos la dieta del puma (*Puma concolor*) en la parte este de la Sierra Nevada en California después de una disminución en la población del venado bura (*Odocoileus hemionus*). El venado bura disminuyó 84% desde 1985 hasta 1991, una época simultánea con disminución en las poblaciones del borrego cimarrón (*Ovis canadensis sierrae*; un taxón en vías de extinción). Un índice de números de pumas se quedó atrás de esas disminuciones, con una reducción de aproximadamente 50% durante los años de 1992–1996. Determinamos la dieta del puma con un análisis de muestras fecales que colectamos durante los años de 1991–1995, cuando la población del venado bura fue menos que 25% de su tamaño anterior. Restos del venado bura se encontraron en 79% de las 178 muestras fecales en el invierno y en 58% de las 74 muestras fecales en el verano. Aunque más muestras fecales (69%) que colectamos en el invierno estuvieron localizadas <5 km de o dentro de (25%) la distribución invernal de los borregos cimarrones, ninguna contuvo evidencia de borrego cimarrón. Una muestra fecal en el verano tuvo restos de borrego cimarrón, lo que indica que esos ungulados no fueron un componente importante de la dieta del puma durante nuestra investigación.

Mule deer (*Odocoileus hemionus*) are the primary prey of cougars (*Puma concolor*) in the Great Basin (Pierce et al., 1999, 2000*a*). Cougars select prey based upon size or sex (Pierce et al., 2000*b*), and can respond to declines of prey by switching to alternative prey (Logan and Sweanor, 2001; Rominger et al., 2004). We studied diets of cougars reconstructed from fecal samples collected following a decline in populations of mule deer (Bowyer et al., 2005) and bighorn sheep (*Ovis canadensis*; Wehausen, 1996) in a Great Basin ecosystem. We hypothesized that occurrence of mule deer in diets of cougars would be more common when mule deer were concentrated on winter range than during summer, when alternative prey were expected to occur more frequently. We further postulated that the decline and persistent low populations of mule deer would cause cougars to consume alternative prey, including domestic animals and bighorn sheep, throughout the year.

Materials and Methods—Round Valley, Inyo and Mono counties, California, at the eastern base of the Sierra Nevada (37°25′N, 118°37′W), was the winter range for a herd of migratory mule deer (Kucera, 1992; Fig. 1). Predominant vegetation in Round Valley was big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*), characteristic of the Great Basin series described by Storer and Usinger (1968). Elevations ranged from 1,300 m at the valley floor to >3,500 m at Wheeler Ridge and Mount Tom, which bound the valley to the north and west, respectively. Further description of this ecosystem is available from long-term studies of predator-prey interactions (Pierce et al., 2000*b*, 2004; Bowyer et al., 2005). Minimum number of mule deer occupying Round Valley during winter declined by 84%, from 5,978 in 1985 to 939 in 1991; annual surveys indicated the population remained between 900 and 1,400 during 1991–1995 (Bowyer et al., 2005). Bighorn sheep experienced a concurrent decline in populations from the late 1980s through early 1990s, which was attributed in part to responses by bighorn sheep to predation by cougars (Wehausen, 1996). This subspecies of bighorn sheep (*Ovis canadensis sierrae*) is an endangered taxon (United States Fish and Wildlife Service, 2008). Decreases in an index to abundance of cougars lagged behind declines in populations of mule deer with a reduction of ca. 50% during 1992–1996 (Pierce et al., 2000*a*).

We collected recently deposited feces of cougars when located by researchers or hounds in the course of trailing cougars during 1991–1995 (Pierce, 2000*a*). Feces often were associated with kill sites or latrines (locations used repeatedly for scent marking; Pierce et al., 2000*b*). Most (94%) fecal samples were <14 days old. Food items were determined from remains of bone, teeth, and claws, and from hair examined for color, length, thickness, and medullary and cuticular characteristics (Mayer, 1952; Bowyer et al., 1983). Samples were analyzed by Big Sky Laboratories (Florence, Montana) and food items were determined with dichotomous keys (Moore et al., 1974; Kennedy and Carbyn, 1981) and an extensive reference collection of hairs, teeth, and bones.

Taxa identified from fecal samples were grouped into five categories: mule deer, bighorn sheep, leporids, livestock and pets, and small animals or other materials. We calculated percentage occurrence for each category and *SE* and confidence intervals (*CI*) for proportions (Bowden et al., 1984; Bowyer, 1991). Samples were analyzed by comparing 95% *CI*s from a binomial distribution, an approach that was especially appropriate because it allows sampling with replacement, and does not assume independence of samples (Zar, 1999). We interpreted lack of overlap in 95% *CI*s as indicative of statistically significant differences. Data were grouped into 2 seasons, winter (November–April) and summer (May–October), based on dates when mule deer typically migrated to winter range (Kucera, 1992; Pierce et al., 1999).

We used ArcGIS Desktop 9.2 (Environmental Systems Research Institute, Redlands, California) to generate a point layer of locations from Universal Transverse Mercator coordinates where samples of feces were collected. Limited data were available for locations of mule deer and bighorn sheep during 1991–1995, when fecal samples of cougars were collected. In absence of concurrent information, we used data from global-positioning-system (GPS) collars deployed on mule deer and bighorn sheep during 2002–2007 to define winter ranges for those taxa (Krausman et al., 2004; Villepique et al., 2008). Although some locations of mule deer were documented concurrently with our study (Pierce et al., 2004), similar data for bighorn sheep were unavailable because 1986 was the last year that telemetry collars were deployed on bighorn sheep in the study area until 1999 (K. Jones, pers. comm.). We believe locations of bighorn sheep from GPS collars to be representative of distributions in 1991–1995 because those locations are consistent with previous studies (Andaloro and Ramey, 1981) that, like contemporary data, indicated use of both high and low elevations by bighorn sheep in winter (T. Stephenson, pers. comm.).

We used Home Range Tools for ArcGIS (Rodgers et al., 2005) to derive size of home ranges using the 95% adaptive-kernel method for bighorn sheep and for mule deer in winter (November–April). Polygons for range in winter were defined with GPS locations from 26 bighorn sheep (7 males, 19 females) and 37 female mule deer during 2002–2007, rarified to one randomly selected location per week, and employing a smoothing factor of 80% h_{ref} (Worton, 1995; Fig. 1). Elevations were derived from a 1:24,000-scale, 10-m-digital model for elevation (United States Geological Survey, http://seamless.usgs.gov).

Results—One fecal sample contained feathers from an unidentified bird, but remains of mammals occurred in >99% of samples (Fig. 2). Mule deer was the most frequent food in diets of cougars and occurred in 79.2 ± 4.7% (*SE*) of fecal samples in winter (n = 178) and 58.1 ± 5.7% of samples during summer (n = 74; Table 1). Leporids were the second most common food in both seasons (Table 1). Use of mule deer was significantly greater in winter compared with summer, but no significant difference between seasons was evident in other categories of diet (Fig. 2). We detected no evidence of increased occurrence of domestic animals in fecal samples during summer, despite a higher proportion of depredation permits issued for cougars preying on domestic animals in summer (70.6 ± 7.6%) compared to winter (29.4 ± 11.8%; M. Kepner, pers. comm.). Samples in winter were at lower elevations (1,833 ± 23.0 m) than samples in summer (2,078 ± 32.6 m).

Most (85.4%) fecal samples collected in winter were <5 km from, or within (56.7%), the winter

Table 1—Percentage occurrence of food items in fecal samples of cougars (*Puma concolor*) in the eastern Sierra Nevada, California, during winter (November–April; $n = 178$) and summer (May–October; $n = 74$) 1991–1995.

Food item	Season	
	Winter	Summer
Mule deer (*Odocoileus hemionus*)	79.2	58.1
Cougar (*Puma concolor*)	27.0	29.7
Unidentified	9.0	16.2
Black-tailed jackrabbit (*Lepus californicus*)	9.0	5.4
Unidentified vegetation	4.5	0.0
Dog (*Canis familiaris*)	4.0	5.4
Desert cottontail (*Sylvilagus audubonii*)	3.9	2.7
Goat (*Capra hircus*)	3.4	5.4
Desert woodrat (*Neotoma lepida*)	3.4	0.0
Ground squirrel (*Spermophilus*)	2.2	5.4
Grass	2.2	1.4
Bobcat (*Lynx rufus*)	1.7	0.0
Vole (*Microtus*)	1.1	2.7
Unidentified rodent	1.1	2.7
Cat (*Felis catus*)	1.1	0.0
Deermouse (*Peromyscus*)	0.6	6.8
Common muskrat (*Ondatra zibethicus*)	0.6	0.0
Western spotted skunk (*Spilogale gracilis*)	0.6	0.0
Unidentified bird	0.1	0.0
American badger (*Taxidea taxus*)	0.0	2.7
Sheep (*Ovis aries*)	0.0	2.7
Jumping mouse (*Zapus*)	0.0	1.4
Long-tailed weasel (*Mustela frenata*)	0.0	1.4
Bighorn sheep (*Ovis canadensis sierrae*)	0.0	1.4
Yellow-bellied marmot (*Marmota flaviventris*)	0.0	1.4
House mouse (*Mus musculus*)	0.0	1.4
Coyote (*Canis latrans*)	0.0	1.4
Unidentified carnivore	0.0	1.4
Insects	0.0	1.4

range of mule deer, whereas 69.1% of fecal samples in winter were <5 km from, or within (24.7%), winter range of bighorn sheep. One sample, collected on 3 July 1993, contained remains of bighorn sheep. This sample was 7.7 km from the home range of bighorn sheep, a radius that encompassed 63.8% of all fecal samples. No evidence of bighorn sheep occurred in 44 fecal samples collected during winter within the polygon for winter range of bighorn sheep.

Discussion—Mule deer occurred most frequently in diets of cougars when deer were concentrated on winter range, consistent with our predictions. Despite the massive decline in the population of mule deer immediately prior to our study, little evidence existed to support prey-switching by cougars to bighorn sheep, as that taxon was detected in one fecal sample. Although bighorn sheep were available, they were not an important component in diets of cougars.

Several potential problems exist in interpreting diets from remains of prey in feces (Bowyer et al., 1983). We collected fecal samples of cougars opportunistically where the same individual likely contributed more than one sample; however, we used the method of Bowden et al. (1984), which has no associated requirement for independence of samples, to calculate confidence intervals for proportions. We could not eliminate the possibility that samples over represented individual cougars because most (85.3%) fecal samples were from unknown individuals; however, 14.7% of samples were produced by 17 marked cougars. Our allocation of sampling effort thus encompassed a minimum of 17 individuals and likely constituted a representative sample of cougars in our study area. Additionally, hounds were used to locate many fecal samples, and species of prey could be overrepresented at kill sites. Nevertheless, any potential biases should be minimal, because hounds are proficient at locating carcasses of domestic animals, as well as bighorn sheep and mule deer.

We could not distinguish between prey killed by cougars and food that might have been obtained by scavenging (Bauer et al., 2005). Similarly, the occurrence of hair from cougars in 27.8% of fecal samples likely resulted predominantly from grooming, although some occurrences could have resulted from consumption of conspecifics (Galentine and Swift, 2007). Inferring diet from fecal samples could be confounded by differential digestibility of prey, but our hypotheses relate primarily to the occurrence of large mammals. Consequently, bias in the inferred diets of cougars should be minimal with respect to mule deer and bighorn sheep. Further, remains of prey in feces of carnivores have been used successfully to track mortality of young mule deer (Bowyer, 1987), and likely provide a reliable index to use of prey by cougars among seasons.

Mule deer were more available to cougars when deer were concentrated on winter range (Kucera, 1992; Pierce et al., 2004), an area of ca. 120 km^2, than during summer, when deer were dispersed over a much larger area (ca. 2,500 km^2). Thus, cougars showed a functional response to the concentration of mule deer on winter range, as evidenced by increased frequency of remains of deer in their feces during winter. We were surprised that no concomitant increase in frequency of alternative prey, such as livestock and pets, was evident during summer. Despite the response to seasonal availability of primary prey, cougars did not respond strongly to the long-term decline in mule deer by switching to bighorn sheep. Several investigators have documented predation by cougars on bighorn sheep (Ross et al., 1997; Hayes et al., 2000; Festa-Bianchet et al., 2006), and others have suggested that increased predation on bighorn sheep can be attributed to a switch to alternate prey by cougars faced with declines in their primary prey (Kamler et al., 2002; Rosas-Rosas et al., 2003; Rominger et al., 2004). Although our study occurred under conditions of a large decline in

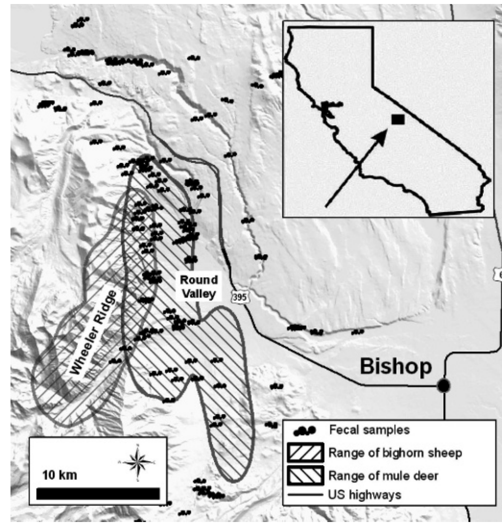

Fig. 1—Locations where fecal samples of cougars (*Puma concolor*) were collected and ranges of mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*) during winter (November–April) in the eastern Sierra Nevada, California.

the population of mule deer, no fecal samples of cougars collected on or adjacent to the winter range of bighorn sheep contained evidence of feeding on that ungulate; instead the one sample containing bighorn sheep was found in July, 7.7 km from the range of bighorn sheep. These results suggest that, in contrast to prevailing theory (Sawyer and Lindzey, 2002), bighorn sheep may not always experience elevated predation by cougars following a precipitous decline in populations of mule deer.

Determining extent of predation by cougars on bighorn sheep in the Sierra Nevada is critically important to efforts to conserve that endangered taxon (United States Fish and Wildlife Service, 2008), and results could aid in conservation of bighorn sheep elsewhere. Wehausen (1996) posited that bighorn sheep abandoned use of winter range at Mount Baxter in response to the risk of predation and concluded that similar behavioral changes were important in the decline of bighorn sheep throughout the Sierra Nevada. Despite a decline in the population of mule deer to <25% of its former size, and examination of diets of cougars over multiple years, we were unsuccessful in our attempt to establish bighorn sheep as an important item in the diet of those large carnivores. Thus, the mechanism for abandon-

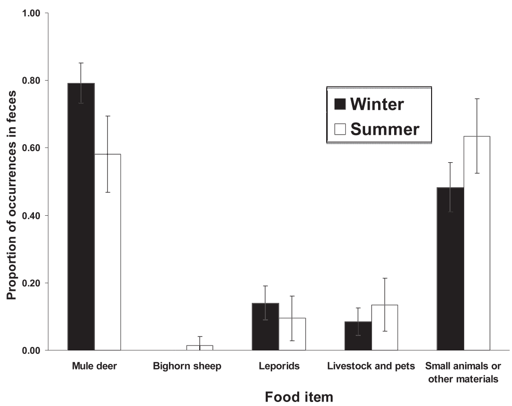

Fig. 2—Mean proportions and 95% *CI*s of food items in diets of cougars (*Puma concolor*) as determined by analysis of feces in winter (November–April; n = 178) and summer (May–October; n = 74) 1991–1995, in the eastern Sierra Nevada, California.

ment of winter range by bighorn sheep remains unclear and more research is necessary to fully understand factors related to the decline of those endangered ungulates.

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