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Authors: Zimmerman, Teresa J., Jenks, Jonathan A., Leslie, David M., and Neiger, Regg D.

and Holgor, Rogg B.

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# HEPATIC MINERALS OF WHITE-TAILED AND MULE DEER IN THE SOUTHERN BLACK HILLS, SOUTH DAKOTA

Teresa J. Zimmerman, 1,4,5 Jonathan A. Jenks, David M. Leslie, Jr., and Regg D. Neiger David M. Leslie, Jr., and Regg D. Neiger

Because there is a paucity of information on the mineral requirements of free-ranging deer, data are needed from clinically healthy deer to provide a basis for the diagnosis of mineral deficiencies. To our knowledge, no reports are available on baseline hepatic mineral concentrations from sympatric white-tailed deer (Odocoileus virginianus) and mule deer (Odocoileus hemionus) using different habitats in the Northern Great Plains. We assessed variation in hepatic minerals of female white-tailed deer (n=42) and mule deer (n=41). Deer were collected in February and August 2002 and 2003 from study areas in Custer and Pennington Counties, South Dakota, in and adjacent to a wildfire burn. Hepatic samples were tested for levels (parts per million; ppm) of aluminum (Al), antimony (Sb), arsenic (As), barium (Ba), boron (B), cadmium (Cd), calcium (Ca), chromium (Cr), cobalt (Co), copper (Cu), iron (Fe), lead (Pb), magnesium (Mg), manganese (Mn), mercury (Hg), molybdenum (Mo), nickel (Ni), phosphorus (P), potassium (K), selenium (Se), sodium (Na), sulfur (S), thalium (Tl), and zinc (Zn). We predicted that variability in element concentrations would occur between burned and unburned habitat due to changes in plant communities and thereby forage availability. We determined that Zn, Cu, and Ba values differed ( $P \le 0.05$ ) between habitats. Because of the nutritional demands of gestation and lactation, we hypothesized that elemental concentrations would vary depending on reproductive status; Cd, Cu, Ca, P, Mn, Mo, Na, and Zn values differed ( $P \le 0.05$ ) by reproductive status. We also hypothesized that, due to variation in feeding strategies and morphology between deer species, hepatic elemental concentrations would reflect dietary differences; Ca, Cu, K, Co, Mo, Se, and Zn differed ( $P \le 0.05$ ) between species. Further research is needed to determine causes of variation in hepatic mineral levels due to habitat, reproductive status, and species.

Key words: Black Hills, elements, fire, liver, mule deer, Odocoileus hemionus, Odocoileus virginianus, reproduction, South Dakota, white-tailed deer.

## INTRODUCTION

Limited information is available on minerals in the nutrition of wildlife; the primary research emphasis has been on domestic and laboratory animals (Robbins, 1983). Liver concentrations of some trace elements have been measured in elk (Cervus elaphus) (Frøslie et al., 1984; Fielder, 1986; Gogan et al., 1989; Vikoren et al., 2005), caribou (Rangifer tarandus) (Frøslie et al., 1984; Barboza and Blake, 2001), moose (Alces alces) (Frøslie et al., 1984; Ytrehus et al., 1999), mountain goat (Oreamnos americanus) (Fielder, 1986), mule deer (Odocoileus hemionus) (Stetler, 1980; Fielder, 1986), muskox (Ovibos moschatus) (Blakley et al., 2000; Rombach et al., 2003), and white-tailed deer (Odocoileus virginianus) (King, 1984; Schultz et al., 1994; McDowell et al., 1995). Trace elements such as copper (Cu) (Stetler, 1980; Frøslie et al., 1984; King, 1984; Gogan et al., 1989; Ytrehus et al., 1999; Blakley et al., 2000; Barboza and Blake, 2001; Rombach et al., 2003; Vikoren et al., 2005), selenium (Se) (Fielder, 1986; McDowell et al., 1995; Ytrehus et al., 1999; Blakley et al., 2000; Vikoren et al., 2005), and molybdenum (Mo) (Stetler, 1980; King, 1984; Gogan et al., 1989; Ytrehus et al., 1999; Blakley et al., 2000) have been the focus of research due to their association with reproduction or disease. Despite these studies, there is a paucity of information on the mineral requirements of free-ranging deer (Robbins, 1983; Jones and Hanson, 1985; Schultz et al., 1994),

<sup>&</sup>lt;sup>1</sup> Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, South Dakota 57007, USA
<sup>2</sup> United States Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit and Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, Oklahoma 74078, USA

Department of Veterinary Science, South Dakota State University, Brookings, South Dakota 57007, USA

<sup>&</sup>lt;sup>4</sup> Current address: Badlands National Park, 25216 Ben Reifel Rd., Interior, South Dakota 57750, USA

<sup>&</sup>lt;sup>5</sup> Corresponding author (email: teresa\_zimmerman@nps.gov)

and data are needed from clinically healthy deer to diagnose dietary mineral deficiencies (Schultz et al., 1994).

Research conducted on white-tailed deer and mule deer has focused on evaluating element toxicity due to strip- and oil shalemining (Stetler, 1980; Woolf et al., 1982; King, 1984) or on documenting Se levels in response to white-muscle disease or poor reproductive rates (Fielder, 1986; McDowell et al., 1995). Schultz et al. (1994) reported baseline data on water, lipid, and mineral concentrations from a large sample of free-ranging white-tailed deer in the southeastern United States. To our knowledge, no one has reported baseline hepatic mineral concentrations from sympatric white-tailed and mule deer using different habitats in the Northern Great Plains.

Our objectives were to (1) measure hepatic mineral concentrations of reproductive and non-reproductive female white-tailed deer and mule deer, with a primary focus on the effect of burning and reproductive status (e.g., pregnant, lactating, and non-lactating); and (2) make interspecific comparisons of the hepatic mineral concentrations in white-tailed deer and mule deer. We predicted that variability in element concentrations would occur between burned and unburned habitat due to changes in plant communities and thereby forage availability. Because of the nutritional demands of gestation and lactation, we hypothesized that elemental concentrations would vary depending on reproductive status. We also hypothesized that because of variation in feeding strategies (Hofmann, 1988a, 1988b) and morphology between species (Zimmerman et al., 2006) (white-tailed deer, concentrate selector; mule deer, concentrate selector-intermediate feeder), hepatic elemental concentrations would reflect dietary differences.

#### **MATERIALS AND METHODS**

The Black Hills are located in west-central South Dakota and northeastern Wyoming and represent the eastern-most extension of the

Rocky Mountains; they are surrounded by grassland and sagebrush (Artemesia spp.) steppe ecosystems (Larson and Johnson, 1999; Petersen, 1984). Topography in the Black Hills ranges from steep ridges, rock outcrops and caves, and canyonlands and gulches, to rolling hills, upland prairies, and tablelands (Froiland, 1990). Elevations range from 973 m to 2,202 m above mean sea level. Mean average temperatures range from 5 C to 9 C with low and high extremes of −40 C and 44 C, respectively (Orr, 1959). Our study area was located in the southern Black Hills (SBH) of South Dakota on the southern edge of the Custer Limestone Plateau in northern Custer and southern Pennington counties.

White-tailed deer and mule deer occur sympatrically in the SBH but use separate winter and summer ranges (Dubreuil, 2003). Ponderosa pine (Pinus ponderosa) comprised about 84% of the overstory canopy (Rumble and Anderson, 1996). The remaining canopy consisted of small stands of white spruce (Picea glauca) and quaking aspen (Populus tremuloides) at higher elevations (Severson and Thilenius, 1976; Sieg and Severson, 1996; Thilenius, 1972). The southwestern part of the winter range was characterized by ponderosa pine, mountain mahogany (Cercocarpus montanus), and Rocky Mountain juniper (Juniperus scopulorum). Understory vegetation on the winter range consisted of big bluestem (Andropogon gerardii), buffalograss (Buchloe dactyloides), fringed sagewort (Artemesia frigida), snowberry (Symphoricarpus albus), serviceberry (Amelanchier alnifolia), cherry species (Prunus spp.), and common juniper (J. communis) (Dubreuil, 2003). Understory vegetation on the summer range was also dominated by snowberry and serviceberry, as well as by Oregon grape (Berberis repens), bearberry (Arctostaphylos uva-ursi), and various grass and forb species (Thilenius, 1972; Severson and Thilenius, 1976; Dubreuil, 2003). Female white-tailed deer in the SBH selected pine, pine-spruce, and pine-aspen habitats with grass-forb understories as foraging areas (Dubreuil, 2003).

On 24 August 2000, a fire burned 34,821 ha, 7% of the Black Hills National Forest (Jasper Fire Rapid Assessment, 2000), in the SBH. Based on LANDSAT data, effects of the fire varied from unburned areas and low-intensity burns (39% of fire area with trees all or partially green) to moderate burns (32%, crowns entirely or nearly entirely scorched) and high-intensity burns (24%, trees devoid of needles); 5% of the area was unclassified. From 2001–2003, average vegetation cover of forbs, grasses, and major shrubs species was 2.2%, 2.3%, and

6.3%, respectively, in unburned habitat and 8.6%, 11.4%, and 2.2% in burned habitat, respectively (Zimmerman, 2004).

We collected deer within and surrounding the Jasper Wildfire perimeter in early February and August 2002 and 2003 (Zimmerman et al., 2006). We sampled  $\geq 5$  mule deer and  $\geq 5$ white-tailed deer from burned and unburned habitats in each season. We used a 4-km buffer around the fire perimeter to avoid collecting deer that used both burned and unburned habitats. Deer were shot in the neck with a high-powered rifle and necropsied at a designated field station. A sample from the caudate lobe of the liver was removed and frozen until analyzed. Age of deer was determined using cementum annuli analysis of collected incisors (Gilbert, 1986). Collection methods followed recommendations of the American Society of Mammalogists (Animal Care and Use Committee, 1998) and were approved by the Institutional Animal Care and Use Committee at South Dakota State University.

Liver samples were analyzed at the Oscar E. Olson Biochemistry Laboratory at South Dakota State University for a standard suite of 24 elements using the established laboratory protocol. All elemental analyses were reported on an as-received (wet weight) basis. The Olson Biochemistry Laboratory first homogenized the liver samples and then sampled a portion of the homogenate weighing about 1 g (wet weight) into a Teflon microwave container. For digestion of the homogenate, 2.5 ml of concentrated nitric acid and 2.0 ml of 30% hydrogen peroxide were added to the Teflon container. The container was sealed, placed in a laboratory microwave, and heated to 110 C for 2 min, 200 C for 2 min, and 220 C for 20 min. After cooling, the test solution was transferred to a volumetric flask and diluted with distilled water to 25 ml. The solution was then analyzed for the standard suite of elements by inductively coupled plasma-atomic emission spectrophotometry as detailed in the instrument manufacturer's laboratory application notes (HORIBA Jobin Yvon, Inc., Edison, New Jersey, USA). At least one digest of reference material, one blank, and duplicates of at least 10% of the total number of samples were included in each batch. Concentrations of elements were corrected for dilution prior to reporting. The following minerals were tested: aluminum (Al), antimony (Sb), arsenic (As), barium (Ba), boron (B), cadmium (Cd), calcium (Ca), chromium (Cr), cobalt (Co), copper (Cu), iron (Fe), lead (Pb), magnesium (Mg), manganese (Mn), mercury (Hg), molybdenum (Mo), nickel (Ni), phosphorus (P), potassium (K), selenium (Se), sodium (Na), sulfur (S), thalium (Tl), and zinc (Zn). Mineral levels were not detectable if they were <25.00 for Na, <1.0 for B, <0.50 for Al and Cu, <0.25 for Sb, As, Tl, and Pb, <0.20 for Hg, <0.10 for Ni, <0.05 for Cd, Cr, and Co, and <0.03 for Ba. If minerals levels were below detectable levels, they were assigned a value of half the detectable limit for statistical analysis and calculation of means (Vikoren et al., 2005; Ytrehus et al., 1999). If >50% of values for a mineral were below the detectable level, the mineral was removed from analysis (Hothem et al., 1998).

Lilliefors test (Lilliefors, 1967; Dallal and Wilkinson, 1986) was used to evaluate normality; non-normal data were rank-transformed (Conover and Iman, 1981), and the alpha-level was set at 0.05. Hepatic variables were compared for main and interactive effects of habitat and reproductive status using analysis of covariance (Zimmerman et al., 2006). Age was used as the covariate (Woolf et al., 1982). If we could not meet assumptions of homogeneity of slopes in analysis of covariance, analyses were conducted by plotting data by independent variables (Zimmerman et al., 2006). If variables were independent of the main effects, the covariate was removed from the analysis (Zimmerman et al., 2006). Tukey's HSD multiple comparisons test was used to determine differences between reproductive groups. Concentrations of elements are presented with ±1 SE. We performed all statistical analyses with SYSTAT (Wilkinson, 1990).

# **RESULTS**

We sampled 41 female mule deer and 42 female white-tailed deer. Age of female white-tailed deer ranged from 1 yr to 11 yr; 22 were pregnant, 11 were lactating, and nine were non-lactating. Age of female mule deer ranged from 1 yr to 10 yr; 18 were pregnant, three were nonpregnant, 14 were lactating, and six were non-lactating. Non-pregnant deer differed from non-lactating deer on the basis of season (winter vs. summer) in which they were collected. We removed non-pregnant mule deer from the analysis due to small sample size (n=3). Because Sb, As, B, Cr, Pb, Hg, Ni, and Tl in white-tailed and mule deer had >50% of the values below detectable levels, these data were not analyzed.

	White-tai	led deer <sup>1</sup>	$Mule deer^1$		
	Burned	Unburned	Burned	Unburned	
$\overline{n}$	21	21	19	19	
Age	5.2 (0.55)	5.1 (0.57)	4.9(0.54)	3.5(0.5)	
Al	0.66 (0.09)	0.46 (0.06)	0.67(0.09)	1.41(0.75)	
Ba	0.10 (0.01)	0.22 (0.10)	$0.07 (0.01)^{a}$	$0.10 (0.01)^{b}$	
Cd	0.80 (0.20)	0.54 (0.08)	0.58 (0.13)	0.51 (0.08)	
Ca	48.67 (1.23)	50.72 (1.62)	43.28 (1.32)	46.38 (1.91)	
Co	0.09 (0.01)	0.09 (0.01)	0.11 (0.01)	0.10 (0.01)	
Cu	62.04 (8.25)	62.19 (4.81)	47.89 (6.43) <sup>a</sup>	$37.55 (4.69)^{b}$	
Fe	140.43 (12.09)	182.27 (27.07)	157.47 (10.78)	151.28 (10.44)	
Mg	183.29 (3.84)	188.05 (4.80)	186.05 (3.24)	181.84 (4.20)	
Mn	4.07 (0.24)	3.87 (0.19)	4.03 (0.15)	3.40 (0.17)	
Mo	0.81 (0.05)	0.77 (0.06)	1.00 (0.04)	1.03 (0.05)	
P	3982.86 (87.30)	4006.67 (102.67)	4091.58 (88.27)	3985.26 (96.65)	
K	2537.14 (61.26)	2492.38 (66.76)	2443.68 (43.47)	2305.79 (53.01)	
Se	0.64 (0.05)	0.98 (0.06)	0.50 (0.04)	0.78 (0.08)	
Na	933.43 (50.55)	868.21 (59.14)	953.90 (48.40)	989.26 (57.84)	
S	2532.86 (38.06)	2477.62 (36.76)	2544.21 (48.21)	2467.37 (45.67)	
Zn	39.09 (1.21) <sup>a</sup>	$35.69 (1.42)^{b}$	43.53 (1.67)	40.56 (1.31)	

Table 1. Means of hepatic major and trace elements (±SE) of female white-tailed deer and mule deer in burned and unburned habitat collected in the southern Black Hills, South Dakota, 2002–2003.

Zinc values ( $F_{1,35}$ =4.296, P=0.046) in white-tailed deer and Cu values ( $F_{1,31}$ =4.784, P=0.036 [significant covariate  $F_{1,31}$ =4.664, P=0.039]) in mule deer were greater in burned than unburned habitat, whereas Ba values ( $F_{1,31}$ =6.277, P=0.018) in mule deer were greater in unburned than burned habitat (Table 1). Remaining variables did not differ (P>0.05) by main effect of habitat.

Cadmium ( $F_{2,37}$ =3.656, P=0.036 [covariant  $F_{1,35}=22.327$ , P<0.001]), Ca  $(F_{2,37}=5.874, P=0.006)$ , Cu  $(F_{2,37}=4.654,$ P=0.016), Mn ( $F_{2.37}=37.004$ , P<0.001), Mo  $(F_{2,37}=25.178, P<0.001), P (F_{2,37}=$ 5.756, P=0.007), Na  $(F_{2,37}=4.740, P=$ 0.015), and Zn  $(F_{2,37}=6.003, P=0.006)$ differed between reproductive groups in white-tailed deer and Cu and Zn levels differed  $(F_{2.31}=13.690, P<0.001$  [significant covariate  $F_{1,31}=4.664$ , P=0.039],  $F_{2.31}$ =4.041, P=0.028, respectively) between reproductive groups in mule deer. Remaining variables did not differ (P>0.05) by main effect of reproductive status.

Cadmium (P=0.031) and Cu (P=0.012)

in white-tailed deer were greater in pregnant than in lactating deer. Copper levels also were greater (P<0.001) in pregnant compared to lactating mule deer, but unlike white-tailed deer, Cu levels were greater in pregnant (P<0.001) compared to non-lactating mule deer. Calcium and P in white-tailed deer paralleled the trend observed in Cu levels in mule deer, with Ca and P values greater (P=0.017, P=0.012, respectively) in pregnant than in lactating white-tailed deer and also greater (P=0.046, P=0.077, respectively) in pregnant than in non-lactating white-tailed deer (Table 2).

Manganese (P<0.001) and Mo (P<0.001) values were greater in lactating than in pregnant white-tailed deer; Mn (P<0.001) and Mo (P<0.001) also were greater in non-lactating than in pregnant white-tailed deer (Table 2). Sodium values were greater (P=0.019) in lactating than in pregnant white-tailed deer and were greater (P=0.044) in lactating than in non-lactating white-tailed deer (Table 2). Zinc values in both white-tailed and mule deer demonstrated a similar trend being greater

<sup>&</sup>lt;sup>1</sup> Different letters indicate significant difference within species between habitat types.

TABLE 2. Major and trace element concentration means (±SE) of nonlactating (NLac), lactating (Lac), pregnant (Preg), and nonpregnant (NPreg) female white-tailed deer and mule deer in reproductive groupings collected in the southern Black Hills, South Dakota, 2002–2003.

1 5.6 0.53 0.41 46.53 0.08 45.55 176.03 182.82 4.78 0.09 3.751.82 2451.82 2451.82				Mule deer	leer	
NLac $\frac{9}{2.9 (0.61)}$ 5.6 $\frac{9}{0.49 (0.16)}$ 0.53 $0.36 (0.24)$ 0.31 $0.42 (0.08)$ 0.41 $46.18 (1.34)^a$ 46.53 $0.07 (0.01)$ 0.08 $59.16 (5.78)$ 45.55 $118.46 (13.27)$ 176.03 $187.00 (3.93)$ 182.82 $4.77 (0.25)^a$ 4.78 $1.05 (0.05)^a$ 3796.67 (91.17) 3751.82 $2561.11 (99.88)$ 2451.82 $0.99 (0.09)$ 0.77		Winter	Summer	ıer	Wir	Winter
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Lac	Preg	NLac	Lac	Preg	NPreg
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	11	22	9	14	18	33
0.49 (0.16) $0.530.36 (0.24)$ $0.310.42 (0.08)$ $0.4146.18 (1.34)^a 46.530.07 (0.01)$ $0.0859.16 (5.78)$ $45.55118.46 (13.27)$ $176.03187.00 (3.93)$ $182.824.77 (0.25)^a 4.781.05 (0.05)^a 0.923796.67 (91.17)^a 3751.822561.11 (99.88)$ $2451.820.90 (0.09)$ $0.77$	5.6 (0.41)	5.9 (0.6)	1.8(0.40)	3.9 (0.43)	5.2(0.61)	3.3(1.45)
0.36 (0.24) $0.310.42 (0.08)$ $0.4146.18 (1.34)^a 46.530.07 (0.01)$ $0.0859.16 (5.78)$ $45.55118.46 (13.27)$ $176.03187.00 (3.93)$ $182.824.77 (0.25)^a 4.781.05 (0.05)^a 0.923796.67 (91.17)^a 3751.822561.11 (99.88)$ $2451.820.90 (0.09)$ $0.77$	(0.08)	0.60 (0.07)	0.81 (0.15)	0.67(0.14)	1.41(0.79)	0.99(0.10)
$\begin{array}{ccccc} 0.42 & (0.08) & 0.41 \\ 46.18 & (1.34)^a & 46.53 \\ 0.07 & (0.01) & 0.08 \\ 59.16 & (5.78) & 45.55 \\ 118.46 & (13.27) & 176.03 \\ 187.00 & (3.93) & 182.82 \\ 4.77 & (0.25)^a & 4.78 \\ 1.05 & (0.05)^a & 0.92 \\ 3796.67 & (91.17)^a & 3751.82 \\ 2561.11 & (99.88) & 2451.82 \\ 0.90 & (0.09) & 0.77 \end{array}$	(0.25)	0.10 (0.01)	0.08(0.02)	0.09(0.01)	0.09(0.01)	0.09(0.05)
$\begin{array}{llllllllllllllllllllllllllllllllllll$	$(0.07)^{a}$	$0.90 (0.19)^{\rm b}$	0.25(0.05)	0.81(0.18)	0.44 (0.04)	0.38 (0.09)
$\begin{array}{cccc} 0.07 & (0.01) & 0.08 \\ 59.16 & (5.78) & 45.55 \\ 118.46 & (13.27) & 176.03 \\ 187.00 & (3.93) & 182.82 \\ 4.77 & (0.25)^a & 4.78 \\ 1.05 & (0.05)^a & 0.92 \\ 3796.67 & (91.17)^a & 3751.82 \\ 2561.11 & (99.88) & 2451.82 \\ 0.90 & (0.09) & 0.77 \end{array}$	$(1.29)^{a}$	$52.72 (1.51)^{b}$	45.48 (2.79)	42.01 (1.30)	46.81 (1.99)	42.30 (3.24)
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	(0.01)	0.09 (0.01)	0.10(0.01)	0.11(0.01)	0.11(0.01)	0.11(0.02)
$118.46 (13.27)   176.03$ $187.00 (3.93)   182.82$ $4.77 (0.25)^{a}   4.78$ $1.05 (0.05)^{a}   0.92$ $3796.67 (91.17)^{a}   3751.82$ $2561.11 (99.88)   2451.82$ $0.90 (0.09)   0.77$	$(4.61)^{a}$	$71.61 (7.85)^{b}$	$23.60 (4.25)^{a}$	$31.21 (3.24)^a$	$58.04 (6.25)^{b}$	27.30 (14.21)
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	(47.60)	171.56 (15.03)	125.48 (11.73)	150.25 (11.95)	167.22 (11.29)	115.67 (1.20)
$4.77 (0.25)^{a}$ $4.78$ $1.05 (0.05)^{a}$ $0.92$ $3796.67 (91.17)^{a}$ $3751.82$ 2561.11 (99.88) $2451.820.90 (0.09)$ $0.77$	(2.88)	186.55 (5.49)	183.17 (5.82)	185.71 (3.82)	182.83 (4.45)	178.67 (1.20)
$1.05 (0.05)^a$ $0.92$ $3796.67 (91.17)^a$ $3751.82$ 2561.11 (99.88) $2451.820.90 (0.09)$ $0.77$	$(0.18)^{a}$	$3.24 (0.12)^{b}$	4.33(0.29)	4.17(0.12)	3.16 (0.13)	3.23(0.29)
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$(0.04)^{a}$	$0.62 (0.04)^{b}$	1.04(0.06)	1.04 (0.06)	0.98(0.04)	1.01(0.12)
2561.11 (99.88) 2451.82 0.90 (0.09) 0.77	$(66.30)^a$	$4197.27 (100.29)^{\rm b}$	3836.67 (129.89)	3874.29 (93.87)	4233.33 (91.32)	4373.33 (235.54)
77.0 (0.09) 0.90	(54.30)	2527.27 (71.47)	2335.00 (52.33)	2404.29 (48.28)	2365.00 (64.12)	2590.00 (151.44)
	(0.08)	0.80 (0.07)	0.48(0.06)	0.77(0.10)	0.59(0.07)	0.42(0.02)
$808.33 (61.12)^{a} 1061.00$	$(42.18)^{b}$	$858.57 (61.08)^{a}$	1138.50 (113.66)	932.43 (63.04)	946.39 (45.95)	907.67 (113.22)
2516.67 (27.54) 2545.46	(37.52)	2480.46 (45.72)	2518.33 (81.91)	2479.29 (55.49)	2522.22 (50.71)	2536.67 (144.38)
$43.46 (1.31)^{a}$ 37.20	(96.0)	$35.00 (1.39)^{b}$	$49.60 (1.54)^{a}$	42.60(1.66)	$39.09 (1.33)^{b}$	38.10(3.44)

<sup>1</sup> Different letters indicate significant difference within species between reproductive status.

Table 3. Means ( $\pm$ SE) and ranges of hepatic major and trace elements of female white-tailed deer and mule deer collected in the southern Black Hills, South Dakota, 2002–2003. Means of elements with >50% of the values below the detectable limits (NA<DL) could not be generated.

	White-tailed deer <sup>1</sup>			Mule deer <sup>1</sup>		
	$\bar{x}$	Min.	Max.	- X	Min.	Max.
n	42			38		
Age	5.0 (0.4)	1.00	11.00	4.20 (0.38)	1.00	10.00
Al	$0.558 \; (0.054)$	0.25	1.49	1.04 (0.38)	0.25	14.80
Ba	0.16 (0.05)	0.02	2.25	0.09 (0.01)	0.015	0.26
Cd	0.67 (0.11)	0.025	3.44	0.55 (0.08)	0.11	2.09
Ca	$49.70 (1.02)^{a}$	38.90	72.50	44.83 (1.18) <sup>b</sup>	34.70	71.60
Co	$0.09 (0.01)^{a}$	0.025	0.17	$0.11 (0.01)^{b}$	0.025	0.17
Cu	$62.11 (4.72)^{a}$	0.25	154.00	$42.72 (4.02)^{b}$	12.00	129.00
Fe	161.35 (15.00)	0.50	639.00	154.38 (7.42)	78.90	262.00
Mg	185.67 (3.05)	146.00	236.00	183.95 (2.64)	150.00	217.00
Mn	3.97 (0.15)	2.43	5.84	3.72 (0.12)	2.06	5.21
Mo	$0.79 (0.04)^{a}$	0.32	1.33	$1.01 (0.03)^{b}$	0.63	1.39
P	3994.76 (66.58)	3400.00	5140.00	4038.42 (65.15)	3210.00	5030.00
K	2514.76 (44.88) <sup>a</sup>	1900.00	3020.00	$2374.74 (35.66)^{b}$	1800.00	2910.00
Se	$0.81 (0.05)^{a}$	0.36	1.57	$0.64 (0.05)^{b}$	0.25	1.59
Na	900.82 (38.76)	12.50	1310.00	971.59 (37.31)	655.00	1420.00
S	2505.24 (26.48)	2140.00	2840.00	2505.79 (33.36)	2150.00	2980.00
Zn	$37.39 (0.96)^{a}$	16.90	50.10	$42.05 (1.07)^{b}$	31.70	54.20
Sb	NA <dl< td=""><td>0.125</td><td>0.37</td><td>NA<dl< td=""><td>0.125</td><td>0.33</td></dl<></td></dl<>	0.125	0.37	NA <dl< td=""><td>0.125</td><td>0.33</td></dl<>	0.125	0.33
As	NA < DL	0.125	0.125	NA < DL	0.125	0.125
В	NA <dl< td=""><td>0.015</td><td>8.40</td><td>NA &lt; DL</td><td>0.015</td><td>2.20</td></dl<>	0.015	8.40	NA < DL	0.015	2.20
Cr	NA <dl< td=""><td>0.025</td><td>0.18</td><td>NA &lt; DL</td><td>0.025</td><td>0.25</td></dl<>	0.025	0.18	NA < DL	0.025	0.25
Pb	NA < DL	0.13	0.13	NA < DL	0.125	0.30
Hg	NA <dl< td=""><td>0.10</td><td>0.10</td><td>NA &lt; DL</td><td>0.10</td><td>0.10</td></dl<>	0.10	0.10	NA < DL	0.10	0.10
Ni	NA < DL	0.05	0.82	NA < DL	0.05	2.10
Tl	NA < DL	0.125	0.44	NA <dl< td=""><td>0.125</td><td>0.28</td></dl<>	0.125	0.28

Different letters indicate significant difference between species.

(P=0.005, P=0.023, respectively) in non-lactating than pregnant deer (Table 2).

Calcium  $(F_{1,77}=8.288,\ P=0.005)$ , Cu  $(F_{1,77}=8.930,\ P=0.004)$ , K  $(F_{1,77}=4.285,\ P=0.042)$ , and Se  $(F_{1,77}=7.196,\ P=0.009)$  values were greater in white-tailed deer than in mule deer, whereas Co  $(F_{1,77}=9.159,\ P=0.003$  [covariate  $F_{1,77}=3.316,\ P=0.003$ ]), Mo  $(F_{1,77}=15.573,\ P<0.001)$ , and Zn  $(F_{1,77}=5.587,\ P=0.021$  [covariate  $F_{1,77}=13.450,\ P<0.001$ ]) values were greater in mule deer than in white-tailed deer (Table 3). Remaining minerals did not differ (P>0.05) between species.

# DISCUSSION

Mineral elements classified as essential (i.e., those that serve a metabolic role in the body) for ruminants include Ca, P, K,

Na, chlorine, S, Mg, Fe, iodine (I), Cu, Mn, Zn, Co, Mo, Se, Cr, fluorine, silicon, Cr, vanadium, tin, As, and Ni (McDonald et al. 1981). Yet some elements, such as Al, Sb, Ba, B, and Tl, have not yet been shown to perform an essential function in ruminants, for example, in cattle or sheep (Puls, 1994). Many of the minerals that we examined have complex interrelationships influencing absorption, utilization, and accumulation. For example, Puls (1994) reported that high levels of Al increased levels of hepatic Zn and Fe but reduced serum Mg and P. These interactions are important in animal nutrition because an imbalance may result in nutritional disorders (McDonald et al., 1981). Furthermore, the mineral content and requirements of an animal's body vary with age, sex, species, maturity, season, and reproductive condition (Robbins, 1983). These interactions make the interpretation of our data challenging; therefore, the primary value of these data are for baseline information from clinically healthy deer. Because we did not evaluate mineral levels of deer forages in the SBH, it is difficult to determine the causes for habitat, reproductive, and interspecific variation demonstrated in this study. Consequently, we can only speculate that the variation observed may be due to diet (Zimmerman, 2004), habitat selection (Dubreuil, 2003), the individual (Robbins, 1983), or feeding strategy (Hofmann, 1988a).

Knowledge of hepatic mineral levels in clinically healthy deer across various ecosystems may be useful for diagnosing toxicity or deficiency throughout the habitats they encompass. Mean hepatic mineral levels of white-tailed and mule deer were within the range of those reported by Puls (1994) for Odocoileus spp. However, when examining the range of values, maximum values for Al, Ca, Co, Fe, Mg, P, Se, Na, and S in both whitetailed and mule deer and Cu in whitetailed deer were greater than the maximum values reported by Puls (1994). Maximum values of hepatic minerals (e.g., Ca, P, K, S, Mg, Na, Cu, and Zn) in white-tailed deer in the SBH also were greater than hepatic minerals of whitetailed deer in Louisiana, with the exception of K (Schultz et al., 1994). It seems that SBH deer are not deficient in any of the hepatic elements that we examined. Although some elements, such as Al, exceeded the toxicity range 11.0 ppm wet weight) reported for cattle (Puls, 1994), toxicity signs (e.g., cholinergic neurotransmission, elevated plasma AST levels, and gastrointestinal irritation) were not apparent (Zimmerman, 2004). Iron and Mg were also high, based on hepatic levels reported for cattle (Puls, 1994). Although toxic effects of Fe have not been reported in deer, excess Mg in cattle can reduce intake of forage, slow the growth rate, and cause diarrhea and emaciation (Puls, 1994). We recommend that data from various locations throughout the wide geographic range of these two species be collected to accurately determine "normal" or adequate mineral levels of healthy deer.

Fire causes an immediate release of nutrients previously held in above-ground plant biomass, often causing significant increases in concentrations of nutrients (Christensen, 1976). Elements such as K, P, Zn, Cu, Fe, and Mn increase in plant biomass following burning (Ohr and Bragg, 1985). Based on our analysis, alteration of the SBH by burning had effects on hepatic mineral concentrations in white-tailed deer (e.g., Zn) and mule deer (e.g., Ba, Cu) within 3 yr following the fire. Because species, season, and stage of maturity affect mineral levels in plants (Kincaid 1988), variation in diets of deer in burned and unburned habitat (Zimmerman 2004) likely caused differences in hepatic mineral levels.

Requirements for increased demand for energy and protein by lactating females are met by selecting vegetation of higher quality and consuming a greater quantity of forage, when compared with their nonreproductive counterparts (Barboza and Bowyer, 2000). According to Blakley et al. (2000), pregnancy in ruminants can be a source of Cu depletion due to its transfer to the developing fetus. Puls (1994) reported that non-pregnant deer had greater liver Cu levels than pregnant animals. Although we could not statistically compare Cu levels in pregnant and nonpregnant mule deer because of a small sample, a comparison of means indicated that pregnant mule deer in the SBH likely had greater hepatic Cu levels than nonpregnant mule deer (Table 2). Copper levels also were greater in pregnant than in lactating and non-lactating deer, which may be attributed to a seasonal effect rather than a reproductive effect because Cu is more readily absorbed when forage is dry, dietary protein is low, and transit time of digesta is long (Puls, 1994; Blakley et al., 2000). Chronic toxicity of Cu has not been reported in deer, whereas clinical signs of Cu deficiency include aberrant hoof growth, enzootic ataxia, weight loss, and infertility (Puls, 1994).

Fetal growth and lactation increase requirements for some elements such as Na, Co, and vitamin  $B_{12}$  (Robbins, 1983; Puls, 1994). Kennedy et al. (1995) reported that mostly adult female white-tailed deer and occasionally fawns visited mineral licks in the Black Hills where soluble salts, soil pH, Na, and nitrate nitrogen were higher than nonlick soils. Therefore, greater hepatic Na in lactating compared to non-lactating and pregnant white-tailed deer was probably due to lactation requirements (Robbins, 1983). Although Puls (1994) reported depleted liver reserves of Co and vitamin  $B_{12}$  in cattle, we did not detect differences in Co levels between reproductive groups of deer. Liver levels of Co are a better reflection of animal status compared with serum levels, whereas levels of vitamin  $B_{12}$  are a more reliable indicator of Co deficiency than Co itself (Puls, 1994). Although Co levels in SBH mule deer exceeded the value (<0.1) reported by Puls (1994), toxicity signs (e.g., anorexia, slow growth rate, and lack of muscular coordination) were not observed in any mule deer we collected.

We did not include season as a treatment in our model; however, seasonality was evaluated by examining differences among reproductive groups (Zimmerman et al., 2006). Under this scenario, individuals in pregnant and non-pregnant groups were collected in winter, whereas those in lactating and non-lactating groups were collected in summer. Manganese and Mo levels were lower in pregnant deer than in lactating and non-lactating deer, yet there was no difference between Mn levels of lactating and non-lactating deer. Because Mn levels do not change with gestational stage, and Mo levels in forage are lowest in winter and rise to their peak in early fall (Puls, 1994), differences in Mn and Mo

levels were probably due to variation in seasonal diets of deer in summer compared to winter (Zimmerman, 2004), and not to reproductive status.

Puls (1994) presented levels of Al, As, Cd, Ca, Co, Cu, Fe, I, Pb, Mg, Mn, Hg, P, K, Se, Na, S, and Zn in liver, kidney, serum, metacarpal, and antler samples for Odocoileus spp. (e.g., white-tailed, blacktailed, and mule deer). According to our results, hepatic mineral levels (e.g., Ca, Co, Cu, Pb, Mo, K, Se, and Zn) differed between sympatric white-tailed deer and mule deer. Mule deer and white-tailed deer differ in feeding strategy (concentrate selector-intermediate feeder; concentrate selector, respectively) (Hofmann, 1988a). Thus, variation in hepatic mineral concentrations was most likely the result of habitat selection (Dubreuil, 2003), diet (Zimmerman, 2004), or forage availability (Zimmerman, 2004). Therefore, based on our findings, we recommend that baseline information on mineral levels in Odocoi*leus* spp. should be separated by species and not grouped together by genus.

Prion diseases (e.g., chronic wasting disease, scrapie, mad cow disease) have been linked to alterations in the metabolism of metals (Brown, 2000). Thackray et al. (2002) documented increases in hepatic Cu levels, prior to the onset of clinical signs, in mice infected with scrapie. They postulated that elevated Cu levels were due to the displacement of Cu from the brain or other tissue. In addition, Brown et al. (2000) proposed that changes in trace elements in diets could potentially induce or increase the incidence of prion diseases, which occur sporadically. Although chronic wasting disease (CWD) has been documented in free-ranging white-tailed deer and mule deer in the South Dakota Black Hills (Jacques et al., 2003; Schuler, 2006), there were no individuals from our study that tested positive for the disease (Zimmerman, 2004). Thus, this baseline information on hepatic mineral levels in white-tailed deer and mule deer may aid in research to identify potential areas where CWD may occur sporadically or for comparison with deer infected with CWD.

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#### LITERATURE CITED

- Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79: 1416–1431
- Barboza, P. S., and J. E. Blake. 2001. Ceruloplasmin as an indicator of copper reserves in wild ruminants at high latitudes. Journal of Wildlife Diseases 37: 324–331.
- ——, AND R. T. BOWYER. 2000. Sexual segregation in dimorphic deer: A new gastrocentric hypothesis. Journal of Mammalogy 81: 473–489.
- BLAKLEY, B. R., S. J. KUTZ, S. C. TEDESCO, AND P. F. FLOOD. 2000. Trace minerals and vitamin concentrations in the liver and serum of wild muskoxen from Victoria Island. Journal of Wildlife Diseases 36: 301–307.
- Brown, D. R. 2002. Metal toxicity and therapeutic intervention. Biochemical Society Transactions 30: 742–745.
- F. Hafiz, L. L. Glassmith, B. Wong, I. M. Jones, C. Clive, and S. J. Haswell. 2000. Consequences of manganese replacement of copper for prion protein functions and protein-ase resistance. European Molecular Biology Organization Journal 19: 1180–1186.
- CHRISTENSEN, N. L. 1976. Short-term effects of mowing and burning on soil nutrients in big meadows, Shenandoah National Park. Journal of Range Management 29: 508–509.
- CONOVER, W. J., AND R. L. IMAN. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. American Statistics 35: 124–133.
- Dubreuil, R. P. 2003. Habitat selection of whitetailed and mule deer in the southern Black Hills, South Dakota. MS Thesis, South Dakota State University, Brookings, South Dakota, 212 pp.
- FIELDER, P. C. 1986. Implications of selenium levels in Washington mountain goats, mule deer, and Rocky Mountain elk. Northwest Science 60: 15–20.
- Froiland, S. G. 1990. Natural history of the Black

- Hills and Badlands. The Center for Western Studies, Sioux Falls, South Dakota, 170 pp.
- Frøslie, A., G. Norheim, J. P. Rambaek, and E. Steinnes. 1984. Levels of trace elements in liver from Norwegian moose, reindeer and red deer in relation to atmospheric deposition. Acta Veterinaria Scandinavica 25: 333–345.
- GILBERT, F. F. 1986. Aging white-tailed deer by annuli in the cementum of the first incisor. Journal of Wildlife Management 30: 200–201.
- GOGAN, P. J. P., D. A. JESSUP, AND M. AKESON. 1989.
  Copper deficiency in tule elk at Point Reyes,
  California. Journal of Range Management 42:
  233–238.
- HIPPENSTEEL, B. A. 2000. Nutritional condition of white-tailed deer in the central Black Hills, South Dakota: Influence of habitat and elk competition. MS Thesis, South Dakota State University, Brookings, South Dakota, 194 pp.
- HOFMANN, R. R. 1988a. Anatomy of the gastrointestinal tract. In The ruminant animal: Digestive physiology and nutrition, D. C. Church (ed.). Prentice-Hall, Englewood Cliffs, New Jersey, pp. 14–43.
- . 1988b. Morphophysiological evolutionary adaptations of the ruminant digestive system. In Aspects of digestive physiology in ruminants, A. Dobson and M. J. Dobson (eds.). Cornell University Press, Ithaca, New York, pp. 1–20.
- Hothem, R. L., D. G. Lonzarich, J. E. Takekawa, and H. M. Ohlendorf. 1998. Containments in wintering canvasbacks and scaup from San Francisco Bay, California. Environmental Monitoring and Assessment 50: 67–84.
- JACQUES, C. N., J. A. JENKS, A. L. JENNY, AND S. L. GRIFFIN. 2003. Prevalence of chronic wasting disease and bovine tuberculosis in free-ranging deer and elk in South Dakota. Journal of Wildlife Diseases 39: 29–34.
- Jasper Fire Rapid Assessment. 2000. United States Department of Agriculture. U.S. Forest Service, Custer, South Dakota, pp. 65.
- JONES, R. L., AND H. C. HANSON. 1985. Mineral licks, geophagy, and biogeochemistry of North American ungulates. Iowa State University Press, Ames, Iowa, 301 pp.
- KENNEDY, J. F., J. A. JENKS, R. L. JONES, AND K. J. JENKINS. 1995. Characteristics of mineral licks used by white-tailed deer (*Odocoileus virginia-nus*). American Midlands Naturalist 134: 324–331.
- KINCAID, R. 1988. Macro elements for ruminants. In The ruminant animal: Digestive physiology and nutrition, D. C. Church (ed.). Prentice Hall, Englewood Cliffs, New Jersey, pp. 326–341.
- King, K. A. 1984. Molybdenum and copper levels in white-tailed deer near uranium mines in Texas. Journal of Wildlife Management 48: 267–270.
- Larson, G. E., and J. R. Johnson. 1999. Plants of the Black Hills and Bear Lodge mountains. Fenske

- Media Corporation, Rapid City, South Dakota, 608 pp.
- LILLIEFORS, H. W. 1967. On the Kolmogorov-Smirnov test for normality with mean and variance unknown. Journal of the American Statistics Association 62: 399–402.
- McDonald, P., R. A. Edwards, and J. F. D. Greenhalgh. 1981. Animal nutrition, 3rd Edition. Longman, Inc., New York, New York, 479 pp.
- McDowell, L. R., D. J. Forrester, S. B. Linda, S. D. Wright, and N. S. Wilkinson. 1995. Selenium status of white-tailed deer in southern Florida. Journal of Wildlife Diseases 31: 205–211.
- Ohr, K. M., and T. B. Bragg. 1985. Effects of fire on nutrient and energy concentration of five prairie grass species. Prairie Naturalist 17: 113–126.
- ORR, H. K. 1959. Precipitation and streamflow in the Black Hills. United States Department of Agriculture Station, Paper 44. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, 25 pp.
- Petersen, L. E. 1984. Northern Plains. In Whitetailed deer: Ecology and management, L. K. Halls (ed.). Stackpole Books, Harrisburg, Pennsylvania, pp. 441–448.
- Puls, R. 1994. Mineral levels in animal health diagnostic data, 2nd Edition. Sherpa International, Clearbrook, British Columbia, Canada, 356 pp.
- Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, New York, 343 pp.
- Rombach, E. P., P. S. Barboza, and J. E. Blake. 2003. Costs of gestation in an Arctic ruminant: Copper reserves in muskoxen. Comparative Biochemistry and Physiology, Part C 134: 157–168.
- Rumble, M. A., and S. H. Anderson. 1996. Microhabitats of Merriam's turkeys in the Black Hills, South Dakota. Ecological Applications 6: 326–334.
- SEVERSON, K. E., AND J. F. THILENIUS. 1976. Classification of quaking aspen stands in the Black Hills and Bear Lodge Mountains. United States Department of Agriculture Resource Paper, RM-166. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, 24 pp.
- Schuler, K. L. 2006. Monitoring for chronic wasting disease in mule deer and white-tailed deer at Wind Cave National Park: Investigating an emerging epizootic. PhD Dissertation. South Dakota State University, Brookings, South Dakota, 173 pp.
- Schultz, S. R., M. K. Johnson, S. E. Feagley, L. L. Southern, and T. L. Ward. 1994. Mineral content of Louisiana white-tailed deer. Journal of Wildlife Diseases 30: 77–85.

- SHORT, H. L., D. R. DIETZ, AND E. E. REMMENGA. 1966. Selected nutrients in mule deer browse plants. Ecology 47: 222–229.
- SIEG, C. H., AND K. E. SEVERSON. 1996. Managing habitats for white-tailed deer in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming. General Technical Report, RM-GTR-274. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, 24 pp.
- STETLER, L. H. 1980. Baseline levels of selected trace elements in Colorado oil shale regions animals. Journal of Wildlife Diseases 16: 175–182..
- THACKRAY, A. M., R. KNIGHT, S. J. HASWELL, R. BUJDOSO, AND D. R. BROWN. 2002. Metal imbalance and compromised antioxidant function are early changes in prion disease. Biochemistry Journal 362: 253–258.
- Thilenius, J. F. 1972. Classification of deer habitat in the ponderosa pine forest of the Black Hills, South Dakota. United States Department of Agriculture Forest Service Research Paper, RM-91, Fort Collins, Colorado, 28 pp.
- Vikøren, T., A. Bernhoft, T. Waaler, and K. Handeland. 2005. Liver concentrations of copper, cobalt, and selenium in wild Norwegian red deer (*Cervus elaphus*). Journal of Wildlife Diseases 41: 569–579.
- WILKINSON, L. 1990. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois, 676 pp.
- WOOLF, A. J., J. R. SMITH, AND L. SMALL. 1982. Metals in livers of white-tailed deer in Illinois. Bulletin of Environmental Contamination and Toxicology 28: 189–194.
- Ytrehus, B., H. Skagemo, G. Stuve, T. Sivertsen, K. Handeland, and T. Vikøren. 1999. Osteoporosis, bone mineralization, and status of selected trace elements in two populations of moose calves in Norway. Journal of Wildlife Diseases 35: 204–211.
- ZIMMERMAN, T. J. 2004. Effects of fire on the nutritional ecology of selected ungulates in the SBH, South Dakota. MS Thesis. South Dakota State University, Brookings, South Dakota, 262 pp.
- ——, J. A. Jenks, and D. M. Leslie, Jr. 2006. Gastrointestinal morphology of female white-tailed and mule deer: Effects of fire, reproductive stage, and feeding type. Journal of Mammalogy 87: 598–605.

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