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GASTROINTESTINAL MORPHOLOGY OF FEMALE WHITE-TAILED AND MULE DEER: EFFECTS OF FIRE, REPRODUCTION, AND FEEDING TYPE

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We assessed variation in length, width, density, and surface enlargement factor of papillae; rumen and intestinal digesta weight; intestinal length; and intestinal tissue weight of reproductive and nonreproductive female white-tailed (*Odocoileus virginianus*) and mule deer (*O. hemionus*) using similar burned and unburned habitat. Deer were collected from study areas in Custer and Pennington counties, South Dakota, in and adjacent to a wildfire burn. Length of papillae and enlargement factor of papillae surface of white-tailed deer and mule deer were greater in burned than unburned habitat, and dry weight of rumen digesta of white-tailed deer was greater in unburned than burned habitat. Papillae surface enlargement factor, papillae length and width, and dry weight of rumen and intestinal digesta were greater for lactating than nonlactating white-tailed deer. Papillae density, intestinal digesta dry weight, and intestinal length were greater in mule deer than white-tailed deer. The mosaic pattern of the burned habitat was beneficial at the mucosal level for white-tailed and mule deer within 3 years postfire. Enhanced papillae morphology of lactating compared with nonlactating and pregnant deer was attributed to high nutritional demands associated with reproductive status. Papillae density may be more important in mule deer because of feeding strategy (concentrate selector–intermediate feeder) compared to white-tailed deer (concentrate selector), whereas greater rumen digesta dry weight and intestinal length may be directly associated with size.

Key words: Black Hills, digesta, fire, intestines, mule deer, *Odocoileus hemionus*, *Odocoileus virginianus*, papillae, South Dakota, white-tailed deer

Limited information exists on gastrointestinal characteristics of wild cervids; studies to date have focused on ruminoreticular dimensions (Demment and Van Soest 1985; Hofmann 1988a; Nagy and Regelin 1975; Parra 1978) or ontogeny of ruminoreticular development (Knott et al. 2004, 2005; Langer 1974; Short 1964). Rumen papillation has been studied in a variety of wild ungulates including elk (*Cervus elaphus*—Lentle et al. 1996, 1997), Norwegian reindeer (*Rangifer tarandus tarandus*—Knott et al. 2004, 2005; Mathiesen et al. 2000; Soveri and Nieminen 1995), moose (*Alces alces*—Hofmann and Nygren 1992), and muskoxen (*Ovibos moschatus*—Knott et al. 2004, 2005). Ruminal papillae are organs of absorption found in the reticulum and rumen of ruminants (Hofmann 1988a). Their distribution, size, and density are

affected by feeding habits, and forage availability and digestibility (Hofmann 1988a).

Variation in diet quality and quantity is hypothesized to affect papillae morphology and perhaps other intestinal features that respond directly to chemical components in plants and thus may be used to evaluate nutritional condition of ruminants (Lentle et al. 1997). Hofmann et al. (1988) evaluated temporal changes in papillae morphology in free-ranging Chinese water deer (*Hydropotes inermis*); variation in a surface enlargement factor, an index of papillary development, paralleled relative availability, abundance, and digestibility of forage. Size of papillae (i.e., absorptive surface area) was positively associated with production of volatile fatty acids in Norwegian reindeer (Mathiesen et al. 2000).

Burning of habitats alters the abundance and quality of forage plants for deer (Carlson et al. 1993; Hobbs and Spowart 1984; Thill et al. 1987; Zimmerman 2004). Total cover of forbs and grasses in lightly to severely burned habitat in the southern Black Hills of South Dakota increased 59.1% ± 21.6% and 79.7% ± 27.7% (SE), respectively, from 2002 to 2003 (Zimmerman 2004).

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Studies on response of deer to burning indicate that white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) may initially avoid newly burned habitat (Dubreuil 2003; Klinger et al. 1989; Roberts and Tiller 1985). Others have reported that mule deer select burned habitat in winter (Davis 1977; Irwin 1975; Keay and Peek 1980). Characteristics used to evaluate use of burned habitat include habitat-selection indices based on tracks and feces (Davis 1977; Klinger et al. 1989; Roberts and Tiller 1985) or radiocollared deer (Dubreuil 2003). To our knowledge, no studies have evaluated response of papillae characteristics, intestinal morphology, or both of ungulates to the effects of wildfires in their habitats.

Our objectives were to examine intestinal morphology and characteristics (papillae characteristics, rumen digesta dry weight, intestinal length, intestinal tissue weight, and digesta dry weight) of reproductive and nonreproductive female white-tailed deer and mule deer, with a primary focus on the effect of burning and reproductive status (e.g., pregnant, lactating, and nonlactating), and to make interspecific comparisons in the intestinal morphology and characteristics of white-tailed deer and mule deer. We predicted that papillae length, width, and surface enlargement factor, and intestinal length would be greater in deer in burned than unburned habitat because of improved access to nutrients, and digesta weights would be greater in unburned than burned habitat because of lower-quality forage. Because of nutritional demands of gestation and lactation, we hypothesized that papillae and intestinal characteristics would be greater in lactating than in nonlactating and pregnant deer. Because of differences in feeding strategies (Hofmann 1988a, 1988b) of white-tailed deer (concentrate selector) and mule deer (concentrate selector–intermediate feeder), we also predicted that papillae morphology and intestinal characteristics would vary between species.

MATERIALS AND METHODS

Study area.—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 (*Artemisia*) steppe ecosystems (Larson and Johnson 1999; Petersen 1984). Topography in the Black Hills ranges from steep ridges, rock outcrops and caves, canyonlands, and gulches to rolling hills, upland prairies, and tablelands (Froiland 1990). Elevations range from 973 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). The study area was located in the southern Black Hills 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 southern Black Hills but use separate winter and summer ranges (Dubreuil 2003). Ponderosa pine (*Pinus ponderosa*) comprises about 84% of the overstory canopy (Rumble and Anderson 1996). The remaining canopy consists 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 portion of winter range is characterized by ponderosa pine, mountain mahogany (*Cercocarpus montanus*), and Rocky Mountain juniper (*Juniperus scopulorum*). Understory vegetation on

winter range consists of big bluestem (*Andropogon gerardii*), buffalograss (*Buchloe dactyloides*), fringed sagewort (*Artemisia frigida*), snowberry (*Symphoricarpos albus*), serviceberry (*Amelanchier alnifolia*), cherry species (*Prunus*), and common juniper (*J. communis*—Dubreuil 2003). Understory vegetation on summer range also is dominated by snowberry and serviceberry as well as Oregon grape (*Berberis repens*), bearberry (*Arctostaphylos uva-ursi*), and various grass and forb species (Dubreuil 2003; Severson and Thilenius 1976; Thilenius 1972). Female white-tailed deer in the southern Black Hills select 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, http://www.fs.fed.us/r2/blackhills/fire/history/jasper/00_11_09_rapid_text.pdf, accessed February 2006) in the southern Black Hills. Based on LANDSAT data reported in the Jasper Fire Rapid Assessment, 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), to high-intensity burns (24%, trees devoid of needles); 5% of the area was unclassified. From 2001 to 2003, average vegetation cover of forbs, grasses, and major shrubs species were 2.2%, 2.3%, and 6.3% in unburned habitat and 8.6%, 11.4%, and 2.2% in burned habitat, respectively (Zimmerman 2004).

Sampling procedures.—We collected deer within and surrounding the Jasper Wildfire perimeter in early February and August 2002 and 2003. We sampled ≥ 5 mule deer and ≥ 5 white-tailed deer from burned and unburned habitats in each season for a total sample of 83 animals (41 mule deer and 42 white-tailed deer). 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. Deer were necropsied at a designated field station. Reproductive status was determined by examining the uterus for fetuses and mammary glands for milk. Incisors were removed and aged using cementum annuli analysis (Gilbert 1986). Body weights (total and eviscerated) were recorded to the nearest kilogram and rumen-reticulum contents were recorded to the nearest 0.1 kg. Samples of rumen wall, > 2 cm², were removed from the dorsal, ventral, left lateral, right lateral, and the dorso- and ventro-caudal blind sacs. Rumen-wall samples were removed within 30 min of harvest and were stored in 10% buffered formalin until processed (Mathiesen et al. 2000; Soveri and Nieminen 1995). We assumed that any changes due to fixation from preservation of tissue samples (Lentle et al. 1997) were consistent among samples and did not influence relative comparisons between burned and unburned habitat or between species. The entire intestinal tract (from pyloric sphincter to rectum) was tied off, removed, and stored frozen until processed. Sampling 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.

A random 2-cm² subsample of the rumen wall was used to determine maximum length and width (in mm) of 20 papillae (5 randomly selected papillae from each side of the subsample) from the 6 rumen-wall locations. Using a 1-cm² ocular grid, papillae density was determined by counting the number of papillae within the perimeter of the grid. Surface enlargement factor was calculated based on the equation of Hofmann and Nygren (1992): $[(2 \times \text{papillae surface}) \times \text{papillae number} + \text{base surface}] / \text{base surface}$, where papillae surface was papillae length multiplied by width and base surface was area of the subsample. Average surface enlargement factor was calculated for each deer by summing the surface enlargement factor from each location and dividing by the total number of samples. To determine

TABLE 1.—Characteristics of ruminal papillae and adjusted means of rumen and intestinal content, intestinal tissue weight, and intestinal length of female white-tailed deer and mule deer in burned and unburned habitat collected in the southern Black Hills, South Dakota, 2002–2003. Values are $\bar{X} \pm 1$ SE.

Characteristic	Burned		Unburned	
	White-tailed deer	Mule deer	White-tailed deer	Mule deer
<i>n</i>	21	20	21	21
Age (years)	5.0 \pm 0.54	4.8 \pm 0.52	5.0 \pm 0.56	3.4 \pm 0.47
Weight of carcass (kg)	35.5 \pm 0.68	43.8 \pm 1.04	36.3 \pm 0.99	41.4 \pm 1.47
Papillae surface enlargement factor	16.4 \pm 1.39	19.2 \pm 1.02	15.7 \pm 1.38	16.3 \pm 1.19
Papillae length (cm)	0.54 \pm 0.03	0.52 \pm 0.02	0.51 \pm 0.04	0.47 \pm 0.03
Papillae width (cm)	0.14 \pm 0.01	0.16 \pm 0.01	0.15 \pm 0.01	0.15 \pm 0.01
Papillae density (no./cm ²)	92.4 \pm 4.90	102.7 \pm 3.26	86.6 \pm 4.71	103.0 \pm 3.20
Contents of rumen (kg, dry weight)	2.4 \pm 0.01	3.83 \pm 0.10	3.0 \pm 0.01	4.0 \pm 0.17
Contents of intestine (g, dry weight)	1,223.1 \pm 19.70	1,575.6 \pm 76.87	1,459.7 \pm 18.12	1,642.0 \pm 129.26
Weight of intestinal tissue (g)	398.1 \pm 0.17	466.4 \pm 0.13	435.0 \pm 0.62	585.1 \pm 0.13
Length of intestine (m)	24.1 \pm 0.17	27.4 \pm 0.20	23.0 \pm 0.15	25.4 \pm 0.32

dry matter weight for rumen ingesta, wet weight was determined for 5 rumen samples for mule deer and white-tailed deer in summer and winter. Samples were dried to constant weight at 60°C, and percentage rumen digesta dry matter was calculated ($\bar{X} \pm SE$; winter: 19.0 \pm 0.4; summer: 15.4 \pm 0.6).

Fat and connective tissues on each intestinal tract were removed, and the entire intestinal tract was weighed to the nearest gram. The intestinal tract was cut longitudinally and all contents were removed by rinsing. After the tract was patted dry, remaining tissue was weighed; difference between weight of the entire intestinal tract and tissue weight was used as an estimate of intestinal digesta wet weight. Fecal dry matter was determined by collecting >10 g (wet weight) of fecal material ($n = 10$) from the rectum of collected deer and drying to constant weight at 60°C. Percentage fecal dry matter was used to adjust intestinal digesta wet weight using the equation (% rumen dry matter + % fecal dry matter)/2. We assumed average moisture content for hindgut digesta. Length of intestinal tissue was determined by stretching sections of the tract using a spring scale with 5 g of tension (Jenks et al. 1994).

Correlations between papillae length and width were performed for the 6 rumen-wall locations. Papillae characteristics (height and width) from the dorso-caudal blind sac were not correlated for this site or with measurements from the other 5 rumen wall sites; therefore, this sampling site was removed from the analysis. Lilliefors' test (Dallal and Wilkinson 1986; Lilliefors 1967) was used to evaluate normality; nonnormal data were rank transformed (Conover and Iman 1981) and the alpha level was set at 0.10. Gastrointestinal morphological variables were compared for main and interactive effects of habitat and reproductive status using analysis of covariance (ANCOVA); interspecific comparisons were conducted using ANCOVA. Age (Lentle et al. 1996) was used as the covariate for papillae length, width, density, and surface enlargement factor. Eviscerated weight (Jenks et al. 1994) was used as the covariate for rumen dry matter, intestinal dry matter, intestinal length, and intestinal tissue weight. If we could not meet assumptions of homogeneity of slopes in ANCOVA, analyses were conducted by plotting data by independent variables. If variables were independent, the covariate was removed from the analysis. Tukey's honestly significant difference multiple comparisons test was used to determine differences between reproductive groups. Papillae morphology means and adjusted means of rumen and intestinal digesta dry weights, weight of intestinal tissue, and intestinal length are presented with ± 1 SE. We performed all statistical analyses with SYSTAT (Wilkinson 1990).

RESULTS

Habitat.—Ages of female white-tailed deer ranged from 1 to 11 years; 22 were pregnant, 11 were lactating, and 9 were nonlactating. Ages of female mule deer ranged from 1 to 10 years; 18 were pregnant, 3 were nonpregnant, 14 were lactating, and 6 were nonlactating. We removed nonpregnant mule deer from the analysis because of small sample size. Surface enlargement factor and papillae length of white-tailed deer ($F = 3.069$, $df. = 1, 35$, $P = 0.089$ and $F = 3.948$, $df. = 1, 35$, $P = 0.055$, respectively) were greater in burned than unburned habitat (Table 1). Dry weight of rumen digesta of white-tailed deer was greater ($F = 3.739$, $df. = 1, 33$, $P = 0.062$) in unburned than burned habitat (Table 1). Surface enlargement factor and papillae length of mule deer ($F = 7.287$, $df. = 1, 31$, $P = 0.011$ and $F = 2.984$, $df. = 1, 31$, $P = 0.094$, respectively) were greater in burned than unburned habitat (Table 1). The interaction of habitat and reproductive status was significant ($F = 2.743$, $df. = 1, 29$, $P = 0.081$) for rumen digesta weight in mule deer. In burned habitat, rumen digesta weight ($F = 5.955$, $df. = 1, 13$, $P = 0.015$) was greater ($P = 0.013$) for lactating (3.793 \pm 0.151) than nonlactating (3.325 \pm 0.140) mule deer. Remaining variables did not differ by main effect of habitat ($P > 0.10$).

Reproductive status.—Papillae surface enlargement factor ($F = 58.890$, $df. = 1, 35$, $P < 0.001$), length ($F = 36.692$, $df. = 1, 35$, $P < 0.001$), width ($F = 38.149$, $df. = 1, 38$, $P < 0.001$), and dry weight of intestinal ($F = 22.183$, $df. = 1, 23$, $P < 0.001$) and rumen ($F = 12.334$, $df. = 1, 33$, $P < 0.001$) digesta of white-tailed deer differed between reproductive groups. Papillae surface enlargement factor ($F = 49.360$, $df. = 1, 31$, $P < 0.001$), length ($F = 36.866$, $df. = 1, 31$, $P < 0.001$), width ($F = 35.623$, $df. = 1, 31$, $P < 0.001$), density ($F = 5.384$, $df. = 1, 29$, $P = 0.010$), dry weight of intestinal digesta ($F = 7.310$, $df. = 1, 20$, $P = 0.004$), tissue weight ($F = 3.675$, $df. = 1, 20$, $P = 0.044$), and intestinal length ($F = 4.842$, $df. = 1, 19$, $P = 0.020$) of mule deer differed between reproductive groups. Remaining variables did not differ by main effect of reproductive status ($P > 0.10$). The covariate was significant for intestinal digesta dry weight ($F = 6.511$,

TABLE 2.—Characteristics of ruminal papillae and adjusted means of rumen and intestinal content, intestinal tissue weight, and intestinal length of female white-tailed deer and mule deer in reproductive groupings collected in the southern Black Hills, South Dakota, 2002–2003. Values are $\bar{X} \pm 1 SE$.

Characteristic	Summer				Winter		
	Nonlactating		Lactating		Pregnant		Nonpregnant
	White-tailed deer	Mule deer	White-tailed deer	Mule deer	White-tailed deer	Mule deer	Mule deer
<i>n</i>	9	6	11	14	22	18	3
Age (years)	2.9 ± 0.61	1.8 ± 0.40	5.6 ± 0.41	3.9 ± 0.43	5.5 ± 0.59	4.9 ± 0.59	3.3 ± 1.45
Weight of carcass (kg)	37.0 ± 1.44	36.8 ± 1.26	36.1 ± 0.96	43.8 ± 0.93	35.4 ± 0.84	43.6 ± 1.59	38.3 ± 6.5
Papillae surface enlargement factor	20.6 ± 1.09	20.4 ± 0.84	22.6 ± 0.83	22.8 ± 0.75	10.9 ± 0.69	13.9 ± 0.74	11.8 ± 1.08
Papillae length (cm)	0.6 ± 0.04	0.5 ± 0.03	0.7 ± 0.03	0.6 ± 0.02	0.4 ± 0.01	0.4 ± 0.02	0.3 ± 0.03
Papillae width (cm)	0.2 ± 0.01	0.2 ± 0.01	0.2 ± 0.01	0.2 ± 0.01	0.1 ± 0.00	0.1 ± 0.01	0.1 ± 0.00
Papillae density (no./cm ²)	99.0 ± 6.06	106.2 ± 2.84	81.5 ± 3.76	93.4 ± 3.41	89.6 ± 5.51	106.4 ± 3.38	119.0 ± 4.74
Contents of rumen (kg, dry weight)	2.6 ± 0.12	3.6 ± 0.17	2.8 ± 0.11	4.2 ± 0.15	2.7 ± 0.06	3.8 ± 0.16	3.1 ± 0.12
Contents of intestine (g, dry weight)	1,267.5 ± 80.05	1,279.6 ± 94.69	1,382.4 ± 57.00	1,785.8 ± 98.93	1,347.5 ± 9.43	1,581.2 ± 127.3	1,697.2 ± 63.29
Weight of intestinal tissue (g)	409.2 ± 7.55	525.8 ± 26.9	420.8 ± 6.66	525.8 ± 16.55	416.7 ± 3.47	529.2 ± 14.67	507.2 ± 23.66
Length of intestine (m)	23.5 ± 0.12	25.8 ± 0.90	23.6 ± 0.02	27.0 ± 0.33	23.6 ± 0.26	26.2 ± 0.34	24.2 ± 0.46

df. = 1, 20, $P = 0.019$) and tissue weight ($F = 5.203$, *df.* = 1, 20, $P = 0.034$) of mule deer.

Papillae width in lactating and nonlactating white-tailed deer was greater ($P < 0.001$) than papillae width of pregnant white-tailed deer (Table 2). Papillae length in lactating and nonlactating white-tailed deer was greater ($P < 0.001$ and $P = 0.001$, respectively) than papillae length of pregnant white-tailed deer. Papillae surface enlargement factor, length, and width in lactating (all $P < 0.001$) and nonlactating (surface enlargement factor: $P < 0.001$; length: $P = 0.003$; width: $P = 0.002$) mule deer were greater than in pregnant mule deer (Table 2).

Papillae surface enlargement factor ($P = 0.072$), length ($P = 0.048$), width ($P = 0.030$), and dry weight of intestinal ($P < 0.001$) and rumen ($P = 0.056$) digesta were greater in lactating than nonlactating white-tailed deer (Table 2). Papillae length ($P = 0.088$), intestinal digesta dry weight ($P = 0.010$), and intestinal length ($P = 0.080$) were greater in lactating than nonlactating mule deer (Table 2).

Intestinal and rumen digesta dry weight of lactating white-tailed deer were greater ($P < 0.001$) than digesta dry weight of pregnant white-tailed deer. Intestinal digesta dry weight ($P = 0.070$) and intestinal tissue weight ($P = 0.048$) of lactating mule deer were greater than intestinal digesta dry weight and intestinal tissue weight of pregnant mule deer (Table 2). Papillae density was greater ($P = 0.008$) in pregnant than lactating mule deer (Table 2).

Interspecific comparisons.—Papillae density ($F = 9.566$, *df.* = 1, 80, $P = 0.003$), rumen digesta dry weight ($F = 13.808$, *df.* = 1, 76, $P < 0.001$), and intestinal length ($F = 7.979$, *df.* = 1, 54, $P = 0.007$) were greater in mule deer than white-tailed deer (mule deer papillae density: 101.45 ± 2.24 papillae/cm²; white-tailed deer papillae density: 87.87 ± 3.18 papillae/cm²; mule deer rumen weight: 3.325 ± 0.140 kg; white-tailed deer rumen weight: 2.703 ± 0.05 kg; mule deer intestinal length: 26.411 ± 0.251 m; white-tailed deer intestinal length: 23.602 ± 0.141 m).

Papillae width ($F = 7.357$, *df.* = 1, 37, $P = 0.010$), papillae density ($F = 5.908$, *df.* = 1, 37, $P = 0.020$), rumen digesta dry

weight ($F = 9.433$, *df.* = 1, 34, $P = 0.004$), intestinal digesta dry weight ($F = 4.230$, *df.* = 1, 17, $P = 0.055$), and intestinal tissue weight ($F = 4.016$, *df.* = 1, 17, $P = 0.061$) were greater for pregnant mule deer than pregnant white-tailed deer (Table 2).

Papillae length ($F = 3.312$, *df.* = 1, 22, $P = 0.082$) was greater for lactating white-tailed deer than lactating mule deer, but papillae density ($F = 4.829$, *df.* = 1, 22, $P = 0.039$) and intestinal length ($F = 11.011$, *df.* = 1, 20, $P = 0.003$) were greater for lactating mule deer than lactating white-tailed deer (Table 2). Remaining variables did not differ by main effect of species ($P > 0.10$).

DISCUSSION

Effects of fire on gastrointestinal morphology.—During the 1st winter postfire, female white-tailed deer in the southern Black Hills avoided all burned habitat (Dubreuil 2003). Unburned habitat was selected by white-tailed deer for foraging and bedding; however, there was weak selection for ponderosa pine–grass–forb habitats, which were lightly burned. Dubreuil (2003) postulated that selection for unburned habitat was related to lack of available cover and forage in severely burned habitat. Irwin (1975) observed that within 2 growing seasons after a fire in northeastern Minnesota, white-tailed deer preferred burned periphery and unburned forest in winter and spring but used burned habitat in summer and autumn. Based on our analysis, alteration of the southern Black Hills by burning had effects on papillae morphology and digesta weight in white-tailed deer and mule deer within 3 years postfire.

Because of the rapid response (e.g., 2 weeks) of papillae to changes in diet quality, papillary morphology likely represents a useful indicator of forage quality (Lentle et al. 1997; Mathiesen et al. 2000). The burn pattern of the Jasper Wildfire created a mosaic of burned and unburned habitat of varying burn intensity within the 34,821-ha zone (Zimmerman 2004). Those patches provided areas of unburned habitat for thermal cover and predator escape and burned edge habitats with

greater diversity and quality of forage, as indicated by greater carbon and nitrogen isotopes in burned than unburned habitat (W. D. Walter, in litt.). Increase in papillary length may be associated to greater concentration of volatile fatty acids (Lane and Jesse 1997) within the rumen or reduced particle size of forage (Greenwood et al. 1997). Similar response in papillae characteristics to burning in both species supports our hypothesis of fire being beneficial at the mucosal level for deer in the southern Black Hills.

Jenks et al. (1994) noted increased digesta in white-tailed deer from ranges with reduced digestibility of diets because of competitive interactions with cattle. Heavier mass of rumen digesta also was reported in mule deer with consumption of low-quality diets compared with high-quality diets (Baker and Hobbs 1987). Jenks et al. (1994, 1996) reported reduced ruminal fill and greater intestinal fill in white-tailed deer on higher-quality diets compared with those occurring sympatrically with cattle that consumed a lower-quality diet. Our results supported those of Jenks et al. (1994) for white-tailed deer; rumen digesta dry weights were greater in poorer-quality habitat (i.e., unburned habitat). The lack of difference in rumen digesta dry weight in mule deer may indicate suitable unburned habitat in the southern Black Hills.

Propionic and butyric acid (i.e., volatile fatty acids) are produced during fermentation of high-quality diets, stimulating growth of papillae (Hofmann 1988a; Van Soest 1982). Because absorption of volatile fatty acids occurs in the rumen and omasum, volatile fatty acids may not act in the same manner to stimulate growth of intestinal tissue (Owens and Goetsch 1988). Thus, stimulation of intestinal tissue is likely due to a different mechanism than for papillae.

Effects of season on gastrointestinal morphology.—Mucosal changes are related closely to seasonal changes in forage quality and quantity (Hofmann and Nygren 1992). Total production of volatile fatty acids for free-ranging animals is lower in winter than summer (Mathiesen et al. 2000). According to Short (1981), vegetation is used with greater efficiency for lipogenesis during summer and early autumn because succulent and starchy forage yields increased levels of volatile fatty acids during rumen fermentation. Short et al. (1966) also reported that butyric acid levels in mule deer were lower in winter and early spring than late spring and summer.

To our knowledge the only documentation of white-tailed deer and mule deer papillae dimensions are by Short (1964, 1981). Based on his data, average papillae length and width were 10 and 2 mm, respectively, for adult white-tailed deer and mule deer. Season, sex, nutritional condition of the deer, and location of those measurements were not reported (Short 1964, 1981). Although we did not include season as a treatment in our model, seasonality was evaluated by examining differences among reproductive groups. Under this scenario, individuals in the pregnant and nonpregnant groups were collected in winter, whereas those in lactating and nonlactating groups were collected in summer. Based on our model, papillae surface enlargement factor was less in pregnant mule deer than in lactating and nonlactating mule deer, and no difference was found between the surface enlargement factor of lactating and

nonlactating deer. Therefore, the difference in surface enlargement factor was probably due to forage availability and quality in summer compared with winter, not reproductive status. Furthermore, by examining means of papillae dimensions it was evident that seasonal variation occurred; average length and width of papillae of white-tailed deer were 0.410 and 0.118 cm in winter and 0.660 and 0.177 cm in summer, respectively, and average length and width of papillae of mule deer were 0.401 and 0.130 cm in winter and 0.587 and 0.177 cm in summer, respectively. Length and perimeter of rumen papillae in moose and Norwegian reindeer also were larger in summer than winter (Hofmann and Nygren 1992; Mathiesen et al. 2000).

Changes in papillary length, followed by density, in moose resulted in the greatest seasonal reduction in surface area (Hofmann and Nygren 1992). Papillae density per square centimeter was higher in March than September in Norwegian reindeer (Mathiesen et al. 2000). Average numbers of papillae in moose in summer and winter were 50.4/cm² and 34.7/cm², respectively, and represented a 31% seasonal reduction in papillae density (Hofmann and Nygren 1992). Mathiesen et al. (2000) also calculated a greater density and shorter length of papillae in adult female Norwegian reindeer in March compared with September. Hofmann and Nygren (1992) found a lesser density and shorter length of papillae in wild moose in winter compared with summer, although they combined data from males and females. Soveri and Nieminen (1995) also reported seasonal effects in papillae size but were unable to detect seasonal effects in papillae density in reindeer calves; length was greater in November–December compared with late April–early May. Although we did not specifically test temporal variation of season, examination of the papillae density data of female white-tailed deer in the southern Black Hills supports findings of Soveri and Nieminen (1995) in reindeer calves demonstrating little variation between seasons. Seasonal variation in papillae density of female mule deer in the southern Black Hills was similar to that of moose and adult female reindeer (Hofmann and Nygren 1992; Mathiesen et al. 2000).

In moose, a decrease in rumen papillae per square centimeter from summer to winter was associated with the majority of the seasonal reduction in surface enlargement factor (Hofmann and Nygren 1992). The surface enlargement factor of white-tailed deer in the southern Black Hills was 10.75 ± 0.64 in winter and 22.10 ± 0.72 in summer, whereas that of mule deer was 13.07 ± 0.62 in winter and 21.92 ± 0.57 in summer. Seasonal reduction in surface enlargement factor seen in mule deer and white-tailed deer was consistent with the absorptive surface reduction from summer to winter in moose, which also approached 50% (Hofmann and Nygren 1992). In free-ranging Chinese water deer, surface enlargement factor was lowest in winter (March) and highest in spring (May—Hofmann et al. 1988); values of surface enlargement factor were <4.0 in winter and about 8.0 in autumn. Mathiesen et al. (2000) noted that surface enlargement factor throughout the rumen decreased from September to November in adult female Norwegian reindeer. In their study, diet quality did not change

from September to November; therefore, the reduction in ruminal mucosa was attributed to a seasonal reduction in dry matter intake.

Effects of reproduction on gastrointestinal morphology.—Changes in papillae morphology may be related directly to forage quality in summer compared with winter, but based on our data, changes in papillae and gastrointestinal morphology were associated with season coupled with reproductive status. Variation in reproductive demands may parallel changes in intestinal capacity (Barboza and Bowyer 2000). Requirements for increased demand for energy and protein by lactating females would be met by selecting vegetation of higher quality and consuming a greater quantity of forage compared with their nonreproductive counterparts (Barboza and Bowyer 2000). Tulloh (1966) reported that dry and wet weights of digesta in cattle were greater in lactating than nonlactating females. As reported by Jenks et al. (1994), greater weights of rumen contents in lactating than nonlactating white-tailed deer supports a lactational effect, which also was demonstrated in white-tailed deer in the southern Black Hills.

After parturition, weights of the rumen, abomasum, intestines, and liver increase, which is mediated by increased food intake as a result of nutrient demands of lactation (Forbes 1986). This lactational effect was demonstrated in white-tailed deer and mule deer in the southern Black Hills. Hammond and Kristan (2000) reported greater small intestine length, mucosal mass, and digestible food intake in lactating compared with nonreproductive female deer mice (*Peromyscus maniculatus*). Thus, increases in quality and quantity of digesta would result in an increase in size of postruminal segments of the digestive tract and liver (Barboza and Bowyer 2000). Intestinal mass of cattle breeds on high-quality forage was greater for lactating than either nonlactating—pregnant or nonlactating—nonpregnant females (Tulloh 1966). Although intestinal length of white-tailed deer could not be evaluated statistically, intestinal length of lactating white-tailed deer and mule deer was longer than that of pregnant and nonlactating white-tailed deer.

Interspecific comparison of gastrointestinal morphology.—According to Short (1964), the larger relative sizes of sheep and cow rumens compared to those of deer allow for a longer retention of food material to enhance fermentation of fibrous forage. The larger dry weight of digesta in mule deer indicated a potential for a diet containing more fibrous foods than that of white-tailed deer, which are less efficient at digesting fiber. Prins and Geelen (1971) reported that the volatile fatty acids composition of elk diets closely resembled that of mule deer, whereas volatile fatty acids composition in fallow deer (*Dama dama*) diets was more comparable to white-tailed deer, with higher fermentation rates in fallow deer than elk. Digesta retention generally decreases with increased fermentation rates and thus may have been less in white-tailed deer than mule deer. Therefore, a lengthened intestinal tract might not have been necessary to maximize absorption in white-tailed deer on a high-quality diet. Furthermore, if variation in length of the colon was due to availability of water for milk production (as suggested by preliminary results one of us [JAJ] has obtained), free water and relatively mild temperatures may have limited

the need to increase colon length. Retention of digesta in the intestinal tract increases with body size in deer (Barboza and Bowyer 2000), and the absolute amount of food required declines with body size (Geist 1981). Greater weight of digesta in mule deer is likely correlated directly to their larger body size.

Rapid response of papillae to changes in forage quality indicates that morphological measurements are a useful indicator of acute response of deer to alterations in habitat. Moreover, changes in papillae and gastrointestinal morphology may be a useful indicator of condition in conjunction with other physiological and morphological indices (i.e., blood and fat indices). Relative to the 2 species studied, perhaps papillae density is more important in mule deer because of feeding strategy (concentrate selector-intermediate feeder—Hofmann 1988a) compared with white-tailed deer (concentrate selector—Hofmann 1988a). Further research on papillae morphology could provide insight on resource partitioning and nutritional condition among ungulates.

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