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Reproductive effects on fecal nitrogen as an index of diet quality: an experimental assessment

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Concentration of fecal nitrogen has been used widely as an indicator of dietary quality for free-ranging ruminants. Differences in digestive function between species of dimorphic ungulates render interspecific comparisons of fecal nitrogen unreliable; however, whether intraspecific sexual differences in digestive function also bias this nutritional index is unknown. Our objective was to compare sex-specific variation in concentration of fecal nitrogen using male, nonlactating female, and lactating female white-tailed deer (*Odocoileus virginianus*) on high- and low-quality diets. During weekly trials over spring and summer (2008–2009), we monitored intake rates, collected feces twice daily, and used micro-Kjeldahl procedures to determine percent fecal nitrogen. We also determined nitrogen content of feces following a neutral detergent fiber (NDF) rinse during pre-, peak, and postlactation. Fecal nitrogen reflected general differences in dietary quality between diets; however, fecal nitrogen of lactating females in both dietary groups was lower than for males or nonlactating females throughout lactation. Nitrogen concentration following an NDF rinse also was lower for lactating females during peak lactation. We hypothesize that the remodeling of the digestive tract and increased rumination by lactating females may enhance their ability to extract nitrogen from their forage. These adjustments may expand the foraging options of lactating females by increasing their ability to process low-quality foods, but also affects the interpretation of fecal nitrogen during the season of lactation.

Key words: diet quality, fecal nitrogen, gastrointestinal tract, lactation, nutrition, *Odocoileus virginianus*, ruminant, sexual segregation, white-tailed deer

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Quality and quantity of forage available to wild ungulates influences all aspects of their life history, including how nutritional resources are allocated to survival and reproduction, the effects of which can carry over between seasons and generations (White 1983; Monteith et al. 2009, 2013; Parker et al. 2009; Raubenheimer et al. 2009; Bårdsen and Tveraa 2012). Measuring forage and diet quality, however, can be difficult, which has led to the development of several indices of forage and dietary quality (Leslie et al. 2008). Concentration of nitrogen in feces is a commonly used indicator of dietary quality (Sinclair et al. 1982; Leslie and Starkey 1985; Blanchard et al. 2003; Leslie et al. 2008), and has been used to compare quality of diets among habitats for both free-ranging (Hodgman and Bowyer 1986; Green 1987; Grant et al.

1996; Hodgman et al. 1996; Jenks et al. 1996; Ueno et al. 2007) and domestic (Cordova et al. 1978; Holecheck et al. 1982; Howery and Pfister 1990) ruminants. Fecal nitrogen indexes relative change in diet quality among seasons and allows the assessment of diet quality in a single population among years or between populations in similar habitats (Leslie et al. 2008). Fecal nitrogen offers a convenient, noninvasive, and low-cost index to diet quality, because fecal matter is readily available and can be collected easily (Jenks et al. 1990; Osborn et al. 2002; Kamler et al. 2003). Potential inaccuracies



in the index have been identified, and discrepancies in performance of fecal nitrogen among studies have led to controversy regarding the reliability and use of this dietary index (Hobbs 1987; Robbins et al. 1987; Dearing et al. 2005; Leslie et al. 2008; Schwarm et al. 2009; Peripolli et al. 2011). Despite this controversy regarding its efficacy, the use of fecal nitrogen has increased substantially since 1986 (Leslie et al. 2008).

Sexual dimorphism in body size of dimorphic ungulates may affect excretion of nitrogen in feces, if those differences parallel interspecific relationships (Leslie and Starkey 1985). Leslie and Starkey (1985) cautioned against interspecific comparisons of fecal nitrogen to index diet quality, because differences in digestive capabilities among species result in variable nitrogen concentration in feces. Despite consuming similar diets, Columbian black-tailed deer (*Odocoileus hemionus columbianus*) had higher concentrations of fecal nitrogen than Roosevelt elk (*Cervus elaphus roosevelti*—Leslie and Starkey 1985). Therefore, between-species comparisons can be misleading because of differences in digestive morphology and function, and plant parts eaten (Leslie and Starkey 1985; Hobbs 1987; Leslie et al. 2008). Metabolic needs also can increase the amount of fecal nitrogen absorbed. Smaller ruminants have high metabolic requirements relative to body mass compared with larger ruminants, which increases the fermentative rate and microbial nitrogen produced by these species (Arman et al. 1975).

Polygynous ruminants segregate by sex for much of the year, and consequently partition space, often occupy different habitats, and consume different forages (Kie and Bowyer 1999; Bowyer 2004; Main 2008; Schroeder et al. 2010). Polygynous ruminants are sexually dimorphic, but have similar rumen volumes relative to their body mass (Weckerly 1998, 2010), experience divergent metabolic demands on a seasonal basis (Moen 1973), and differ in digestive function (Barboza and Bowyer 2000, 2001). Consequently, the amount of fecal nitrogen that is absorbed may differ inter- and intrasexually. Lactating females remodel their gastrointestinal tracts by additional investment in rumen, small intestine, liver, and cecum-proximal colon (Jenks et al. 1994; Barboza and Bowyer 2000; Zimmerman et al. 2006) to enhance digestion and absorption of nutrients to support the protein and energetic demands of lactation (Moen 1973), including production of high-protein milk (Robbins 1983). Remodeling of the gastrointestinal tract may allow lactating females to increase absorption of nitrogen beyond the capabilities of males and nonlactating females (Barboza and Bowyer 2000), which would affect comparisons of dietary quality among sexes and their reproductive status based on fecal nitrogen.

Our objectives were to experimentally assess the relationship between diet quality and fecal nitrogen among sexes and relative to reproductive status of white-tailed deer (*Odocoileus virginianus*) during spring and summer. We hypothesized that differences in digestive function and metabolic rate would influence absorptive capability of dietary nitrogen and thereby, the concentration of fecal nitrogen. Based on the difference in

body size and metabolic rates between males and females (Leslie and Starkey 1985), we predicted that females would have higher concentrations of fecal nitrogen than males on a similar diet. In addition, we predicted that lactating females would be capable of absorbing more nitrogen compared with nonlactating females or males on similar diets, because of the investment in digestive surfaces and the need to maximize digestion and absorption to support lactation.

MATERIALS AND METHODS

Experimental design.—We evaluated effects of diet quality, sex, and reproductive status on concentrations of fecal nitrogen in captive white-tailed deer, which were hand-raised and accustomed to small enclosures, during spring and summer 2008 and 2009. Our study was conducted at the Wildlife Research Facility at South Dakota State University in Brookings, South Dakota (44°20'N, 96°47'W). Research animals were adult white-tailed deer of varying age (2–7 years old), which we separated into 2 treatments that differed in diet quality (high quality versus low quality). Each treatment was separated into 3 subgroups by reproductive status and sex: males on high-quality ($n = 4$) and low-quality ($n = 4$) diets, nonlactating females on high-quality ($n = 3$) and low-quality ($n = 4$) diets, and lactating females on high-quality ($n = 3$) and low-quality ($n = 4$) diets. We assigned females to a reproductive group and all deer to each diet randomly.

We fed deer rations of shelled corn and pelleted soy hulls in separate containers for both treatments. In vitro dry matter digestibility (IVDMD) was determined over 24 h with rumen fluid collected from a domestic cow (Van Soest 1994; Dairyland Laboratories, Inc., St. Cloud, Minnesota). We determined crude protein content of foods using micro-Kjeldahl analysis (Jackson 1958), and estimated digestible protein for each diet from the product of in vitro dry matter digestibility and crude protein. Shelled corn, which we considered high-quality food, had an in vitro dry matter digestibility of 88.2%, with 8.7% crude protein, resulting in 70% protein digestibility. Pelleted soy hulls, which we considered lower-quality food, were 62.2% digestible with 12.0% crude protein, yielding 75% protein digestibility. The bioavailability of protein was slightly higher for the lower-quality food, which could have increased measures of fecal nitrogen. Nevertheless, such bias would not affect comparisons among sex and reproductive status because we maintained animals on a constant diet. Furthermore, for nonlactating animals in this study, average apparent digestible protein, as determined by absolute difference in intake and excretion of crude protein, was higher for the high-quality diet (70.4%) than for the low-quality diet (66.3%). Corn is a highly preferred food for white-tailed deer in the midwestern United States and is consumed throughout the year (Schmitz 2000; Delger et al. 2011). To represent the high-quality diet, we offered the animals shelled corn and pelleted soy hulls ad libitum (corn composed 60% of ad libitum intake). For the low-quality diet, we offered animals soy hulls ad libitum, but restricted

availability of corn to 40% of the ad libitum intake of corn measured for each respective group on the high-quality diet (adjusted for body mass; g/kg). Rather than restricting total absolute intake of food, our goal was to create a diet of poor quality by limiting the more-digestible food, while offering the less-digestible food ad libitum (Tollefson et al. 2011). We placed animals in enclosures and offered diets to animals a minimum of 2 weeks before the beginning of the study to allow rumen microbes to adapt to rations (Mautz et al. 1976), and allow individuals to become accustomed to each enclosure; deer remained on their assigned diet throughout spring and summer of each year.

We conducted trials every other week from week 22 (late May) through week 38 (early October) of the calendar year, which resulted in monitoring for 1 week before parturition, 7 weeks during lactation, and 1 week postweaning. During trials, each animal was confined to a 3.0-m² enclosure (1.22 × 2.44 m) with access to feed and ad libitum water. Each enclosure had a slanted cement or wood floor. We monitored feed intake for 5 days during each trial, and collected total fecal output for 3 days following the 1st day of trials. To maintain lactation, we kept 1 neonate in an adjacent enclosure to each lactating female from weeks 23 through 37, after which they were weaned. Lactating females were allowed to nurse their neonate according to the same feeding schedule used for hand-rearing neonatal deer (Buckland et al. 1975). We used 1 neonate to represent the minimum metabolic requirements of a lactating female during spring and summer (Sadlier 1982). Neonates consume primarily milk in the 1st few weeks of life; however, they had access to shelled corn, pelleted soy hulls, and water (ad libitum) to mimic the changing patterns of nutrients required by young, because young consume more forage as they grow (Sadlier 1982). Facilities and procedures for research on captive deer followed guidelines of the American Society of Mammalogists (Sikes et al. 2011), and were approved by the Institutional Animal Care and Use Committee (approval 08-A029) at South Dakota State University.

Data collection.—We measured daily intake rates of water and experimental diets weekly by weighing remaining feed and water daily with a hanging dairy scale accurate to 45.4 g (model 600; Hanson Scale Company, Shutuba, Mississippi). We collected a sample of each feed daily and dried it to a constant weight at 50°C to calculate dry matter intake. We weighed deer weekly using a walk-on scale accurate to 454 g (Adrian J. Paul Company, Duncan, Oklahoma). We then calculated daily food intake of dry matter as a function of body mass (g/kg) per day.

We collected total fecal output from each animal every 6 h for 3 days during each week of trials. We dried fecal samples to constant weight at 50°C (Hinnant and Kothmann 1988), ground them in a Wiley mill with a 1-mm-mesh screen (Davitt and Nelson 1980), and composited them into weekly samples per individual (Jenks et al. 1989). We conducted micro-Kjeldahl analysis (Jackson 1958) for 2 samples of feces from each composite sample and averaged those 2 samples to determine percent fecal nitrogen per week. Average difference between

duplicate samples was 0.02%. We also prepared a sample of each feed source in the same manner as fecal samples to determine concentration of dietary nitrogen. We then calculated apparent nitrogen absorption based on the intake of dietary nitrogen relative to total nitrogen output in feces (Robbins 1983). Similarly, we used mean fecal output per day relative to mean dry matter intake for each animal to calculate apparent digestive efficiency (Robbins 1983).

We assessed an additional index of dietary quality by measuring percent nitrogen of feces after conducting a neutral detergent fiber (NDF) rinse (NDF-N—Van Soest 1994). An NDF rinse removes the cell-soluble portion of the diet and endogenous sources of nitrogen and thus, NDF-N represents the amount of nitrogen contained in hemicellulose, cellulose, and lignin of the cell wall that was not digested (Schwarm et al. 2009). Evaluation of the NDF-N provided an indication of undigested nitrogen remaining in forage (Schwarm et al. 2009; P. S. Barboza, University of Alaska Fairbanks, pers. comm.). We calculated NDF-N of fecal samples collected from weeks 22, 30, and 38 to encompass preparturition, peak energy demand during lactation, and postweaning for lactating females (Sadlier 1982).

Data analyses.—We combined data for corresponding weeks during 2008 and 2009 to provide adequate sample size for statistical analyses. We adjusted the trial period for 1 lactating female to align periods of parturition and weaning, because she gave birth 1 week later than other females in the study. We used mean daily values per week to represent a datum for each individual deer. We evaluated trends in body mass, dietary intake, digestive efficiency, and fecal nitrogen by assessing differences in temporal patterns among treatments (Johnson 1999). Because we repeatedly monitored the same individuals through time, we conducted a repeated-measures analysis of variance to evaluate differences in response variables among males, nonlactating females, and lactating females within dietary treatments (Zar 1999). We adopted an $\alpha = 0.05$; for all subsequent pair-wise comparisons, we used Bonferroni corrections to maintain the overall experiment-wide error (Zar 1999).

RESULTS

Male white-tailed deer on the high-quality diet were initially larger than males on the low-quality diet (Fig. 1); males on the high-quality diet increased in body mass by an average of 25.7% ($SE = 0.1$ kg) throughout the summer, whereas males on the low-quality diet increased, on average, only 13.0% ($SE = 0.1$) during the study (Fig. 1). As a result, male deer on the high-quality diet were 50% larger than nonlactating and lactating females ($F_{2,7} = 29.10$, $P < 0.001$; Fig. 1), whereas males on the low-quality diet were only 25% larger than nonlactating and lactating females ($F_{2,9} = 4.73$, $P = 0.04$; Fig. 1). Despite costs of lactation, females on the low-quality diet were able to maintain their body mass during summer, similar to those on the high-quality diet (Fig. 1).

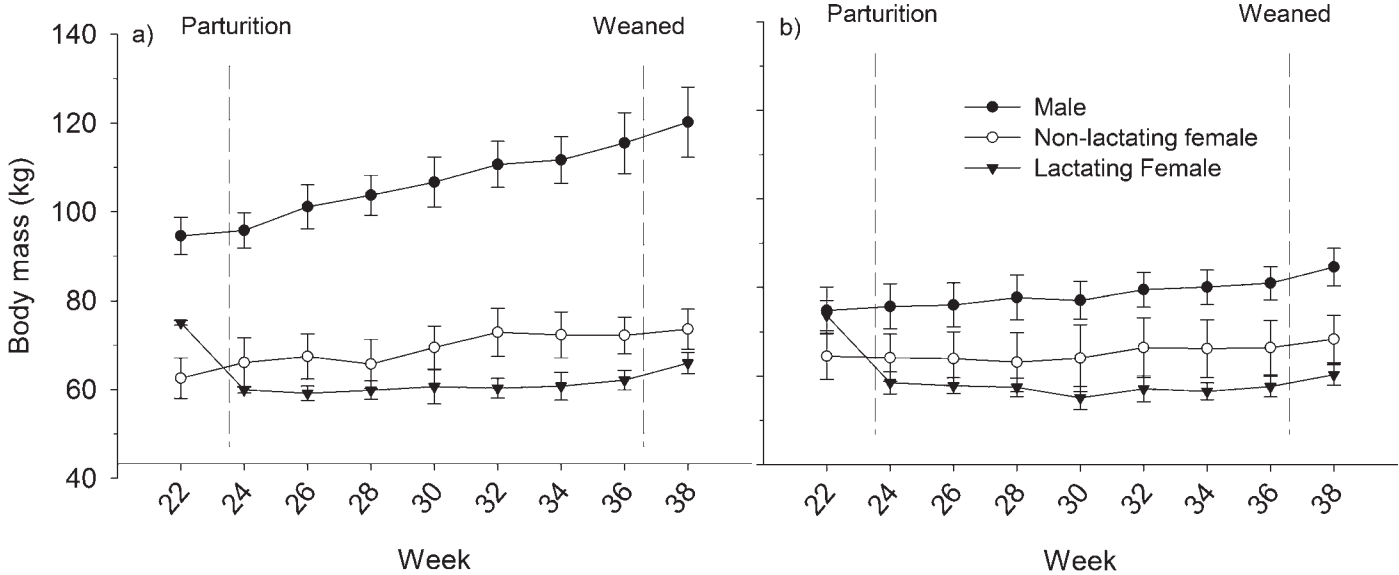


FIG. 1.—Mean (\pm SE) body mass measured every 2 weeks for male, nonlactating female, and lactating female white-tailed deer (*Odocoileus virginianus*) for 2008 and 2009, Brookings, South Dakota, in 2 treatment groups: a) high-quality and b) low-quality diets. Dashed lines represent the time of parturition and weaning of young for lactating females.

Mean dry matter intake per day relative to body mass differed among sexes and reproductive status of females for both high-quality ($F_{2,7} = 6.88, P = 0.022$) and low-quality ($F_{2,9} = 12.91, P = 0.002$) diets (Fig. 2). Those differences were largely a result of lactating females (Fig. 2); intake rates of males and nonlactating females were similar (all $P > 0.37$). Before parturition, mean (\pm SE) dry matter intake of lactating females was lowest compared with their intake for the remainder of spring and summer (Table 1); food intake increased nearly 2-fold 3–5 weeks following parturition (Fig. 2). Conversely, dry matter intake of males and nonlactating

females remained consistent, with little change throughout spring and summer (Fig. 2). Despite the high rate of dry matter intake for lactating females, apparent digestive efficiency was similar between sexes and reproductive status for high-quality ($F_{2,7} = 1.32, P = 0.33$) and low-quality ($F_{2,9} = 0.67, P = 0.53$) diets (Fig. 3). Individuals on the high-quality diet, however, had greater digestive efficiency than those on the low-quality diet ($P = 0.004$; Fig. 3).

Overall, mean (\pm SE) fecal nitrogen reflected diet quality for white-tailed deer; individuals on the high-quality diet had higher levels of fecal nitrogen ($2.88\% \pm 0.05\%$) compared

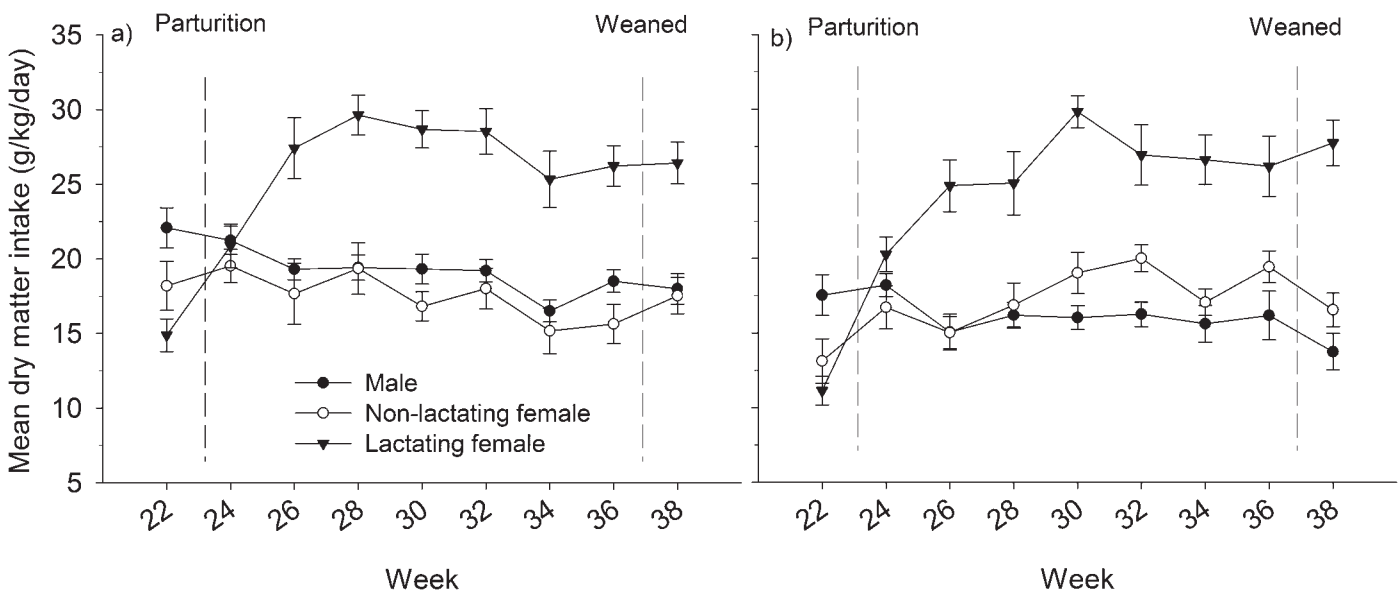


FIG. 2.—Mean (\pm SE) dry matter intake per week of male, nonlactating female, and lactating female white-tailed deer (*Odocoileus virginianus*) for 2008 and 2009, Brookings, South Dakota, in 2 treatment groups: a) high-quality and b) low-quality diets. Dashed lines represent the time of parturition and weaning of young for lactating females.

TABLE 1.—Mean, SE, and sample size (number of deer) of dry matter intake ($\text{g kg}^{-1} \text{ day}^{-1}$) measured weekly for male, nonlactating female, and lactating female white-tailed deer (*Odocoileus virginianus*) before lactation, during lactation (7 weeks), and postlactation, 2008–2009, Brookings, South Dakota, in 2 treatment groups: a) high-quality and b) low-quality diets.

Diet	Reproductive status	n	Prelactation		Lactation		Postweaning	
			\bar{X}	SE	\bar{X}	SE	\bar{X}	SE
High quality	Male	3	22.34	1.91	19.35	0.27	18.32	0.06
	Nonlactating female	4	17.30	2.78	17.63	2.03	16.25	2.33
	Lactating female	3	15.17	1.46	26.05	1.42	25.60	1.50
Low quality	Male	4	17.54	2.28	16.27	0.70	13.72	2.02
	Nonlactating female	4	13.12	2.98	17.94	1.41	16.61	1.24
	Lactating female	4	11.13	1.37	25.63	1.77	27.62	1.95

with individuals on the low-quality diet ($2.51\% \pm 0.03\%$, $P = 0.015$; Fig. 4). Despite consuming similar diets within treatments, fecal nitrogen of lactating females was significantly lower than that of males and nonlactating females for both high-quality ($F_{2,7} = 12.84$, $P = 0.048$) and low-quality ($F_{2,9} = 18.69$, $P = 0.009$) treatments (Table 2). Lactating females on high-quality diets had similar concentrations of fecal nitrogen ($2.25\% \pm 0.11\%$) as lactating females on the low-quality diet ($2.12\% \pm 0.04\%$) 3–5 weeks following parturition ($P = 0.38$; Fig. 4). Males and nonlactating females exhibited similar values of fecal nitrogen within treatment groups (all $P > 0.65$; Table 2). Because lactating females consumed more nitrogen, while excreting proportionally less than did males or nonlactating females, apparent nitrogen absorption was highest for lactating females on both diets (both $F > 14.57$, $P < 0.003$; Fig. 5).

Values of fecal nitrogen following an NDF rinse exhibited patterns comparable to standard values of fecal nitrogen; males and nonlactating females were similar throughout the summer, whereas NDF-N of lactating females declined during lactation. For the high-quality diet, lactating females had significantly

lower NDF-N compared with males and nonlactating females ($F_{2,7} = 4.42$, $P = 0.042$). A similar, albeit not significant, pattern also occurred for groups on the low-quality diet ($F_{2,9} = 3.35$, $P = 0.073$).

DISCUSSION

Our captive experiment with known and simple diets indicated that, in general, fecal nitrogen reflected diet quality, with individuals on the high-quality diet having higher concentrations of fecal nitrogen than those on the low-quality diet. Although fecal nitrogen was similar between sexes, the disparity between lactating females and males and nonlactating females (Fig. 4) pointed to an important limitation of this index, even when it is applied to a single species. In support of our prediction, lactating white-tailed deer excreted less nitrogen in their feces compared with males and nonlactating females, even while consuming diets of identical quality (Fig. 4). Differences in digestive function between lactating females and other deer also were revealed when deer were placed on a less-digestible diet. Despite consuming a poor-quality diet and

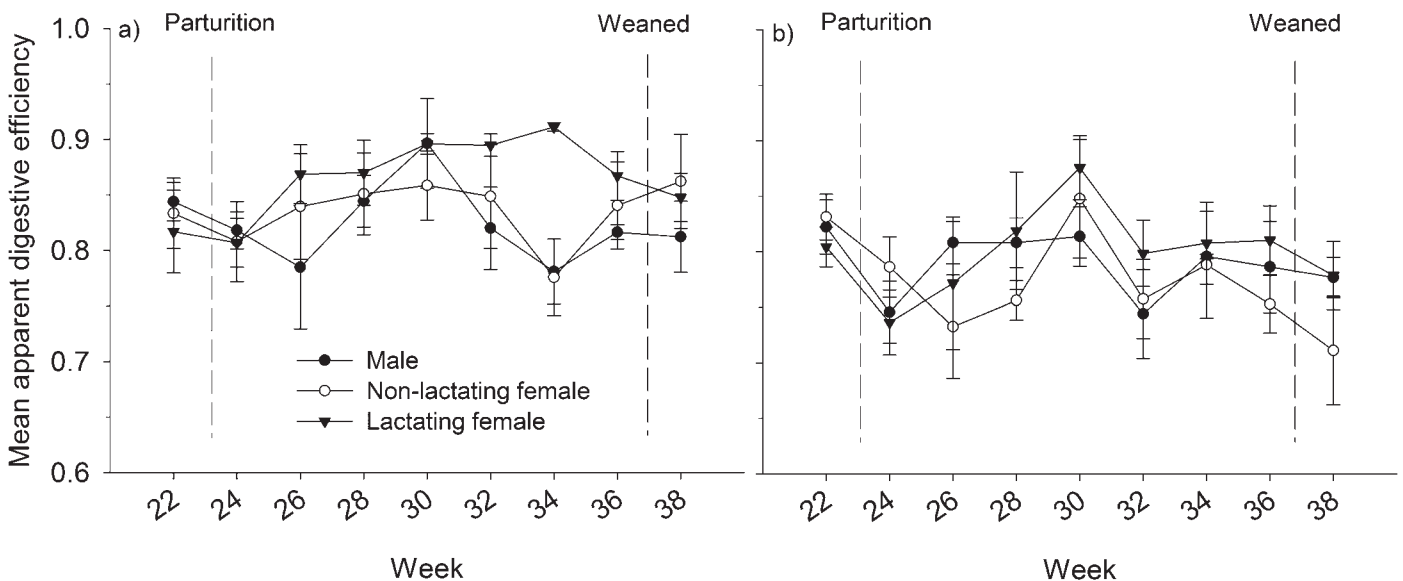


FIG. 3.—Mean (\pm SE) apparent digestive efficiency per week of male, nonlactating female, and lactating female white-tailed deer (*Odocoileus virginianus*) for 2008 and 2009, Brookings, South Dakota, in 2 treatment groups: a) high-quality and b) low-quality diets. Dashed lines represent the time of parturition and weaning of young for lactating females.

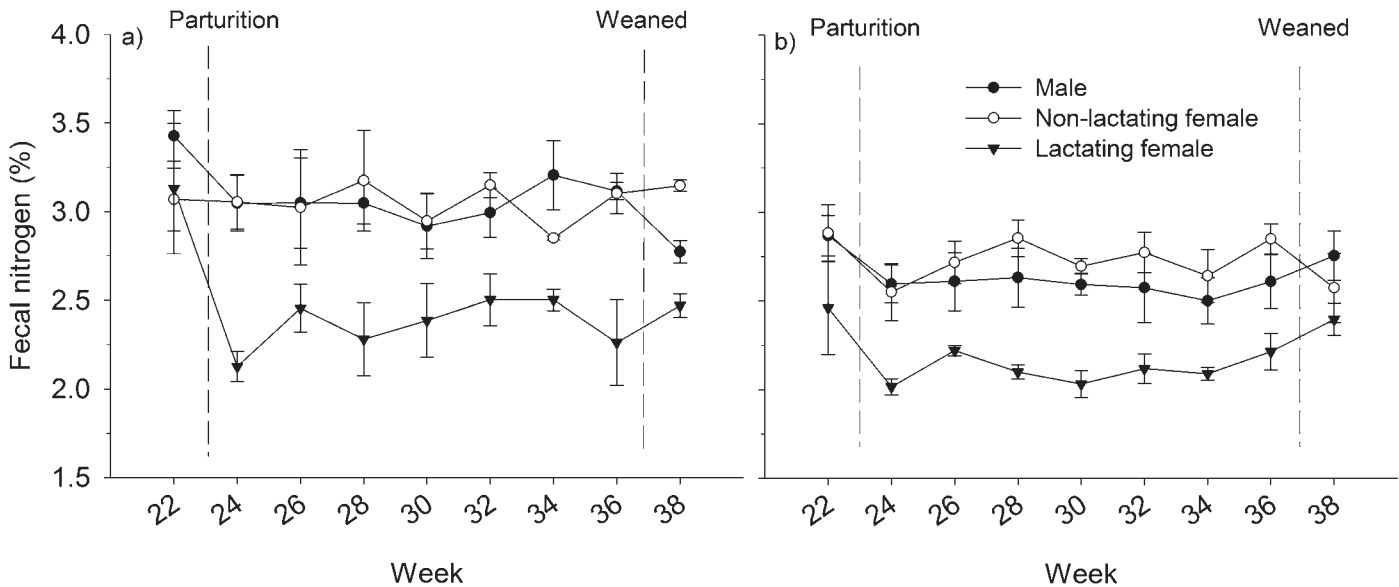


FIG. 4.—Mean (\pm SE) fecal nitrogen concentration per week of male, nonlactating female, and lactating female white-tailed deer (*Odocoileus virginianus*) for 2008 and 2009, Brookings, South Dakota, in 2 treatment groups: a) high-quality and b) low-quality diets. Dashed lines represent the time of parturition and weaning of fawns for lactating females.

incurring the energetic demands of lactation, lactating females were capable of maintaining their body mass throughout summer (Fig. 1). Males on the same diet, however, did not increase their body mass during summer, which contrasts with the 15% increase in body mass for males maintained on the high-quality diet. Although lactating females will catabolize somatic reserves when necessary to support lactation (Tollerson et al. 2010), lactating females in our study were capable of partially compensating for a lower-quality diet by maintaining digestive efficiency and increasing absorption of dietary nitrogen above that exhibited by males and nonlactating females.

Nitrogen excreted in feces is composed of both exogenous and endogenous sources (Robbins 1983; Barboza et al. 2009). Ruminants acquire nitrogen by ingesting plants and through the subsequent fermentative action of anaerobic microbes (Van Soest 1994). Plant nitrogen is composed primarily of true protein (60–80%), but it also includes soluble nonprotein nitrogen and a small amount of lignified nitrogen (Van Soest 1994). Exogenous sources include indigestible nitrogen in cell walls and free nitrogen contained in dietary protein (true

protein), most of which the ruminant uses and absorbs (Schwamm et al. 2009; Verheyden et al. 2011). Indigestible protein also may be bound by plant secondary compounds (Robbins 1983; Schwamm et al. 2009) and, consequently, can be unavailable to ruminants (Schwamm et al. 2009). Endogenous sources of fecal nitrogen include both metabolic and microbial nitrogen (Robbins 1983). As herbivores digest forage, metabolic nitrogen is produced from the fermentative action of anaerobic microbes, with higher rates of fermentation yielding greater production of metabolic nitrogen (Helmer and Bartley 1971; Van Soest 1994; Wehausen 1995; Schwamm et al. 2009). Microbial nitrogen results from digestion and absorption of the bacteria and protozoa that are passed from the rumen, and nitrogen recycled via saliva of the ruminant (Van Soest 1994). Forages with high levels of digestible energy generate high rates of fermentation (Robbins et al. 1987; Gauthier and Bédard 1990; Berteaux et al. 1998; Schwamm et al. 2009); therefore, high rates of intake and consumption of high-quality forages result in high values of fecal nitrogen via increased fermentation, absorption of microbial biomass, and bypass of nitrogen (Church 1988). Collectively, amounts of

TABLE 2.—Mean, SE, and sample size (number of deer) of fecal nitrogen concentration (%) measured weekly for male, nonlactating female, and lactating female white-tailed deer (*Odocoileus virginianus*) before lactation, during lactation (7 weeks), and postlactation, 2008–2009, Brookings, South Dakota, in 2 treatment groups: a) high-quality and b) low-quality diets.

Diet	Reproductive status	n	Prelactation		Lactation		Postweaning	
			\bar{X}	SE	\bar{X}	SE	\bar{X}	SE
High quality	Male	3	3.47	0.17	3.07	0.04	2.90	0.15
	Nonlactating female	4	3.21	0.19	3.04	0.15	3.14	0.02
	Lactating female	3	3.01	0.47	2.32	0.12	2.47	0.09
Low quality	Male	4	2.87	0.12	2.59	0.10	2.76	0.14
	Nonlactating female	4	2.88	0.16	2.73	0.07	2.57	0.19
	Lactating female	4	2.46	0.26	2.11	0.02	2.36	0.07

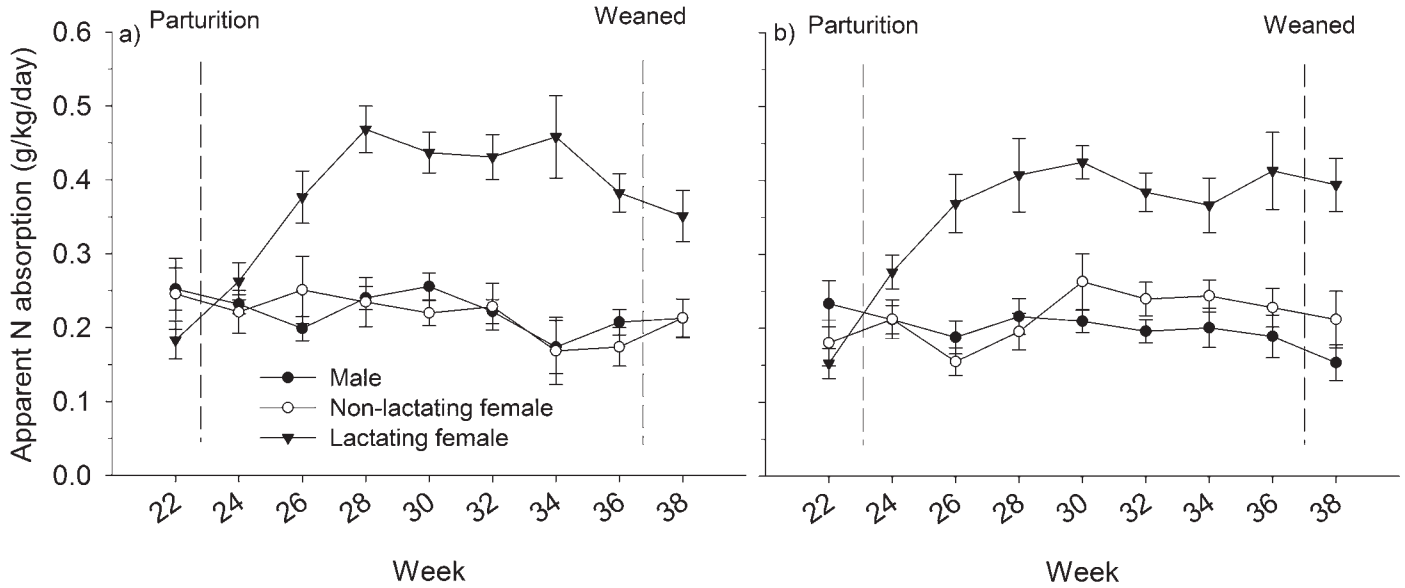


FIG. 5.—Mean (\pm SE) apparent nitrogen absorption per week of male, nonlactating female, and lactating female white-tailed deer (*Odocoileus virginianus*) for 2008 and 2009, Brookings, South Dakota, in 2 treatment groups: a) high-quality and b) low-quality diets. Dashed lines represent the time of parturition and weaning of fawns for lactating females.

endogenous and exogenous sources of nitrogen, and the ability of the herbivore to absorb or recycle dietary nitrogen, determine the concentration of nitrogen in feces (Robbins 1983).

Nutrient intake is limited by the rate of digestion and excretion (Hamel and Côté 2009), but also can affect digestive efficiency. When animals consume less-digestible forages, they may increase intake until ingesta fills the rumen in an attempt to compensate for poor-quality diets (Baker and Hobbs 1987; Barboza et al. 2009; Hamel and Côté 2009). Increased intake, in turn, can decrease retention time and increase rate of passage (Domingue et al. 1991). Increased intake also results in more fecal output that is composed primarily of plant fiber, which may lower or dilute the concentration of nitrogen in feces (Barboza et al. 2009). Therefore, digestive efficiency and retention time are expected to decrease and fecal nitrogen to increase as lactating females increase intake rates to support lactation (Fig. 3). In contrast to those expectations, lactating females within each dietary treatment maintained digestive efficiency and increased nitrogen absorption while increasing intake, thereby excreting less nitrogen in their feces compared with males and nonlactating females (Figs. 2 and 3).

Lactating females not only absorbed more nitrogen from their diets than did males or nonlactating females, they absorbed more of the fractions of nitrogen contained within cell walls, as indicated by lower NDF-N. Gross et al. (1996) reported that lactating Nubian ibex (*Capra nubiana*) digested fiber components of forages to the same extent as males even though females consumed more forage and had faster passage rates than did males. To do so, Gross et al. (1996) proposed that by more thoroughly processing food via mastication, females further broke down cell-wall surfaces and increased digestion of finer particles (Gross et al. 1995). Increased

rumination may not only have contributed to the ability of lactating females to extract and denature more plant proteins from cell walls, but also for nonlactating females to compensate for smaller body size and display digestive capabilities similar to those of males (Gross et al. 1995). We hypothesize that remodeling of the gastrointestinal tract during lactation (Barboza and Bowyer 2000; Zimmerman et al. 2006) further contributed to increased nitrogen absorption for lactating females resulting in additional reductions in nitrogen excretion.

Following parturition, weight and size of the rumen, abomasum, intestines, and liver increase (Jenks et al. 1994; Zimmerman et al. 2006), which coincides with the rapid rise in nutrient demands associated with lactation (Moen 1973). Remodeling of the gastrointestinal tract (Barboza and Bowyer 2000), when accompanied by increased food intake, rumination, and rate of passage of digesta may promote an increase in protein absorption to help satisfy demands of lactation. As lactating females consume forages, some protein is degraded in the rumen and some is left undigested (Van Soest 1994). Undegraded protein can be absorbed directly by the animal in the small intestine, whereas degraded protein is broken down to ammonia, which is utilized by anaerobic bacteria to produce microbial protein (Van Soest 1994). We hypothesize that an increase in rate of intake, and thus, digesta passage, allowed more undegraded protein to bypass the rumen for direct absorption in the small intestine, which is lengthened during lactation, providing greater surface area for absorption (Jenks et al. 1994; Zimmerman et al. 2006).

Sexes of white-tailed deer occupy different niches based on seasonal habitat requirements and reproductive status that influences their forage requirements and digestive abilities (Beier 1987; Beier and McCullough 1990; Weckerly 1993; Kie

and Bowyer 1999). Lower metabolic demand relative to body mass ostensibly allows larger-bodied individuals to subsist on a greater intake of fibrous forage to maximize digestion of forages compared with smaller-bodied individuals (Jenks et al. 1994; Barboza and Bowyer 2000; Clauss et al. 2009). Scaling of gut capacity with body mass observed between species (i.e., Bell–Jarman hypothesis), however, does not apply within species of ruminants, especially white-tailed deer (Weckerly 2010). Considering that the scalar between rumen–reticulum capacity and body mass is similar to that for metabolic rate within species (Weckerly 2010), lactating females may be capable of enhancing digestion and absorption above that that is possible for males and nonlactating females by investing in digestive tissue (Jenks et al. 1994; Barboza and Bowyer 2000; Zimmerman et al. 2006). Indeed, lactating females digested foods with similar efficiency to males but were able to extract more nitrogen from their diet (Fig. 4).

Lactation corresponds to periods of high food abundance and high forage quality for ungulates, but even this increased availability of forage can be inadequate for females to meet the high energetic demands of lactation (Cook et al. 2004; Hamel and Côté 2009). Furthermore, lactating females often encounter a trade-off between forage quality and predation risk, which may preclude selection of sites offering high-quality forage (Stearns 1992; Bleich et al. 1997; Corti and Shackleton 2002; Bowyer 2004). For example, caribou (*Rangifer tarandus*) traded nutrition for a low risk of predation by choosing calving areas at high elevation with low vegetation biomass (Barten et al. 2001; Gustine et al. 2006), and female bighorn sheep (*Ovis canadensis*) traded forage quality and abundance for ranges with low predation risk (Bleich et al. 1997). Selection should favor those females that are able to compensate for poor forage quality, rather than face potential reproductive failure. Our results, when considered along with those from other studies (e.g., Jenks et al. 1994; Gross et al. 1995; Barboza and Bowyer 2000), indicate that increases in digestive surfaces and rumination by lactating females may improve their ability to process less-digestible foods, and thereby, expand the range of foraging options suitable to meet the metabolic demands of reproduction. Although this strategy may enhance fitness of female herbivores by increasing their ability to allocate resources to reproduction while maintaining nutritional condition (Monteith et al. 2013), these physiological and morphological processes compromise the value of fecal nitrogen as an index to diet quality when females are lactating. Consequently, intersexual comparisons of fecal nitrogen during summer to explain behavior (sensu Main 2008) are potentially flawed, because diet quality for lactating females will be underestimated when compared with males or nonlactating females.

Ability to accurately assess nutritional quality of seasonal ranges is an important component of conservation and management programs, because of the pervasive effects of nutrition on dynamics and sustainability of populations (White 1983; Monteith et al. 2009, 2013; Parker et al. 2009; Raubenheimer et al. 2009). Fecal nitrogen has been a widely used index to evaluate diet quality of free-ranging ruminants

(Leslie et al. 2008), but the influence of lactation status on nitrogen excretion in the feces during summer presents an additional obstacle for reliable interpretation of fecal nitrogen. Fecal nitrogen did, however, reflect overall dietary quality for males and nonlactating females, indicating that the index is of value outside the period of lactation or where samples can be further processed to identify sex and lactation status (Kohn and Wayne 1997; Huber et al. 2002; Brinkman et al. 2010).

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