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Comparing Protein and Energy Status of Winter-Fed White-Tailed Deer

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Abstract

*Although nutritional status in response to controlled feeding trials has been extensively studied in captive white-tailed deer (*Odocoileus virginianus*), there remains a considerable gap in understanding the influence of variable supplemental feeding protocols on free-ranging deer. Consequently, across the northern portion of the white-tailed deer range, numerous property managers are investing substantial resources into winter supplemental-feeding programs without adequate tools to assess the nutritional status of their populations. We studied the influence of a supplemental winter feeding gradient on the protein and energy status of free-ranging white-tailed deer in the Adirondack Mountains of New York. We collected blood and fecal samples from 31 captured fawns across 3 sites that varied considerably in the frequency, quantity, and method of supplemental feed distribution. To facilitate population-wide comparisons, we collected fresh fecal samples off the snow at each of the 3 sites with supplemental feeding and 1 reference site where no feeding occurred. Results indicated that the method of feed distribution, in addition to quantity and frequency, can affect the nutritional status of deer. The least intensively fed population showed considerable overlap in diet quality with the unfed population in a principal components ordination, despite the substantial time and financial resources invested in the feeding program. Data from fecal samples generally denoted a gradient in diet quality and digestibility that corresponded with the availability of supplements. Our results further demonstrated that fecal nitrogen and fecal fiber, indices of dietary protein and digestibility, can be estimated using regressions of fecal pellet mass, enabling a rapid qualitative assessment of diet quality.* (WILDLIFE SOCIETY BULLETIN 34(3):716–724; 2006)

Key words

Adirondacks, energy, Odocoileus virginianus*, physiology, protein, supplemental feeding, white-tailed deer, winter.*

The ability of deer (*Odocoileus* spp.) to survive a northern winter is influenced largely by energetic costs in terms of the length and severity of winter and the amount of fat reserves accumulated during autumn (Mautz 1978*a*). In addition to metabolizing fat reserves, deer also obtain energy by foraging for browse throughout the winter (Mautz 1978*b*, Verme and Ullrey 1984). The nutritional benefit of the diet depends on its digestibility and associated protein and energy levels (Seal et al. 1978, Ouellet et al. 2001). Energy is typically the most critical dietary component for deer during the winter, with other nutrient needs being satisfied while foraging for energy (Mautz 1978*b*, Short 1981, Robbins 1983). Due to their relatively small size, limited fat reserves, and low hierarchal status, fawns typically are among the first in a population to succumb to the hardships of winter (Smith et al. 1975, Verme and Ozoga 1980*a*). Consecutive severe winters can devastate a population if an adequate number of fawns do not survive to be recruited into the population (Holter and Hayes 1977, Underwood 1990).

In an attempt to offset the energy deficit that deer typically experience in the winter, many individuals and organizations throughout northern portions of the white-tailed deer (*O. virginianus*) range developed supplemental wintertime feeding programs (Sage and Gustafson 1991). These programs range in scale from small, periodic, backyard hobbies to large-scale, well-structured feeding operations costing several thousand dollars annually. While the operators of these expansive feeding programs have assumed that deer benefit from the supplemental nutrition, few quantitative data on the energetic status of free-ranging deer have been available. Thus far, most physiological studies of supplemental feeding have been conducted with captive deer during the autumn (Smith et al. 1975, Holter and Hayes 1977, Verme and Ozoga 1980*b*). Variables of a feeding program influencing the potential benefits to deer include type of feed, amount provided, frequency of feedings, distribution methods, and the duration of feeding through the winter. The coordination of these factors largely determines whether deer are able to realize the potential benefits from a feeding program.

Physiological indicators of nutritional status have been used by a variety of researchers for numerous species (LeResche et al. 1974, DelGiudice et al. 1990, Wiklund et al. 1996, Domingo-Roura et al. 2001). Commonly used protein indices include blood urea nitrogen (BUN) and albumin from blood or serum (Seal et al. 1978, Warren et al. 1982, DelGiudice et al. 1994, Sams et al. 1998). Serum creatinine has been used as an index of energy status and stress-related muscle catabolism (Woo et al. 1979, Sams et al. 1998, Domingo-Roura et al. 2001). Fecal components, including neutral detergent fiber (FNDF), acid detergent fiber (FADF), and fecal nitrogen (FN), have been used to evaluate diet digestibility and protein content (Leslie and Starkey 1985, Van Soest 1994, Gray and Servello 1995, Hodgman et al. 1996). Fecal 2,6 diaminopimelic acid (DAPA) is an amino acid primarily found in bacterial cell walls that has been used to estimate rumen fermentation and has shown a strong positive correlation with dietary digestible energy (Davitt and Nelson 1984, Leslie et al. 1989, Hodgman et al. 1996).

The objectives of this study were 1) to compare the protein and energy status of fawns from 3 long-term supplemental feeding programs that utilized different feeding protocols, 2) to compare

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Table 1. Supplemental-feeding data for white-tailed deer reported by property managers from 3 study sites in the north-central Adirondack Mountains, New York, USA, winter 2000.

Feeding-site characteristics	Site		
	South	West	North
Start feeding	13 Dec 1999	1 Jan 2000	11 Feb 2000
End feeding	21 Apr 2000	1 Apr 2000	3 Mar 2000
Total days	131	92	22
Feeding days per week	6–7	5–7	2
Deer fed (average)	250	60	N/A
Deer fed (max.)	360	120	250
Corn fed (kg)	20,000	4,000	10,000
Hay fed (kg)	41,000	15,000	2,000
Corn (kg/max. deer/day)	0.4	0.4	1.8
Hay (kg/max. deer/day)	0.9	1.4	0.4
Feeding area	1-ha lot	1-ha lot	13 stations along 10-km trail near riverbank
Dispersal method	1 row corn, 100 m long, hay ad libitum	3 rows corn, 15 m long, hay ad libitum	corn by salt spreader, hay fed with corn 2× per week

diet protein and digestibility among deer populations associated with supplemental feeding programs to a population without access to supplemental feed, and 3) to identify a physiologically based tool to assist managers in assessing wintertime nutritional status of deer herds. Implications for assessing protein and energy status of deer relative to feeding protocols are discussed.

Study Area

We conducted this study on 4 sites (South, West, North, Unfed) totaling approximately 23,000 ha in the north-central Adirondacks in New York State, USA (center of study area, 44°30′N, 74°35′W). Elevations in this area range from 400 m along the lakes and rivers to 900 m on mountaintops. The mean annual temperature in the north-central Adirondacks is 5°C with approximately 110 frost-free days and 170 growing days. This area receives an average of 96 cm of annual precipitation with nearly 30% of that as snow (Kudish 1992). Most of the soils in the Adirondacks are acidic Spodosols formed from glacial till. Bedrock through most of the region is granitic gneiss and metasedimentary rock (Driscoll et al. 1991). Well-drained, forested sites were typically dominated by second-growth stands of northern hardwoods: sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), and black cherry (*Prunus serotina*). Lowland sites with poorer drainage generally supported red spruce (*Picea rubens*)–balsam fir (*Abies balsamea*) communities, some containing speckled alder (*Alnus incana*).

The West site (7,500 ha), owned by a paper company and leased to an active hunting and sporting club, was under timber management for hardwood species at the time of this study. Supplemental feed was provided daily throughout the winter in an open meadow near the center of the property. Conifers along an adjacent river corridor provided deer with nearby cover. At each feeding, a fixed amount of shelled corn was distributed in 3 rows approximately 15 m long along the ground and alfalfa hay was available nearly ad libitum.

The South site (8,500 ha) was a private holding used primarily for nonhunting, recreational purposes. Most upland areas at this site developed into second-growth hardwood and mixed-wood forests after intense timber harvests in the 19th century and subsequent fires in many areas of the property. Supplemental feeding was constrained to a central jack pine (*Pinus banksiana*) plantation surrounded primarily by an open-burn meadow with a dense ground cover of lichen (*Cladonia* sp.). A river corridor with red spruce, balsam fir, and speckled alder was located 400–500 m from the feeding site. The quantity of shelled corn fed daily was based on the number of deer present at feeding time the previous day and was distributed along a roadway approximately 100 m long. Deer also had access to alfalfa hay ad libitum.

The North site (6,100 ha) was privately owned by a hunting and sporting club. There was some selective timber harvesting at this site but considerably less than at the West site. This site had dense stands of balsam fir and white spruce that were quite extensive, especially along river corridors. The surrounding region, because of its proximity to the river and dense conifer cover, has been a historical winter yard for white-tailed deer (R. Inslerman, New York State Department of Environmental Conservation [NYSDEC], Bureau of Wildlife, USA, personal communication). Upland areas at this site supported second-growth mixed-hardwood communities. The winter feeding program involved distribution of shelled corn, by means of a salt spreader, and alfalfa hay across the property at approximately 13 sites twice weekly. The feeding route (approx. 10 km) followed the river corridor and connecting lowlands, thereby serving the traditional deer-wintering areas.

Feeding at the West and South sites began prior to the typical winter migration period each year, while feeding at the North site began after deer began to congregate in winter yards. Table 1 provides a detailed comparison of the feeding programs from each of the sites listed above from data provided by property managers.

The Unfed site was a traditional deer-wintering area (R. Inslerman, NYSDEC Bureau of Wildlife, personal communication) located approximately 45 km southwest of the 3 fed sites. This 1,100-ha property consisted of approximately 50% northern hardwoods and 50% conifers made up of plantations and natural stands over elevations ranging from 450 to 580 m. Conifer stands included plantations of white pine, red pine (*Pinus resinosa*), Scotch pine (*P. sylvestris*), and Norway spruce (*Picea abies*), along with naturally occurring balsam fir and red spruce. Property managers at this site and regional environmental conservation personnel affirmed that no supplemental-feeding programs were being conducted in the vicinity of the deer winter-yarding area that was sampled.

At each of the 3 fed sites, deer mobility was enhanced by snowmobile trails and plowed roadways around each of the feeding areas. While similar paths were not available at the Unfed site, we suggest that they are an inherent result of the feeding process and, consequently, add an additional energetic benefit to the deer by improving mobility and potential to access additional sources of native browse. Deer at the fed sites also utilized well-worn herd trails radiating from the feeding areas, which enabled

relatively facile movement by the deer between feeding sites and nearby conifer cover throughout the winter. Herd trails also were present at the Unfed site, though they appeared less worn relative to those at the fed sites.

Each of the above feeding sites was located in close proximity (<500 m) to a streambed. While at times we observed open drinking holes in the ice over the streams, we have no assurance that free-flowing water was available at all times at any of the sites and do not expect potentially small differences in water availability to significantly affect our findings. A complete vegetation assessment was beyond the scope of this study, and, while we acknowledge that there were likely some differences in browse availability and species, we suggest that these differences did not overwhelm the variations in feeding programs with respect to deer protein and energy status. The potential exception to this, as discussed below, may be the presence of lichen at the South site which was not observed at any of the other sites. At all study sites, a browse line at approximately 2 m in height indicated use of accessible vegetation around the wintering areas.

While population density can be an important variable in describing deer wintering yards, this characteristic is most relevant in assessing resource availability. Because supplemental feeding in the above fed sites represents a major influx of available resources, we suggest that more important than deer numbers is the amount of feed provided on a per deer basis as presented in Table 1. Additionally, data from visual records of deer movement along roadways and telemetry data collected concurrent with this study indicated that the area that individual deer utilized at each site was highly variable. Therefore, a population density estimate could be misleading as the relatively small feeding areas would represent a widely variable proportion of individual or family-unit winter range size. We acknowledge that variation among sites and individuals complicates the interpretation of the data; however, such variability is inherent in studies of free-ranging animals across multiple sites where true replication is not possible.

Methods

From January through March 2000, we captured 31 fawns (<1 year old) at supplemental-feeding sites by firing syringe-darts containing 2–3 mL of an anesthetization cocktail containing 200 mg/mL ketamine HCl and 40 mg/mL xylazine HCl (Clark and Jessup 1992). We aged deer from tooth replacement and wear patterns (Severinghaus 1949) and fitted all captured animals with numbered plastic livestock ear tags for visual identification and monal metal ear tags issued by the NYSDEC. A complete handling protocol (ESF-99–01) was approved and is on file with the chair of the State University of New York College of Environmental Science and Forestry Institutional Animal Care and Use Committee.

Fawn Protein and Energy Status

From captured fawns, we collected approximately 16 mL of blood from the jugular vein using sterile, evacuated test tubes. We allowed the blood to coagulate for 3–6 hours before centrifuging to isolate the serum, which was stored frozen until analysis. We also extracted an average of 11 g (range 2–46 g) of fecal pellets from the rectum of each captured fawn. These samples were also stored frozen and later oven dried at 40°C for analysis. Of the 31 fawns captured, we collected blood and feces from 29 and 27 deer, respectively. We collected both blood and fecal samples from 25 fawns. Additional capture details are provided in Page (2001).

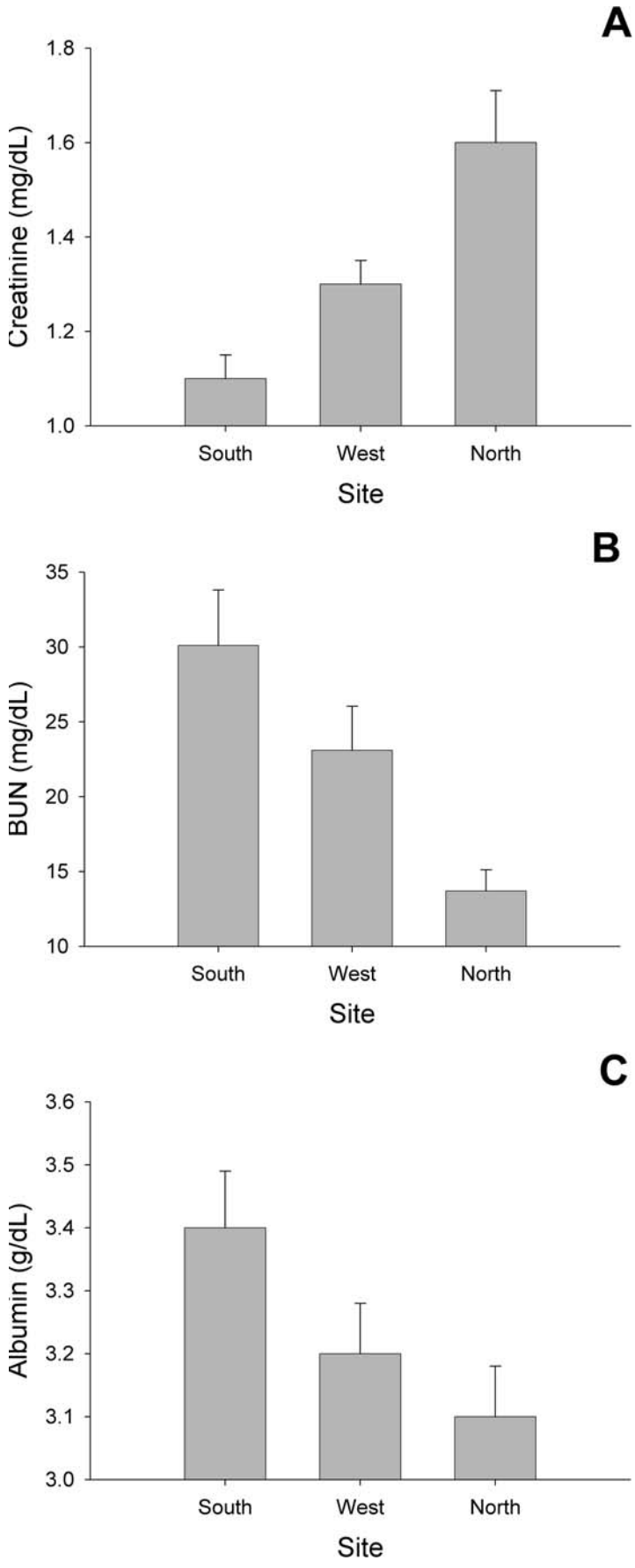
Serum samples were analyzed at Cornell University College of Veterinary Medicine Clinical Pathology and Endocrinology laboratories for concentrations of BUN, creatinine, and albumin using a Roche Hitachi 917 chemistry analyzer. We sent oven-dried fecal matter to the Wildlife Habitat Nutrition Laboratory at Washington State University to be analyzed for FN (following Horowitz 1980), DAPA (following Davitt and Nelson 1984), and FNDF and FADF (using ANKOM Fiber analyzer, ANKOM Technology, Macedon, New York). We tested each blood and fecal parameter by site for normality using Shapiro–Wilk test in the PROC UNIVARIATE function (SAS Institute 1985). Using $\alpha = 0.05$, none of the data sets were significantly different from a normal distribution and, therefore, none of the data were transformed. We used ANOVA and Tukey's means separation tests to identify differences among blood and fecal parameters based on study site (SAS Institute 1985).

Comparison of Diet Protein and Digestibility Among Fed and Unfed Populations

Throughout the winter sampling period, we collected 278 fecal pellet groups off the snow from unknown individuals from the 3 fed and 1 unfed sites. In order to obtain a representative sample from each population and to minimize the risk of pseudoreplication, we collected pellet groups based on the following criteria: appeared fresh and undisturbed, were on top of a recent snow-fall, were at least 25 m apart, and from a spectrum of pellet sizes. We assumed that within a population, average pellet size would approximately correlate to deer size. We determined an average fresh-pellet mass per group. Samples were stored frozen and later oven dried at 40°C to prepare for analysis.

For analysis, we formed 12 composite samples for each site by subsampling an average of 5.8 (SD = 2.7) individual fecal pellet groups per composite. We first sorted pellet groups temporally into early-, middle-, and late-winter periods and then ranked and sorted groups by average pellet mass into quartiles. Samples were analyzed for FN, DAPA, FNDF, and FADF at the Wildlife Habitat Nutrition Laboratory at Washington State University as described above.

We tested each fecal parameter by site for normality using Shapiro–Wilk test in the PROC UNIVARIATE function (SAS Institute 1985). Using $\alpha = 0.05$, none of the data sets were significantly different from a normal distribution and, therefore, none of the data were transformed. We used principal components analyses (PCA) to identify relationships among fecal parameters (FN, DAPA, FNDF, and FADF; SAS Institute 1985). We then used the PCA results to construct 2-dimensional ordinations to spatially depict the dietary protein and digestible energy of deer populations by study site. We used ANOVA and Tukey's means separation tests to identify differences in fecal parameters among study sites (SAS Institute 1985). In an attempt to formulate a rapid assessment technique to determine relative differences in dietary protein and digestibility, we developed regression equa-



tions to predict FN, FNDF, FADF, and DAPA individually from fecal-mass data.

Results

Fawn Protein and Energy Status

Serum creatinine levels were higher among fawns captured at the North site relative to fawns captured at the South site ($P = 0.002$). Fawns captured at the West site had slightly higher creatinine levels than fawns from the South site ($P = 0.309$) and lower levels than fawns from the North site ($P = 0.051$; Fig. 1A). Among the indices of protein status, BUN concentrations were higher at the South site than at the North site ($P < 0.001$). The BUN levels at the West site were lower than at the South site ($P = 0.201$) and higher than at the North site ($P = 0.056$; Fig. 1B). Serum albumin levels exhibited the same trend as BUN: higher at the South site than at the North and West sites ($P = 0.053$ and $P = 0.431$, respectively) and higher at the West site than at the North site ($P = 0.444$; Fig. 1C). None of the fecal constituents from samples collected from captured fawns differed among sites, likely a reflection of small sample size and high variability.

Comparison of Diet Protein and Digestibility Among Fed and Unfed Populations

Results from fecal pellets collected off the snow from unknown deer at the 3 fed and 1 unfed study sites generally exhibited the same trends, suggesting similarities between the West and South sites and between the North and Unfed sites. Values for percent FNDF were higher for samples collected from the Unfed and North sites relative to the West and South sites ($P < 0.001$ for each paired comparison; Fig. 2A). Percent FNDF at the West site was slightly higher than at the South site ($P = 0.420$) and was higher at the Unfed site than at the North site ($P = 0.066$). Percent FADF was higher at the Unfed site as compared to the fed sites ($P < 0.001$), and was higher at the North site than at the South and West sites ($P < 0.001$ and $P = 0.004$, respectively; Fig. 2B). Percent FADF did not differ between the South and West sites ($P = 0.406$). Because FADF is a less digestible component of FNDF, we also expressed these 2 fiber types as a ratio where FNDF/FADF was lower for the Unfed site relative to the 3 fed sites (Fig. 2C).

As an index of dietary protein, percent FN was higher at the West and South sites as compared to the North and Unfed sites ($P < 0.001$ for each paired comparison; Fig. 3A). Fecal DAPA levels, indicating dietary digestible energy, were higher at the West and North sites relative to the South site ($P = 0.031$ and $P = 0.036$, respectively) with the Unfed site having intermediate values, which did not differ from the fed sites ($P > 0.445$; Fig. 3B).

Ordination revealed that the deer populations at South and West sites had relatively high dietary protein and digestibility as indicated by higher FN and lower FNDF and FADF values on the horizontal axis. The vertical "digestible energy" axis had less

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Figure 1. Average blood serum concentrations from captured white-tailed deer fawns at supplemental winter feeding programs, north-central Adirondack Mountains, New York, USA, winter 2000. Error bars = 1 SE. (A) Creatinine, (B) blood urea nitrogen (BUN), (C) albumin. Sample sizes: South site = 9, West site = 10, North site = 10.

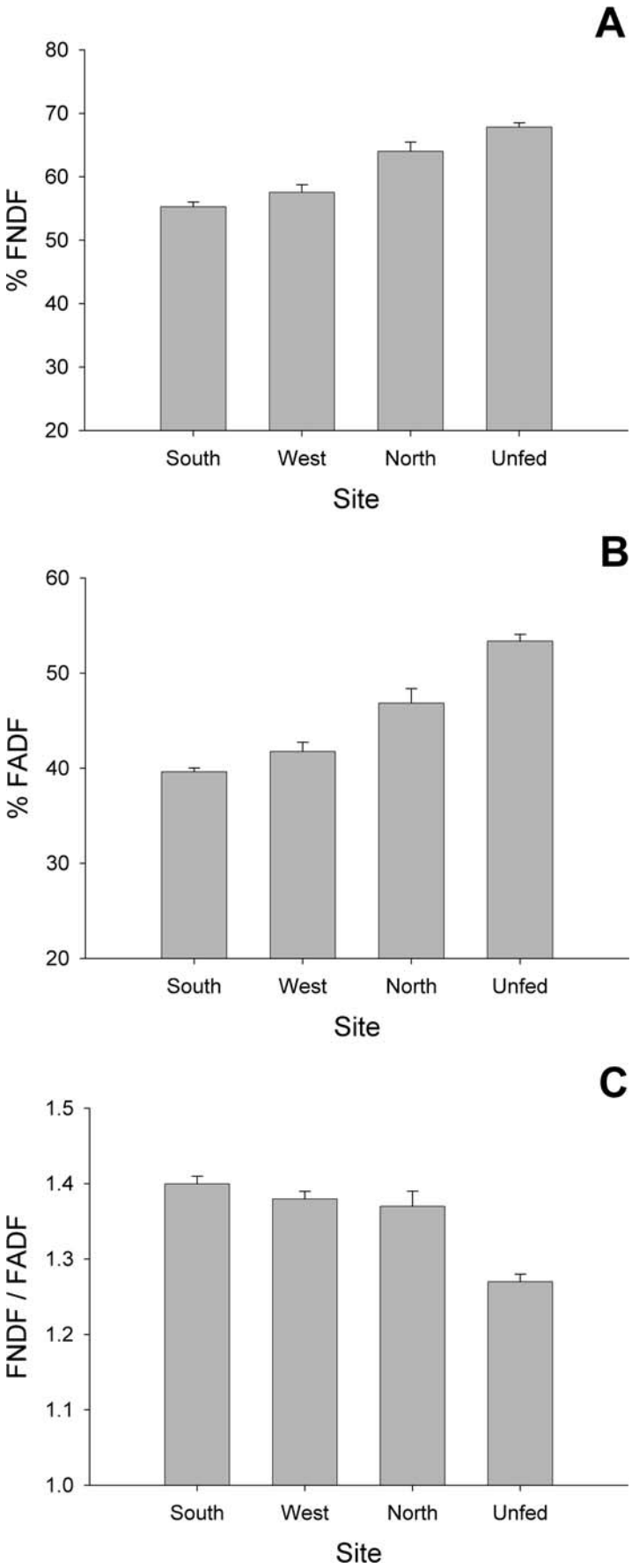


Figure 2. Average fecal fiber proportions (%) from composited white-tailed deer pellet groups collected off the snow from unknown individuals at 3 sites with supplemental winter feeding and 1 unfed population, north-central Adirondack Mountains, New York, USA, winter 2000. Error bars = 1 SE. (A) Neutral detergent fiber (FNDF), (B) acid detergent fiber (FADF), (C) FNDF/FADF. Sample sizes: South site = 12, West site = 12, North site = 11, Unfed site = 12.

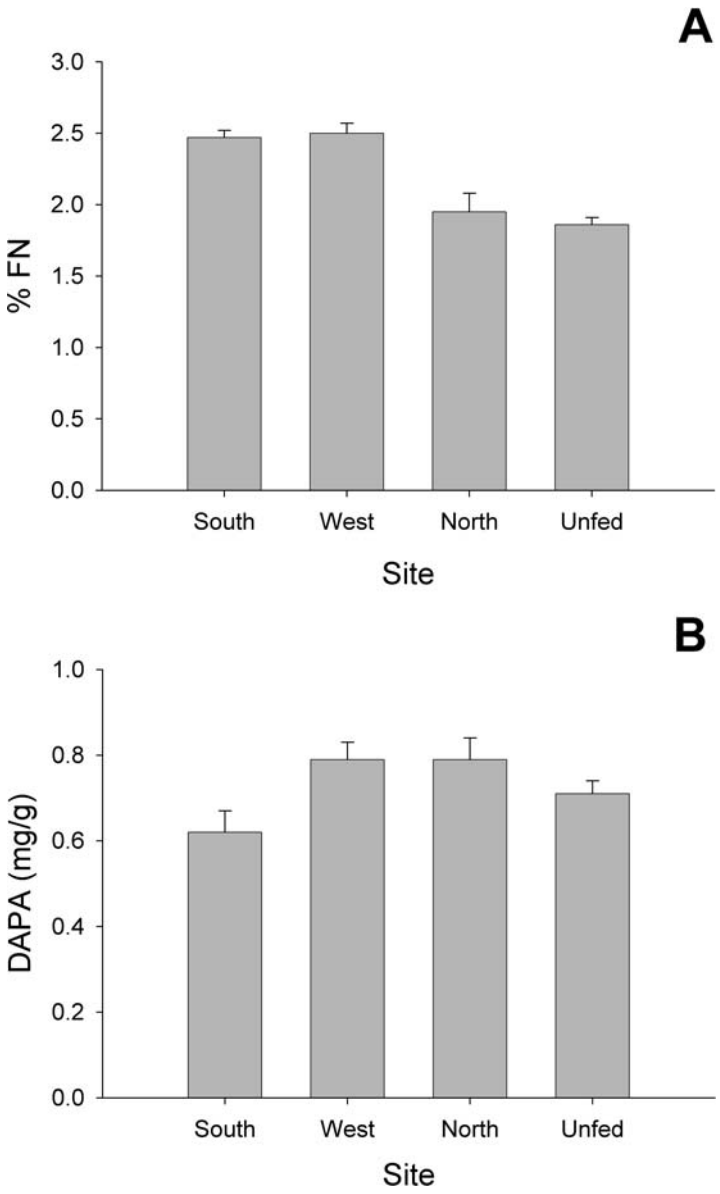


Figure 3. Average fecal nitrogen and 2,6 diaminopimelic acid from composited white-tailed deer pellet groups collected off the snow from unknown individuals at 3 sites with supplemental winter feeding and 1 unfed population, north-central Adirondack Mountains, New York, USA, winter 2000. Error bars = 1 SE. (A) Fecal nitrogen (FN), (B) 2,6 diaminopimelic acid (DAPA). Sample size = 12 composites for all sites.

separation among sites, but the lower values for the South site corresponded with the relatively low DAPA concentrations (Fig. 4). These first 2 principal components explained 93% of the variation in the population data set.

Regressions of fecal fibers and nitrogen on mean pellet mass were significant: FNDF (Fig. 5A; $R^2 = 0.48$, $P < 0.001$), FADF (Fig. 5B; $R^2 = 0.48$, $P < 0.001$), and FN (Fig 5C; $R^2 = 0.29$, $P = 0.001$). The regression of fecal DAPA on mean pellet mass was

not significant and, therefore, will not be discussed further ($R^2 = 0.0006$, $P = 0.87$).

Discussion

Fawn Protein and Energy Status

Creatinine production has a direct relationship with muscle mass and is related to lean body weight (Benjamin and McKelvie 1978, Woo et al. 1979). This indicates that fawns captured at the North site were the most lean (highest creatinine) and, consequently, had less body fat than fawns captured from the South and West sites (Fig. 1A). This conclusion is supported by other researchers finding that elevated serum creatinine levels were associated with nutritional stress and low levels of body fat (Sams et al. 1998, Domingo-Roura et al. 2001). Wiklund et al. (1996) reported that reindeer with access to supplemental feed had significantly lower levels of serum creatine relative to reindeer without supplements. During refeeding of nutritionally deprived white-tailed deer, DelGiudice et al. (1990) interpreted decreasing serum creatinine levels as a response to increased water intake and kidney functioning rather than being reflective of improved energy status. While creatinine levels can be affected by dehydration (Benjamin 1981), this seems an unlikely concern in this comparison of free-ranging deer with similar water availability and habitat conditions.

Protein status reflected by BUN and albumin (Fig. 1B,C) showed the same trends, with fawns from the South site having the highest levels and fawns from the North site with the lowest levels. While increases in BUN and albumin result from increased dietary protein intake, BUN levels also can be influenced by muscle catabolism, energy intake, and the ability of deer to recycle urea (Robbins et al. 1974, Seal et al. 1978, Ritchie 1979, Warren et al. 1982). Sams et al. (1998) found that albumin levels in deer increased as population densities were reduced and protein status improved. In feeding trials Brown et al. (1995) also found that serum albumin levels were elevated among deer on high-protein relative to those on low-protein diets. With no known reports of albumin being influenced by muscle catabolism, we interpret the common pattern of BUN and albumin to be reflective of dietary protein intake, specifically from high-protein alfalfa hay. These indicators of protein intake corresponded with the ad libitum supply of hay at the South and West sites and the feeding of a relatively small quantity of hay twice a week at the North site (Table 1).

Indices of both protein and energy status among captured fawns correlated with the attributes of the respective feeding programs. At the South site, deer were fed for a longer duration and for more days as compared to the other sites. Although at the North site deer were fed more corn per deer per day, the duration of feeding was shorter, feedings were only 2 days per week, and the distribution of corn with a salt spreader likely resulted in a high percentage of corn loss into the deep snow. While deer at the South and West sites would form "livestock" lines to consume dense rows of corn laid on hard-packed snow, deer at the North site had to search through relatively undisturbed snow for scattered corn, in a manner more similar to birds pecking than to livestock at a trough.

While we expected to identify correlations between the blood and fecal indices for protein and energy, these results did not materialize. Similarly, in a comprehensive supplemental feeding study of grazing beef steers, Bodine and Purvis (2003) also found that protein indices using FN and BUN were not closely related. They attributed this lack of a strong relationship to variations in diet quality affecting fermentation in the gut and consequently FN output. While FN can provide a good qualitative index of protein status, using multiple physiological variables, both blood and fecal in origin, should provide a more complete metabolic profile of a population.

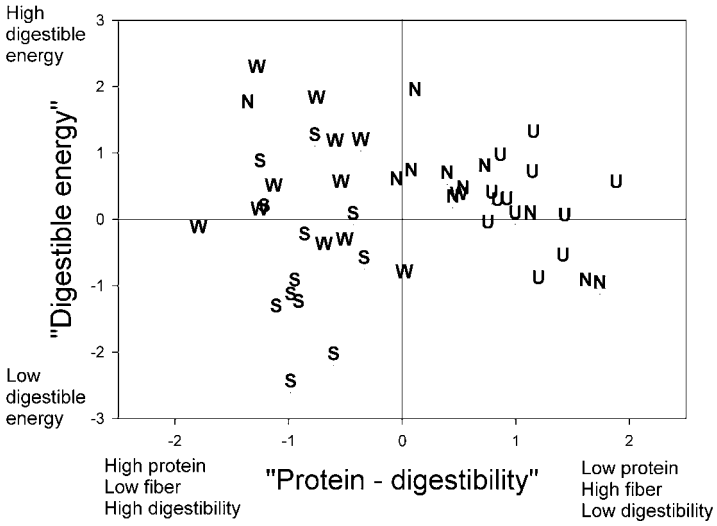
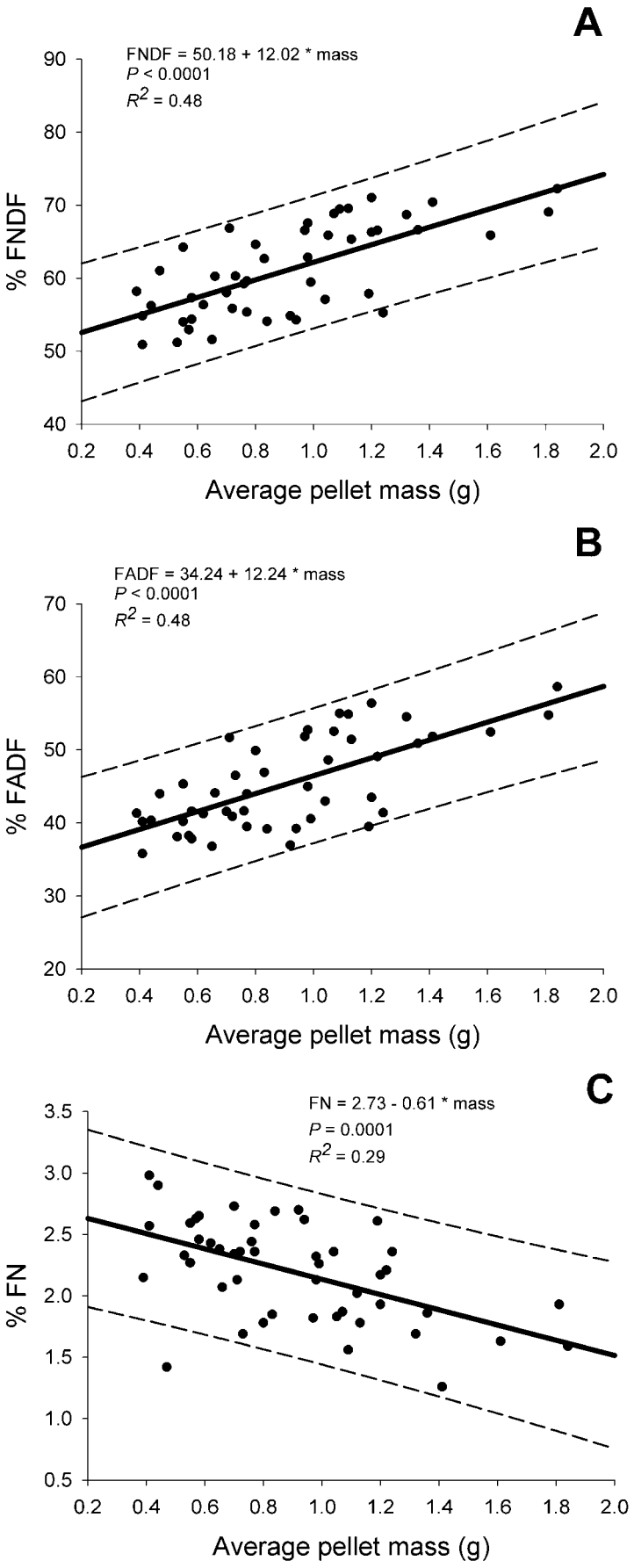


Figure 4. Ordination of fecal constituents as index for diet quality from 3 white-tailed deer populations with supplemental winter feeding and 1 unfed population, north-central Adirondack Mountains, New York, USA, winter 2000. "S" = South site, "W" = West site, "N" = North Site, "U" = Unfed site.

Comparison of Diet Protein and Digestibility Among Fed and Unfed Populations

Data from the 2 fecal fiber constituents, FNDF and FADF, both indicated that a greater proportion of fiber was consumed by deer at the Unfed site relative to deer at the South and West sites (Fig. 2A,B). Increased fiber consumption generally increases food retention time and limits dry matter intake by an animal (Ammann et al. 1973). The percentage of FNDF is inversely related to dietary intake and FADF is inversely related to digestibility (Van Soest 1994, Gray and Servello 1995). Tarr and Pekins (2002) reported an inverse relationship between FADF and percent grain in the diet. This suggests that deer at the South and West sites likely consumed more grain (corn) relative to the North site despite the larger amount of corn fed at the North site. The ratio of FNDF:FADF (Fig. 2C) indicated that populations at the fed sites consumed more digestible fiber relative to the population at the Unfed site. This is most likely attributable to the provision of alfalfa hay at the sites with supplemental feeding.

Percent FN (Fig. 3A) indicated that deer at the South and West sites consumed significantly more protein than deer at the North and Unfed sites. The relationship between FN and protein intake has been disputed based on variations due to site, season, and possible confounding effects from tannin ingestion (Hobbs 1987). Because this study considered free-ranging deer with similar diets and habitats, FN likely provided a reasonable index of protein



intake and diet quality (Leslie and Starkey 1987, Howery and Pfister 1990, Hodgman et al. 1996, Osborn and Jenks 1998).

Fecal DAPA results (Fig. 3B) indicated that the population at the South site consumed less digestible energy relative to deer at the North and West sites. This was an unexpected result as all other indicators of diet quality suggested that deer at the South site consumed the most digestible and highest-quality diet. We suggest that the abundance and probable consumption of lichen around the feeding area at the South site may have contributed to this anomalous result. The high digestibility and possible synergistic effects of lichen in reducing feed retention time in the digestive tract have been documented (Hodgman and Bowyer 1985, Robbins 1987, Jenks and Leslie 1988, 1989). Additionally, lichens contain antimicrobial compounds (Person et al. 1980, Robbins 1987, Elix 1996), which could alter rumen faunal composition and, therefore, affect fecal DAPA (Van Soest 1994). While we did not observe consumption of the lichen at the South site, it may be a plausible explanation for the aberrant DAPA levels reported.

The ordination (Fig. 4) showed a transition from a high-protein, highly digestible diet at the South and West sites to a lower-protein, less-digestible diet at the North and Unfed sites. Along the vertical "digestible energy" axis, there was greater variability among the sites with supplemental feeding than the Unfed site. This may reflect either a more consistent diet consumed by deer at the Unfed site or may be an artifact of a smaller population in the absence of supplemental feeding that may have increased deer density at the 3 fed sites (Sage and Gustafson 1991).

The positive relationships observed between fresh fecal pellet mass and the fecal fiber constituents suggest that large pellets may indicate relatively lower diet digestibility. Additionally, the significant negative relationship between fresh pellet mass and FN indicates that large pellets also may be associated with relatively low dietary protein. While these relationships were substantiated only for winter fecal samples collected at 4 sites, they may be helpful in assessing relative differences in diet quality over spatial or temporal scales. It is likely that variations among individual deer, sites, and diet would preclude these relationships from being used for quantitative analysis. Additionally, because single nutritional indices may give conflicting results, management decisions are best made after using multiple assessment techniques (Brown et al. 1995, Sams et al. 1998).

Our results indicate that supplemental winter feeding can significantly influence the protein and energy status of white-tailed deer. Using physiological variables, we identified a decreasing gradient of diet quality from the most intensively managed feeding programs to the Unfed site. We suggest that both the seasonal duration of a winter feeding program and the methods of feed distribution can significantly affect the protein and energy benefits that deer can obtain from the feed provided.

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Figure 5. Regressions with 95% confidence limits of fecal fibers and fecal nitrogen on average pellet mass from composited white-tailed deer pellet groups collected off the snow from unknown individuals at 3 sites with supplemental winter feeding and 1 unfed population, north-central Adirondack Mountains, New York, USA, winter 2000. (A) Neutral detergent fiber (FNDF), (B) acid detergent fiber (FADF), (C) fecal nitrogen (FN).

Specifically, the relatively short duration of the feeding program at the North site, coupled with the dispersal of corn using a salt spreader, likely resulted in a high percentage of grain waste and decreased benefits realized by the wintering population. With energetic status being a critical factor in winter survival, feeding programs should be designed to optimize the net energy gain by a population. By providing high-quality, readily accessible feed through the duration of the winter in sufficient quantity to both maintain metabolic needs and minimize competition, managers can begin to maximize the benefits of winter feeding programs (see Sage and Gustafson 1991).

While blood constituents from captured deer can be used to develop a detailed physiological profile, the collection of these data can be costly in terms of time and resources. Our data suggest that a rapid, though nonquantitative, determination of diet quality can be assessed based on positive relationships between fecal nitrogen and fresh pellet mass and negative relationships between fecal fiber and pellet mass. Further work on refining these fecal indices and identifying the effects of lichens and other species on index variables likely will provide managers with a powerful and relatively inexpensive tool for monitoring changes in the diet quality of a population.

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