12-2009

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Recommended Citation

Walter, W.D.; Zimmerman, T. J.; Leslie, D. M. Jr.; and Jenks, J. A., "Dietary Response of Sympatric Deer to Fire Using Stable Isotope Analysis of Liver Tissue" (2009). *Natural Resource Management Faculty Publications*. 172.
http://openprairie.sdstate.edu/nrm_pubs/172

Wildl. Biol. Pract., December 5(2): 128-135
DOI:10.2461/wbp.2009.5.13

ORIGINAL PAPER

DIETARY RESPONSE OF SYMPATRIC DEER TO FIRE USING STABLE ISOTOPE ANALYSIS OF LIVER TISSUE

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Keywords
Burned;
C_3;
C_4;
Carbon isotopes;
Nitrogen isotopes;
Odocoileus hemionus;
O. virginianus;
Unburned.

Abstarct

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in biological samples from large herbivores identify photosynthetic pathways (C_3 vs. C_4) of plants they consumed and can elucidate potential nutritional characteristics of dietary selection. Because large herbivores consume a diversity of forage types, $\delta^{13}C$ and $\delta^{15}N$ in their tissue can index ingested and assimilated diets through time. We assessed $\delta^{13}C$ and $\delta^{15}N$ in metabolically active liver tissue of sympatric mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) to identify dietary disparity resulting from use of burned and unburned areas in a largely forested landscape. Interspecific variation in dietary disparity of deer was documented 2–3 years post-fire in response to lag-time effects of vegetative response to burning and seasonal (i.e., summer, winter) differences in forage type. Liver $\delta^{13}C$ for mule deer were lower during winter and higher during summer 2 years post-fire on burned habitat compared to unburned habitat suggesting different forages were consumed by mule deer in response to fire. Liver $\delta^{15}N$ for both species were higher on burned than unburned habitat during winter and summer suggesting deer consumed more nutritious forage on burned habitat during both seasons 2 and 3 years post-fire. Unlike traditional methods of dietary assessment that do not measure uptake of carbon and nitrogen from dietary components, analyses of stable isotopes in liver or similar tissue elucidated $\delta^{13}C$ and $\delta^{15}N$ assimilation from seasonal dietary components and resulting differences in the foraging ecology of sympatric species in response to fire.

Introduction

Wildlife researchers often want to evaluate ungulate use of food plots, supplemental feed, agricultural crops, or unique landscapes (e.g., burned habitat; [1-3]). Indirect methods to assess use of specific food sources or habitats by ungulates are valuable alternatives to those that require capture and intensive monitoring protocols. Furthermore, a method to identify landscapes important to ungulates nutritionally would be useful to wildlife agencies. Darr and Hewitt [4] suggested that diets of conspecific herbivores occupying disparate landscapes (e.g., dominated by C_3 plants vs. C_4 plants) or diets dominated by non-native plants can be identified and differentiated using stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in various tissues. Despite broad-scale applicability of stable isotopes to understanding trophic ecology across varying taxa [5,6], few researchers have provided practical applications for $\delta^{13}C$ and $\delta^{15}N$ to enhance management of ungulates.

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes have been used to identify photosynthetic pathways (i.e., C_3 or C_4) of plants consumed by herbivores [5,7,8]. Carbon isotopes from C_3 plants average about –27‰ (range: −35 to −21%) whereas $\delta^{13}C$ from C_4 plants average −13‰ (range: −14 to −10‰; [5,9]). Therefore, grazers consuming predominately C_4 forage (e.g., bison (*Bison bison*)) would be expected to have higher $\delta^{13}C$ than browsers consuming predominately C_3 shrubs and browse (e.g., white-tailed deer (*Odocoileus virginianus*)). Furthermore, mixed-feeders such as Rocky Mountain elk (*Cervus elaphus*) and mule deer (*O. hemionus*) would be expected have $\delta^{13}C$ somewhere in between those of grazers and browsers [10-12]. Similarly, plants can have mean $\delta^{15}N$ ranging from -7 to 7‰ due to differential fractionation of nitrogen by N_2-fixing and non-N_2-fixing plants [13-15]. Several studies attempted to use $\delta^{15}N$ to understand herbivore diets and found that physiology (i.e., heat stress), anatomy (i.e., hindgut vs. foregut fermenters), and diet (i.e., grazers vs. browsers) can confound reliable conclusions about nutritional ecology [16-18]. Studies on captive ungulates show that tissue $\delta^{15}N$ increases as dietary protein increases [8,19] suggesting tissue $\delta^{15}N$ can be used as an index of nutrition in free-ranging ungulates.

Research in the Black Hills of South Dakota, USA, in the 1990s indicated that white-tailed deer were in poorer nutritional condition and exhibited lower reproductive rates than deer from other parts of the state [20,21]. Fire was considered a preferred method to improve winter nutrition of white-tailed deer, mule deer, and mountain sheep (*Ovis canadensis*) because fire elevated concentrations of protein and *in vitro* digestibility of forages [22]. Burned habitat improved condition of mule deer and white-tailed deer, as indexed by changes in gastrointestinal morphology [23] and hepatic characteristics [24], but use of burned habitat differed between both deer species, depending on season and number of years post-fire.

We present a case study that differentiated dietary characteristics of sympatric mule deer and white-tailed deer foraging in burned and unburned habitats using $\delta^{13}C$ and $\delta^{15}N$ in liver tissues. Liver is highly active metabolically, and its isotopic characteristics reflect diets consumed within 1−2 weeks of sample collection [25,26]. Differences in seasonal dietary characteristics of the two deer species, as reflected in changes in liver $\delta^{13}C$ and $\delta^{15}N$, were assessed for deer foraging in burned and unburned habitats. We also identified a lag-time response in the foraging ecology of sympatric deer in burned habitats using liver tissue isotopes because forage quality would be expected to decrease several years post-fire [22,27].

Study Area

We sampled liver tissue collected from mule deer and white-tailed deer in the southern Black Hills in west-central South Dakota, USA, in early February and August 2002 and 2003 [23]. Mountainous terrain in the Black Hills is 973 to 2,202 m above mean sea level with steep ridges, rock outcrops, and rolling hills interspersed with native prairie habitat. About 84% of the overstory canopy in the study area was C_3 plants such as ponderosa pine (*Pinus ponderosa*) with remaining canopy containing small stands of white spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*) at higher elevations. The southwestern part of the winter range of both species contained ponderosa pine, mountain mahogany (*Cercocarpus montanus*), and Rocky Mountain juniper (*Juniperus scopulorum*) with understory vegetation of C_4 grasses such as big bluestem (*Andropogon gerardii*) and buffalograss (*Buchloe dactyloides*). Prairie sagewort (*Artemesia frigida*), common snowberry (*Symphoricarpus albus*), serviceberry (*Amelanchier alnifolia*), cherry species (*Prunus* spp.), and common juniper (*J. communis*) were common C_3 shrubs found on winter range.

On 24 August 2000, a fire burned 34,821 ha or 7% of the Black Hills National Forest in the southern Black Hills. Unburned to low intensity burns, moderate burns, high-intensity burns, and unclassified habitats occurred on 39, 32, 24, and 5% of the area burned, respectively (http://www.fs.fed.us/r2/blackhills/fire/history/jasper/00_11_09_jrapid_text.pdf, accessed April 2009). From 2001 to 2003, mean vegetation cover of forbs, grasses, and major shrubs were 2.2, 2.3, and 6.3% in unburned habitat and 8.6, 11.4, and 2.2% in burned habitat, respectively [28].

Materials and Methods

We sampled ≥5 female mule deer and ≥5 female white-tailed deer from burned and unburned habitats during 4 periods (i.e., summer 2002 and 2003 and winter 2002 and 2003) for a total sample of 83 animals (41 mule deer, 42 white-tailed deer; [23,24]). We used a 4-km buffer around the fire perimeter to avoid collecting deer that used both burned and unburned habitats [28]. Random deer were shot in the neck with a high-powered rifle and necropsied at a designated field station in a manner approved by the Institutional Animal Care and Use Committee at South Dakota State University. A 5-g sample from the caudate lobe of the liver was removed and stored frozen prior to being oven-dried at 70°C to a constant weight and subsequently ground by hand using a mortar and pestle.

Values of $\delta^{13}C$ and $\delta^{15}N$ were calculated where δ was the ratio of heavy to light isotopes in the sample divided by the standards from Peedee Belemnite marine fossil limestone formation from South Carolina ($^{13}C/^{12}C = 0.01124$) and atmospheric nitrogen ($^{15}N/^{14}N = 0.00368$), respectively [9,25]. The quotient was then subtracted from one and then multiplied by 1,000 to represent δ that was expressed in per mil notation (‰). Standard deviations for replicated internal standards were 0.08 for $\delta^{13}C$ and 0.22‰ $\delta^{15}N$. About 1–2 mg of liver was loaded into individual 5- x 8-mm tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analyses with an isotope ratio mass spectrometer at the Stable Isotopes Facility, University of California-Davis. Differences in mean $\delta^{13}C$ and $\delta^{15}N$ in liver among species, habitat, and periods were assessed using a 3-way analysis of variance [29]. A priori significance was set at $P \leq 0.05$ for all statistical analyses.

Results

There was a 3-way interaction among species, habitat, and period ($F_{3,81} = 8.08$, $P < 0.001$) for mean $\delta^{13}C$ in liver samples. Greater variability among means occurred for $\delta^{13}C$ in winter 2002 than winter 2003 for all possible comparisons (Fig. 1a). Means of $\delta^{13}C$ in summer 2002 and 2003 were higher for mule deer on burned habitat than on unburned habitat but not for white-tailed deer on burned and unburned habitat (Fig. 1b).

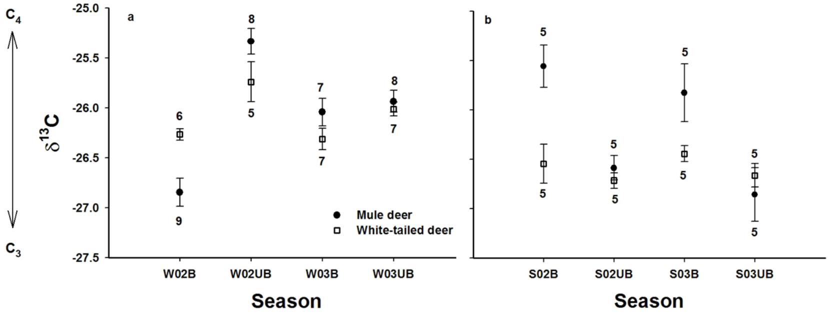

Fig. 1. Mean (± SE) $\delta^{13}C$ in liver samples from female mule deer and white-tailed deer from burned (B) and unburned (UB) habitats collected in a) winter (W), 2002 and 2003 and b) summer (S), 2002 and 2003 in the Black Hills of west-central South Dakota. Numbers at standard error bars represent sample size. The arrow along the y-axis in (a) shows the continuum of expected $\delta^{13}C$ signatures with a change in the proportion of C_3 and C_4 plants in the diet.

The 3-way interaction of species, habitat, and period was insignificant ($F_{3,81} = 0.13$, $P = 0.942$) for mean $\delta^{15}N$ in liver samples. Means of $\delta^{15}N$ for mule deer and white-tailed deer were higher on burned habitats than unburned habitats regardless of period (Fig. 2a, 2b). Means of $\delta^{15}N$ were typically higher for mule deer than white-tailed deer during winter and in all habitats.

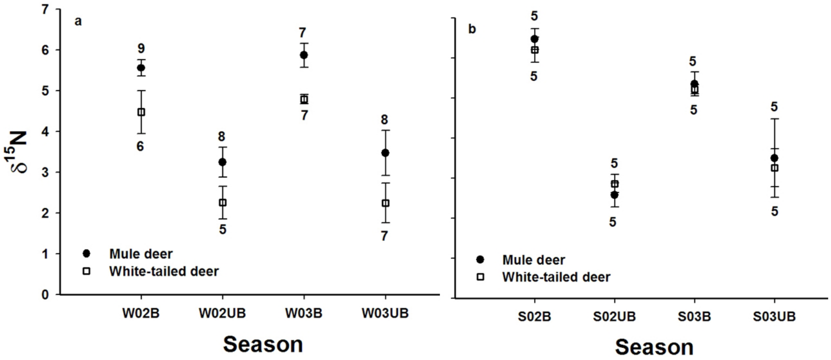

Fig. 2. Mean (± SE) $\delta^{15}N$ in liver samples from female mule deer and white-tailed deer from burned (B) and unburned (UB) habitats collected in a) winter (W), 2002 and 2003 and b) summer (S), 2002 and 2003 in the Black Hills of west-central South Dakota. Numbers at standard error bars represent sample size.

Discussion

Paralleling results from examination of gastrointestinal morphology of the same deer [23], seasonal and species differences in dietary characteristics from burned and unburned habitats were apparent in $\delta^{13}C$ and $\delta^{15}N$ of liver samples. Liver tissue has a short half-life and greater isotope turnover-rate (i.e., replace carbon at a faster rate) than less metabolically active tissues such as hair and hoof [10,25,30]. Therefore, $\delta^{13}C$ and $\delta^{15}N$ in liver samples of mule and white-tailed deer would index dietary characteristics during that season when samples were collected (i.e., summer and winter). Diets of mule deer during winter 2002 contained a greater quantity of C_3 plants than white-tailed deer on burned habitat, but the two deer species were similar during winter 2003 (Fig. 1). This was likely because of the greater proportion of high-quality grasses and forbs consumed by mule deer on burned habitat 2 years post-fire during winter [27,31]. Changes in rumen papillae and differences in some hepatic mineral concentrations in liver from the same sample of deer also suggested that burned habitat provided forage of higher quality for mule deer [23].

Liver $\delta^{13}C$ in white-tailed deer was apparently less influenced by quality and quantity of forage on burned habitats than on unburned habitats. Although changes in gastrointestinal morphology suggested that fire benefited white-tailed deer [23], values of liver $\delta^{13}C$ were similar on both habitats regardless of season. Plant type and protein content would increase in grasses and forbs on burned habitats compared with unburned habitats, but feeding strategies would determine which deer species would benefit most [22]. Forage on burned areas would benefit the concentrate selector–intermediate feeding strategy of mule deer to a greater extent than the concentrate selector feeding strategy of white-tailed deer because larger rumen size allows longer retention of digesta made up of both grasses and forbs in the former [32]. In contrast, concentrate selectors have relatively smaller rumens than mule deer and rely on forages characterized by high digestibilities and nitrogen concentrations; these attributes were illustrated by higher $\delta^{15}N$ in liver samples of the more selective species, white-tailed deer. Overall, our results suggest that diet selection in response to fire influenced the liver isotope dynamics of both carbon and nitrogen in mule deer but only for nitrogen in white-tailed deer.

Burning of habitat in the Black Hills of South Dakota had a positive effect on the protein content of grasses and forbs commonly selected by mule deer and white-tailed deer, respectively, as indicated by liver $\delta^{15}N$ and changes in gastrointestinal morphology [22,28]. Results from gastrointestinal morphology supports our finding that increased nutrition of plants on burned habitat resulted in higher liver $\delta^{15}N$ and that nitrogen recycling by deer using burned habitat was not occurring [33]. Furthermore, nitrogen recycling typically occurs during winter, but higher $\delta^{15}N$ also occurred during summer suggesting nitrogen recycling was not responsible for the higher $\delta^{15}N$ compared to those from deer on unburned habitats. Both species of deer had greater liver $\delta^{15}N$ during winter and summer on burned habitat than unburned habitat during both years of our study. Although dietary selection appeared different based on $\delta^{13}C$, the protein content of those forages consumed by both deer species resulted in higher liver $\delta^{15}N$ at the burned sites. Data on captive and free-ranging ungulates have documented an increase in tissue $\delta^{15}N$ with an increase in the protein content of the diet [8,34].

Differences in $\delta^{13}C$ suggested that greater amounts of grasses were consumed by mule deer than white-tailed deer in summer 2002 and 2003, paralleling results after summer burning in previous studies [22,27]. Similarly, burning seemed to have less influence on dietary characteristics of mule deer during winter 3 years post-fire because liver $\delta^{13}C$ were similar to those of white-tailed deer 3 years post-fire. The diminishing influence of fire through time on quality and quantity of forage has been documented [22,27]. Diminishing returns of fire (i.e., lower quality grass several years post-fire) may have caused greater consumption of legumes and forbs that can have lower $\delta^{15}N$ than grasses as indicated by our liver $\delta^{15}N$ 3 years post-fire. Nevertheless, fire can increase protein content of forages for months to several years post-fire, and this likely was reflected in the liver $\delta^{15}N$ of both deer species.

Limited data exists on $\delta^{13}C$ and $\delta^{15}N$ of plants consumed by ungulates in the Northern Great Plains of the USA with most research focusing on $\delta^{13}C$ [34,35]. Although baseline plant $\delta^{13}C$ and $\delta^{15}N$ were not collected on the study site, differences in foraging ecology were identified through liver $\delta^{13}C$ and $\delta^{15}N$, and nutritional quality was inferred through gastrointestinal morphology. Examination of gastrointestinal morphology and collection of liver tissue required lethal removal of deer to determine influences of forage quality from burned and unburned habitats on the two deer species. However, $\delta^{13}C$ and $\delta^{15}N$ can be assessed in other metabolically active tissue (e.g., muscle biopsy) or blood during immobilization procedures if lethal removal is not an option. Digestive physiology of ungulates is multi-faceted so additional knowledge of $\delta^{13}C$ and $\delta^{15}N$ in tissue that reflect dietary characteristics would enhance understanding of stable isotope dynamics of sympatric species. Furthermore, data collected for >3 years post-fire would provide additional insight on the length of time that burning enhances dietary quality and on how foraging ecology of these of sympatric deer populations adapt to change in forage quality.

Acknowledgments

We thank personnel from the South Dakota Department of Game, Fish and Parks who assisted with deer collection. Funding was provided by the Federal Aid, Pittman-Robertson Wildlife Restoration Act under Project W-75-R (Study 75102) administered by the South Dakota Department of Game, Fish and Parks. Additional funding was provided through the Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma Department of Wildlife Conservation, Oklahoma State University, United States Geological Survey, United States Fish and Wildlife Service, and Wildlife Management Institute cooperating).

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