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Near Infrared Spectroscopy and Fecal Chemistry as Predictors of the Diet Composition of White-Tailed Deer

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Abstract

Overbrowsing by white-tailed deer (*Odocoileus virginianus* Zimmermann) on Anticosti Island (Canada) created a need to develop efficient methods for estimating their foraging patterns. We tested the ability of near infrared (NIR) spectra of feces and of fecal chemical properties to predict diet composition of different individuals. We first used a principal component-based discriminant analysis to sort the NIR spectra of fecal samples ($n=102$) obtained from two groups of captive deer that had been fed two different diets. The diets differed only in their relative abundance of balsam fir (*Abies balsamea* [L.] P.Mill.) and white spruce (*Picea glauca* [Moench] Voss.) foliage. The calibrated model allowed us to assign 28 of 30 validation fecal samples (93.3 %) to the correct diet. In a second study, we attempted to estimate the proportion of coniferous, deciduous, herbaceous, and lichenous forages in diets of free-ranging white-tailed deer, as determined by fecal microhistology. Both NIR spectra and chemical properties of feces were used as predictors of diet composition. NIR spectra were analyzed using partial least-squares regression (PLSR), whereas fecal chemical properties were analyzed using mixed-linear regressions (MLRs). The PLSR models were robust ($R^2=0.89$; ratio of prediction to deviation=3.2) for predicting the amount of coniferous fragments, but not for predicting the relative amounts of balsam fir, white spruce, and deciduous and lichenous fragments within feces. MLR models revealed a positive relationship (47% variance explained) between acid detergent lignin (ADL) and coniferous fragments within feces. ADL and cellulose explained 24% of variance in deciduous fecal fragments, whereas ADL alone explained 22% of variance in balsam fir fecal fragments. These results suggest that NIR spectroscopy and fecal chemical properties have several applications on Anticosti Island, such as measuring the degree of variation in diets within a given home range or determining dietary conifer intake during winter.

Key Words: diet quality, fecal analysis, fecal microhistology, near infrared spectroscopy, overbrowsing, white-tailed deer

INTRODUCTION

Studying the foraging behavior of large wild herbivores in heterogeneous landscapes informs us on habitat selection, seasonal movements, or the impacts of herbivory on plant communities. To this end, a variety of methods have been developed over past decades to describe the diet of wild herbivores. These include fecal analyses (Stewart 1967), the probing of stomach contents (McInnis et al. 1983), browse surveys (Shipley et al. 1998), behavioral observations in the field (Parker et al. 1999), as well as isotope fractionation of animal tissues (Dalerum and Angerbjörn 2005). Among these techniques, fecal analyses are an interesting option because fecal samples are easy to obtain in high-density populations and do not require the handling or killing of animals. The main disadvantage of this approach is that highly digestible plant species could be underrepresented in the estimated diets, whereas less digestible plants could be overrepresented. Nevertheless, Hanley and McKendrick (1985) showed 65% to 77% similarity between the estimated plant species composition of rumen contents and fecal samples of Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Rafinesque).

Estimating the diets of large herbivores through fecal analyses usually entails the microhistological analysis of plant fragments (Dearden et al. 1975; Lefort 2002). This method is, however, expensive and time consuming, and it requires a good knowledge of the micromorphology of different plant tissues. More rapid proxy methods have been developed, such as determining fecal n-alkanes (Bugalho et al. 2004; Dove and Mayes 2005) or DNA barcoding of plant fragments within feces (Valentini et al. 2009a), but these remain relatively expensive, and their ability to accurately quantify the proportion of different plant species in complex diets is uncertain (Bugalho et al. 2002; Valentini et al. 2009b). There is, therefore, a need to develop rapid and cost-efficient ways for estimating the diets of large herbivores through fecal analyses.

Recent research has shown that near infrared spectroscopy (NIRS) of fecal samples could be used to assess the dietary composition of free-ranging domestic livestock (Landau et al. 2006; Dixon and Coates 2009; Walker et al. 2010). NIRS is a nondestructive procedure requiring minimal sample preparation, and it produces a spectrum expressing the entire chemical makeup of the sample. NIRS may thus be used to predict both the chemical (Malley et al. 2002; Stuth et al. 2003) and

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functional (McIlwee et al. 2001; Stolter et al. 2006) properties of materials. There is an opportunity, therefore, to explore the potential and limitations of NIRS to discriminate different diets of wild herbivores through the spectral analysis of their feces.

A second potentially rapid and cost-effective approach to assess the diets of wild herbivores would be to use fecal chemical properties such as fecal nitrogen (N) or proximate carbon (C) fractions. These have traditionally been used to assess the nutritional and energetic quality of different diets or habitats, but not to estimate the actual botanical composition of the diet. For example, fecal N may be a good index of seasonal variations in diet quality (Verheyden et al. 2011), provided that the amount of tannins in the diet is low (Leslie et al. 2008). Likewise, Hodgman and Davitt (1996) proposed that neutral detergent fiber (NDF) content of feces be used as a predictor for digestible energy of the diet. Given that different forage types vary in their nutritional and energetic qualities, there is an opportunity to explore the ability of fecal chemical properties to estimate the actual botanical composition of the diets of wild herbivores. For example, fecal N might be used to detect the intake of nitrophilous plant species, whereas NDF might be used to identify the most digestible plant species. We posit that this potential to detect diet composition via fecal chemical properties increases as the number of available forage types decreases.

Using NIRS or fecal chemical properties to estimate the diets of wild herbivores first requires a calibration data set of fecal samples from animals with known diets. Knowledge of an animal's recent food intake may be obtained directly through feeding trials on captive individuals, or by reliable microhistological data. Feeding trials may yield more accurate data than microhistogical analyses, but are relatively expensive and logistically complicated to perform on wild animals in remote regions. Furthermore, feeding trials usually comprise a limited number of distinct diets, which underrepresents the wide range of diets that are possible in the wild. On the other hand, microhistological data have been criticized as being imprecise (e.g., Wam and Hjeljord 2010), leading Walker et al. (2010) to speculate that these cannot be used as calibration data sets for NIRS. This remains, however, a contentious matter given that Taillon et al. (2006) found an almost perfect concordance between the amounts of fir and spruce needles fed to captive white-tailed deer (*Odocoileus virginianus* Zimmermann) fawns and the percentages of these two forage types within feces. There is, therefore, a need to test the resolution at which NIRS or fecal chemical properties can predict simple diets of wild herbivore based on both types of calibration data sets (i.e., feeding trials and microhistological data).

We report on a study where we evaluated both the potential and limitations of NIRS and fecal chemical properties to predict the proportion of different plant groups composing the winter diets of white-tailed deer on Anticosti Island, Canada. The island boasts a high population of this herbivore, which makes it a prized area for game hunting. There are concerns, however, that overbrowsing of certain winter forage types could result in an important crash of the population before 2100 (Potvin et al. 2004). For this reason, it is important to propose rapid and cost-effective tools that could help rangeland managers on Anticosti Island to monitor the depletion of resources during winter. Fecal samples were obtained, therefore, from two prior studies; one in which distinct diets had been administered to captive deer, and the other in which diets of free-ranging deer had been estimated from microhistological analyses.

METHODS

Study Area

Anticosti Island (lat 49°28′N, long 63°00′W) is located in the Gulf of St. Lawrence, Canada. The entire island (7 943 km^2) is located in the Eastern balsam fir-White birch bioclimatic zone (Grondin et al. 1996). The subboreal maritime climate provides cool summers (mean of 16°C in July) and cold winters (mean of –11°C in January), with an average annual precipitation of 630 mm of rain and 406 cm of snow (Environment Canada 2006).

About 200 white-tailed deer were introduced onto the island in 1896, and the population increased rapidly in the absence of natural predators. Accordingly, the average white-tailed deer density over different sectors of the island has been 20 to 60 individuals $\cdot$ km^{-2} for the past 80 yr (Potvin et al. 2004). Heavy browsing has resulted in a loss of palatable species in the shrub layer such as Mountain maple (*Acer spicatum* Lam.), Beaked hazel (*Corylus cornuta* Marsh.), and Canadian yew (*Taxus canadensis* Marsh; Potvin et al. 2003), and in the spread of browse tolerant graminoids such as Canada bluejoint (*Calamagrostis canadensis* [Michx.]; Dufresne et al. 2009). Balsam fir (*Abies balsamea* [L.] P.Mill.) is the preferred winter forage (Lefort et al. 2007), such that the recruitment of balsam fir seedlings has substantially diminished in the understory giving way to a higher recruitment of less palatable white spruce seedlings (*Picea glauca* [Moench] Voss.; Hidding et al. 2013). In accordance with this shift in the understory vegetation, it is expected that white-tailed deer will increase their winter consumption of white spruce seedlings in coming years (Sauvé 2005; Taillon et al. 2006).

Fecal Samples

In study 1, Taillon et al. (2006) tested the effects of two winter diets on the behavior and body condition of captive white-tailed deer fawns. In 2004, seven fawns were fed a control winter diet, approximating the proportional intake of balsam fir (70%), white spruce (20%), and arboreal lichens (10%) for white-tailed deer on Anticosti Island (Lefort et al. 2007). Six other fawns were fed a "poor quality" diet consisting of 50% balsam fir, 40% white spruce, and 10% arboreal lichens. Feces were collected on a daily basis (control diet: $n=69$, poor diet: $n=63$) and kept frozen at –20°C until further analyses.

In study 2, performed in 2009–2010, Giroux et al. (2012) conducted a field survey on Anticosti Island to determine the influence of winter diet on body condition of free-ranging white-tailed deer. Using a combination of telemetry and the bio-marking of feces with food dyes, they followed 27 individuals and recovered fresh feces ($N=90$). Within 6 h after collection, fecal samples were dried at 20°C and subsequently stored at –4°C. A subsample of each fecal sample was kept for NIRS scanning and chemical analyses (explained below), whereas the remaining fecal material was analyzed for its plant content by microhistological analysis (Lefort et al. 2007).

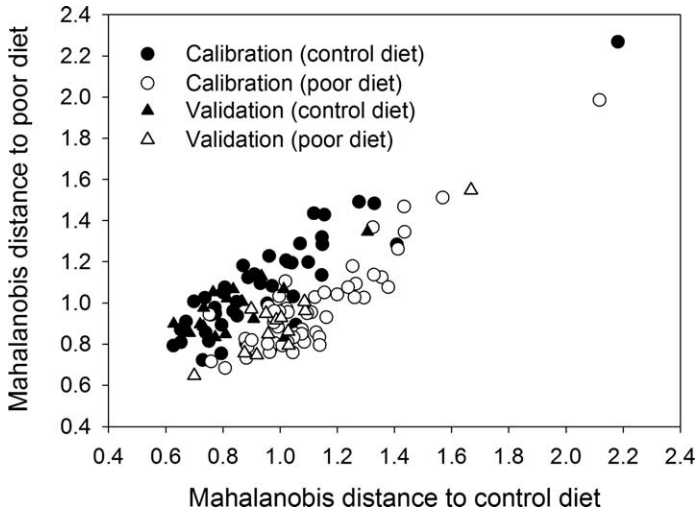

Figure 1. Results of principal component-based discriminant analysis showing the Mahalanobis distances between the near infrared spectra of fecal samples collected from captive deer that had been fed two different diets (Control diet=70% balsam fir+20% white spruce+10% lichens; Poor diet=50% balsam fir+40% white spruce+10% lichens). A total of 102 samples were used for model calibration and 30 samples for validation.

Coniferous, deciduous, as well as herbaceous and lichenous fragments were identified by comparing with reference samples under a microscope. Among the coniferous fragments, balsam fir and white spruce needles were distinguished based on their micromorphology. The proportion of lichens was estimated at 16× magnification, whereas the proportions of the other forage types were estimated at 100× magnification, according to the protocol developed by Lefort (2002).

Fecal Chemical Properties

The stored fecal subsamples from study 2 (Giroux et al. 2012) were thawed, dried again in an air-draft oven (50°C), and ground in a mortar to pass a 2-mm sieve. Fecal N was measured by high temperature combustion followed by gas analysis, using a Vario Macro C&N Analyzer (Elementar Analysensysteme Corp, Hanau, Germany). NDFs, acid detergent fibers (ADFs), and acid detergent lignin (ADL) were measured following the protocol of Goering and Van Soest (1970), using an Ankom Fiber Analyzer 200 (Ankom Technology, Macedon, NY). Cellulose was estimated as the difference between ADL and ADF (Van Soest 1994).

Near Infrared Spectroscopy

Air-dried and sieved fecal subsamples of both study 1 and study 2 were scanned for the reflectance of wavelengths ranging from 1 000 to 2 500 nm, using a Nicolet Antaris FT-NIR spectroscope supported with Omnic software (Thermofisher Scientific, Waltham, MA). In study 1, a principal component (PC) based discriminant analysis using Mahalanobis distances was used to discriminate the NIR spectra of feces from white-tailed deer fed with control versus poor quality winter diets. This predictive model was calibrated using 102 fecal subsamples, and the remaining 30 subsamples were used for its validation. The nonrandomness in the classification of fecal samples among the two diets was evaluated using a χ^2 test. For study 2, we used partial least-squares regressions (PLSR; Wold 1966) to build predictive models relating microhistological data to the NIR spectra of 75 fecal samples. First derivatives and mathematical smoothing features from the TQ Analyst software (Thermofisher Scientific) were used to improve the predictive power of the calibrated PLSR models (Savitzky and Golay 1964; Williams and Norris 1987). The remaining spectra from 15 randomly selected fecal samples were used to validate each PLSR model and evaluate its robustness based on the ratio of prediction to deviation (RPD=ratio of the standard deviation of predictions to the observed standard deviation). According to Williams (2001), model calibrations are deemed reliable only if $R^2 > 0.49$ and RPD > 2.3.

Fecal Chemistry Models

Linear mixed-effects models (*nlme* R package; Pinheiro and Bates 2000) were used to relate fecal chemistry to microhistological data stemming from study 2 (Giroux et al. 2012). We considered the identity of the deer as a random effect variable, which required us to drop one fecal sample, the identity of which was unknown ($N=89$). We limited the number of explanatory variables to ADL, cellulose, and fecal N in order to avoid multicollinearity among fecal chemical properties and to maintain variance inflation factors below 2.5 (Graham 2003). ADL and cellulose were expressed on an NDF basis in order to reduce the bias induced by variations in labile substrates in the feces (e.g., microbial biomass, endodermal losses, etc.; Van Soest 1994). Microhistological data were either arcsine or arcsine square root-transformed, in order to meet the assumption of homoscedasticity (Gilbert 1989). We used the Akaike information criterion (Akaike 1974; Hurvich and Tsai 1989) corrected for small sample size (AICc) to select the best fitting model for each forage type.

RESULTS

PC-based discriminant analysis is a modeling method that classifies each fecal sample into one of two predefined classes (i.e., diets), based on a set of PCs that were derived from NIR absorbance values. The classification of a given fecal sample is based on the shortest Mahalanobis distance (i.e., H value) to the mean of each class. Thus, PC-based discriminant analysis of NIR spectra of feces from two different diets used in study 1 correctly classified 28 of 30 validation samples (Fig. 1). Altogether, 115 of 132 fecal samples were correctly assigned to the correct diet ($\chi^2=72.8$, $P<0.001$).

Microhistological analyses from study 2 reported fecal samples with 47–100% conifer content ($\bar{X}=81\%$), 0–44% deciduous content ($\bar{X}=7\%$), and 0–17% lichen content ($\bar{X}=5\%$). Among the conifer fragments, balsam fir and white spruce respectively represented 0–93% ($\bar{X}=40\%$) and 0–90% ($\bar{X}=41\%$) of the total forage fragments in the feces. PLSR regression models using NIR spectral information successfully predicted ($R^2=0.89$, RPD=3.2) the proportion of conifer fragments as determined by microhistological analyses (Fig. 2). However, PLSR models were not robust for predicting the proportions of deciduous ($R^2=0.64$, RPD=1.1), balsam fir

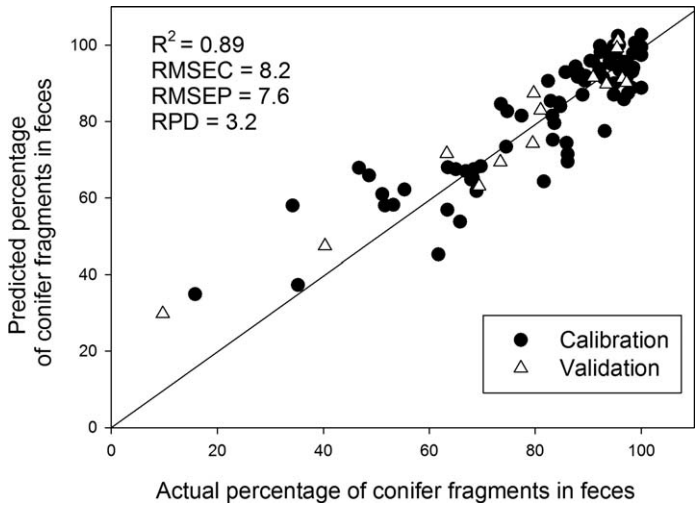

Figure 2. Correlation between coniferous content of fecal samples as determined by microhistology and that predicted by a partial least-squares regression model of fecal near infrared spectra. A total of 75 samples were used for model calibration and 15 samples for validation. RMSEC indicates root mean squared error of calibration; RMSEP, root mean squared error of prediction.

(R^2=0.68, RPD=1.4), white spruce (R^2=0.55, RPD=1.1) or lichen (R^2=0.36, RPD=1.0) content of fecal samples.

Linear mixed-models applied to fecal chemistry data from study 2 best predicted the conifer content of fecal samples, with 47% of the variance explained when using ADL as the only explanatory variable (Table 1). For predicting the deciduous content of feces, the best fitting model explained 24% of the variance, and included ADL and cellulose as explanatory variables. Fecal ADL explained 22% of the variance in balsam fir content, whereas ADL and cellulose could only explain 8% of the variance for white spruce. No model could explain the variance in lichen content by fecal chemistry. Fecal N was not a predictor of microhistological data in any of the models.

DISCUSSION

Our study showed that NIR spectra of feces from study 1 could discriminate between animals consuming two diets differing only in the relative proportion of balsam fir and white spruce. In the context of Anticosti Island, this may have practical implications, given that the relative abundance of white spruce to balsam fir should continue to increase over coming years. NIRS could, therefore, be used to track a possible concomitant shift in white-tailed deer winter diets. For example, it would be relatively inexpensive and easy to collect a large number of winter fecal samples over consecutive years, and to scan these by NIRS. Using our PC-based discriminant model, the average statistical distance of fecal samples to each calibration diet type could then be computed in order to detect an increasing use of white spruce in the winter diets of white-tailed deer.

The potential for NIRS to discriminate between two related simple diets could also be applied to answer more fundamental questions on the ecology of white-tailed deer on Anticosti Island. For example, one of the outcomes of the "Optimal Foraging Theory" (MacArthur and Pianka 1966) is that individuals sharing a common home range should converge towards the same diet. Empirical evidence has shown, however, that nonrandom variations may occur in the feeding behavior of neighboring individuals of the same age group (Searle et al. 2010). Hanley (1997) discussed the possible role of learned behavior and other social factors that may create this variation in diet choices among individuals. Thus, analyzing the multivariate dispersion among fecal NIR spectra (e.g., Anderson 2004) could be a novel and cost-efficient way of measuring the degree of variation in diets within a given home range.

Although PC-based discriminant analysis successfully sorted fecal spectral data according to two different diets used in study 1, a regression approach to analyzing both NIR spectra and fecal chemical properties in study 2 had limited success in estimating the relative abundance of different forage types. This is consistent with past studies that had limited success in developing robust predictive models for estimating the specific forage composition of diets based on NIR spectra (e.g., Walker et al. 1998; Landau et al. 2004). It may be argued that our limited success was due to the unreliability of microhistological data as a calibration tool for NIRS, as suggested by Walker et al. (2010). But, as previously mentioned, Taillon et al. (2006) reported a high correlation between the spruce and fir contents of fecal samples as determined by microhistology, and the actual proportion of these two forage types in the diets of captive white-tailed deer on Anticosti Island. These forage types are especially relevant to rangeland management on Anticosti Island, as they are among the main winter staples for white-tailed deer and because they differ in nutritional quality (Sauvé and Côté 2007). It is, therefore, unfortunate that NIRS and fecal chemical properties could not accurately predict the proportion of these two forage fragments in fecal samples from study 2.

The salient finding of our study is that both NIRS and fecal chemical properties were relatively good at predicting the coniferous content of feces from free ranging white-tailed deer (i.e., study 2). We speculate that coniferous forage is a lot less digestible than the other forage types found on Anticosti Island,

Table 1. Best-fitting mixed-linear regression models predicting the fecal content of various forages based on fecal chemical properties (N=89).

Response variable	Explanatory variable	Coefficient	Standard error	P	Explained variance (%)
Conifers	ADL[1]	5.7	0.9	<0.001	47
	Intercept	−1.0	0.3	0.003	
Deciduous	ADL	−4.2	1.3	0.001	24
	Cellulose	3.2	1.6	0.049	
	Intercept	0.6	0.8	0.468	
Balsam fir	ADL	7.3	2.1	<0.001	22
	Intercept	−1.4	0.7	<0.001	
White spruce	ADL	−2.6	1.6	0.111	8
	Cellulose	−4.9	2.2	0.028	
	Intercept	4.0	1.0	<0.001	
Lichens	Intercept (null model)	0.38	0.02	<0.001	

[1]ADL indicates acid detergent lignin.

which facilitated its detection by NIRS. This is a relatively new application for fecal NIR spectra, as previous research on wild ruminants has so far only succeeded in using NIRS to estimate diet nutritional quality rather than the botanical composition of different diets (Kamler et al. 2004; Showers et al. 2006). The fact that we succeeded is probably due to the fact that ecosystems on Anticosti Island are relatively simple, with only a few winter forage types available to browsers. Although we were hoping to predict specific forage types, being able to predict the percent conifer content is nevertheless useful, as it is a good indicator of quality food shortages during the winter (Häsler and Senn 2012).

The fact that fecal ADL was positively correlated to conifer fragments (i.e., needles and twigs), and negatively correlated to deciduous fragments (i.e., twigs and young bark), suggests that the former may have been richer in lignin than the latter. We have difficulty explaining, however, why fecal ADL correlated to balsam fir fragments but not to white spruce fragments, as both forage types contain approximately the same amounts of lignin (Sauvé and Côté 2007). Dumont et al. (2005) demonstrated a positive relationship between different assumed bite sizes of balsam fir forage by white-tailed deer and the ADL concentration of each morsel. Thus, the relationship between fecal ADL and balsam fir fragments may reflect larger bites by white-tailed deer when browsing balsam fir, their preferred winter forage type.

IMPLICATIONS

Our study has shown the potential and limitations of fecal NIR spectra, and of fecal chemical properties, as rapid and cost-efficient indices of the winter diet composition of white-tailed deer on Anticosti Island. Both of these tools could be used, therefore, to launch a low cost monitoring program of winter resources for the white-tailed deer in Anticosti. Only a few fecal samples per relevant home range would be required each year to detect changes in winter-feeding behaviors. The low costs associated to both analytical methods allow rangeland managers to substantially increase their sampling efforts.

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