Agricultural subsidies affect isotopic niche size in elk and white-tailed deer

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Abstract

Agricultural crops are a concentrated food subsidy for wild ungulates that can bring animals into close proximity, providing an opportunity for pathogen transmission and thereby facilitating disease spread. We examined the diet of elk and white-tailed deer in three areas in the Canadian prairies using stable isotope analysis to reconstruct diet, and calculated the niche breadth of each species using stable isotope niche metrics. We expected more diet variation among individuals in white-tailed deer than elk due to their opportunistic feeding tendencies, but individual diet variation would decrease in both species if agriculture was a larger contributor to their diet. Agricultural sources accounted for 40-80% of the diets of both species in all areas. Diet variability (isotopic niche breadth) was greater for deer than elk in all study areas and in both early fall (reflected in hair) and on an annual timescale (reflected in muscle samples), indicating that deer are a generalist species composed of individuals with varied and specialized diets, while elk are individual generalists. For white-tailed deer, niche breadth in early fall decreased with increasing consumption of agricultural foods, as deer increased the proportion of agriculture in their diet by more deer specializing in agricultural feeding.However, annual niche breadth and agricultural feeding were unrelated in white-tailed deer. Elk diet breadth did not change with agricultural contributions to their diet for either timescale and was remarkably consistent over time. These results show that in addition being a concentrated food source, agricultural plants are also a significant subsidy.Agricultural feeding may increase the risk of disease not only by increasing the apparent density of these species at feeding sites, but also increase the overall population size. Efforts to

control agricultural feeding by elk and deer may reduce disease by reducing both overall density and local density at concentrated food sources.

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Introduction

Ecological subsidies, resources whose renewal rate is independent of its consumers, can strongly affect consumer-resource dynamics by increasing the consumer population beyond what other resources can support (Polis et al. 1997). Naturally occurring subsidies include detritus flowing downstream (Wipfli and Musslewhite 2004) or carrion (Roth 2003). Subsidies can also be anthropogenic, such bears using human food waste (Merkle et al. 2011) or supplemental feeding at the National Elk Refuge in Wyoming (Cross et al. 2010). Subsidies can also increase the risk of disease by increasing host population density (Pearson and Callaway 2006). Consumers that specialize on the subsidized resource can somewhat offset the burden of increased consumer population on other resources (Huxel et al. 2002), but this specialization can also increase the risk of disease by concentrating consumers around the subsidized resource, increasing their local density (Sorensen et al. 2013). Consumption of a subsidy could decrease the variability in diet between individual consumers, and this increased diet similarity potentially could increase pathogen transmission and disease spread.The variability in individual diets is important because different individual diets can have different risks and benefits associated with them, and variation between individuals allows natural selection (Bolnick et al. 2003).

The aspen parkland exists in the Canadian prairie provinces of Manitoba and Saskatchewan along the border between prairie and boreal forest. Historically this border shifted with as changing biotic and abiotic factors tipped areas from grassland to forest and back again (Bird 1961). More recently, these areas have undergone a drastic conversion to agriculture, removing 81% of the native prairie in Saskatchewan and over

99% in Manitoba (Samson and Knopf 1994), although changing economic conditions have led to the abandonment of some agricultural land and its reversion to forest (Bird 1961).The conversion to agriculture introduced a large subsidy of agricultural crops into the diets of herbivores in the region (Sorensen 2014). The North American elk (*Cervus canadensis*), a large prairie herbivore, has retreated to protected pockets of its historic range or to the margins between the now-agricultural landscape and less disturbed habitat, such as the boreal forest-prairie boundary (Bird 1961; Thomas and Toweill 1982). However, white-tailed deer (*Odocoileus virginianus*), another large-bodied, generalist herbivore, can be considered "disturbance specialists" (Whitehead 1972) and have expanded their range to encompass the newly converted agricultural habitat (Bird 1961). Now, elk populations along the border between the agricultural prairies and protected areas coexist with large numbers of white-tailed deer using both protected and agricultural habitats(Bird 1961; Vander Wal et al. 2013; Sorensen 2014).

In addition to being an ecological subsidy, agricultural feeding by elk and deer is a significant cost to farmers as these animals are consuming material that would otherwise be sold (Wagner et al. 1997; Sorensen 2014), as well as potentially increasing disease transmission. For example, availability of agriculture was a key factor in predicting the prevalence of chronic wasting disease, a transmissible spongiform encephalopathy that affects cervids, in white-tailed deer during an outbreak in Wisconsin (Joly et al. 2006). Chronic wasting disease is also found in elk and deer in Saskatchewan (Kahn et al. 2004). Around Riding Mountain National Park in Manitoba, deer and elk can carry bovine tuberculosis, which can affect livestock and human health, and use of

agricultural areas by elk has been shown to be a risk factor for passing the disease to cattle (Brook and McLachlan 2009).

Although both white-tailed deer and elk are generalist herbivores, their feeding strategies differ. Ruminant herbivores, such as deer and elk, exist along a spectrum from concentrate selector, feeding on smaller quantities of higher quality food, to bulk grazers who digest large quantities of lower quality food. White tailed deer are closer to the concentrate selector end of this spectrum, while elk, as mixed feeders, fall in the middle of the spectrum but much closer to the bulk grazer end than white-tailed deer (Hofmann et al. 1985). Both elk and white-tailed deer are generalist consumers, but a generalist population can comprise individuals that all eat a wide range of resources (type A generalists) or individuals that specialize on different food sources (type B; Bearhop et al. 2004). Diets are more similar between individuals in type A generalists than in type B (Bearhop et al. 2004). Because they are more selective feeders and have a smaller home range (Brook and Mclachlan 2006; Edye and Bayne 2008) from which to select their food, we expected white-tailed deer to be closer to the type B end of the spectrum than elk, which eat a larger quantity of bulk foods.

We evaluated the effect of subsidized food sources on the diet variability between individual white-tailed deer and elk using stable isotope analysis. Because animals use material in their diet to build their tissues, the stable isotope ratios of the elements in their tissues reflect the ratios of those same elements in their diet (DeNiro and Epstein 1978; DeNiro and Epstein 1981). By comparing the stable isotope ratios of an animal's tissue with those of its food we can reconstruct the relative proportions of different diet components (Gannes et al. 1997; Ben-David and Flaherty 2012), and by comparing

isotopic signatures with those of other animals in the same or similar species we can examine diet variability (Bearhop et al. 2004; Newsome et al. 2007; Jackson et al. 2011). We expected that where consumption of the subsidized food source was higher, isotopic variability (reflecting dietary niche breadth) would be lower in both species as individuals specialize in the subsidized resource. We also expected that deer, being closer to a type B generalist, would show more diet variability that elk, which are closer to a type A generalist.

Methods

Stable isotope analysis provides an advantage over scat or rumen content analysis by providing information on diet integrated over long periods of time, depending on the tissue being measured (Tieszen et al. 1983). We estimated the diets and diet variability of elk and white-tailed deer using two different tissues (muscle and hair) to capture diet and diet variability on two different time scales.

Data Collection

We measured the carbon and nitrogen stable isotope ratios of elk and white-tailed deer tissues from three areas in Manitoba and Saskatchewan where both species occur (Figure 1).Carbon and nitrogen are the elements most commonly used in wildlife diet reconstruction because their stable isotope ratios vary greatly within terrestrial ecosystems (Crawford et al. 2008). Manitoba Conservation and Water Stewardship, Saskatchewan Environment, and the Canadian Cooperative Wildlife Health Center provided samples as well as harvest location and date from hunter-harvested elk and

white-tailed deer collected as part of their wildlife disease monitoring efforts. In 2011 and 2012 we obtained hair and muscle samples from 49 elk (7 had only hair samples, 2 only muscle) and 48 white-tailed deer (2 hair only, 3 muscle only) in western Manitoba, 14 elk and 33 white-tailed deer (1 only hair) near Hudson Bay, SK, and 4 elk (1 only hair, 1 only muscle) and 11 white-tailed deer (1 only muscle) near Nipawin, SK. Samples were collected from animals harvested in September through December of each year, except for 4 elk killed in July 2012 (1 from Nipawin and 3 from Hudson Bay) and 4 deer killed in February 2012 (3 from Nipawin and 1 from Hudson Bay). We also obtained hoof samples from 5 elk and 4 deer, but did not include them in this analysis due to a small and imbalanced sample (Appendix 1).

Muscle carbon and nitrogen have long turnover times in large mammalian herbivores. The half-life of carbon in alpaca (*Lama pacos*) muscle was 178.7 days (Sponheimer et al. 2006), while in cattle (*Bos tauros*) muscle the half-life of carbon was 134-151 days and was 145-157 days for nitrogen(Bahar et al. 2009). In contrast the half-life of carbon in gerbil (*Meriones unguienlatus*) muscle is only 27.6 days (Tieszen et al. 1983). Based on these half-lives we assumed that muscle stable isotope ratios in elk and deer would represent the average diet over the year leading up to the time the sample was collected. Hair stable isotope ratios reflect diet during the time that hair was growing.In elk and white-tailed deer sampled in autumn, hair would represent from early August to mid-September based on when the hair color changes (Thomas and Toweill 1982; Hewitt 2011). Our own field observations confirmed that white-tailed deer were shedding in early September in our study areas (A. Coulson, personal observation). Although we expect that underfur would grow in sometime during the fall, we could not find any

literature that had measured when this growth took place; therefore we measured the stable isotope ratios of guard hair alone. Some of our hair samples were run without removing underfur, so for a subset of samples we measured the differences in stable isotope ratios of guard hair alone, underfur alone, and unsorted hair samples. Where there was a difference, we added a correction factor for unsorted hair samples to make their stable isotope ratios comparable to guard hair.

From each of our study areas we also collected samples of potential forage plants that could be consumed by ungulates. Using Geobase land cover data sets (Canadian Council on Geomatics 2000), we categorized potential sample locations in each study area as forest, wetland and grassland according to their covertype in Geobase and randomly selected 20 sample points in each covertype from each study area using QGIS software (QGIS Development Team 2012), with the additional constraint that sample pointswere within 50 meters of a road or trail.Because grassland made up less than 1% of the area of our Nipawin study area, we only collected plants from wetland and forest points there. We only collected samples from 7 grassland points in Hudson Bay becausegrassland made up only 2% of that study area and randomly generating more points would have resulted in sampling the same locations repeatedly.At each point we collected1 sample eachof the 3 most abundant graminoid and3 most abundant forb species, based on percent cover within a 0.5 m^2 quadrat, and1 sample of every woody species within 5 meters of each point. If there were less than 3 graminoid or forb species we collected a sample from each species present within the quadrat. We collected agricultural samples by randomly selecting roads using QGIS and then sampling from each field on either side of the road at random intervals between 1.6 and 14.4 km. We

supplemented these random samples with opportunistically collected agricultural plant samples (Figure 1, Table 1).

From our wild habitat samples, we randomly selected 5 points from each habitat in each study area and measured the stable isotope ratios of all plant samples collected from those points (samples from one Nipawin forest point were lost during processing). We supplemented these samples with samples haphazardly chosen from the remaining points. We measured the stable isotope ratios of all agricultural crop samples (Figure 1, Table 1).

We prepared muscle samples by freeze-drying, homogenizing using a mortar and pestle, and then removing lipids using a soxhlet apparatus (Roth 2003). We removed lipids because lipids are usually depleted in ^{13}C relative to other tissues, and lipid content can vary between samples (Post et al. 2007). To prepare hair samples for stable isotope analysis we washed them with soap and water, rinsed them thoroughly, dried them in a drying oven, and homogenized them using scissors. We rinsed plant samples with water, dried them at 60° C, and homogenized them using scissors and a mortar and pestle. We weighed subsamples on a microbalance (0.6 mg for muscle, 0.8 mg for hair, and 2.0 mg or greater for plants) and sent them to the University of Windsor Chemical Tracers Laboratory, where their carbon and nitrogen stable isotope ratios were measured on a continuous flow isotope ratio mass spectrometer.

Data Analysis

We used the Stable Isotope Analysis in R (SIAR) software package (Parnell et al. 2010) in R (R Development Core Team 2014) to estimate the proportion of plants from

each habitat in the diets of elk and deer for each study area. We first calculated the mean carbon and nitrogen stable isotope ratios of all plant samples collected at each wild sample point, and then combined those values to calculate stable isotope means and standard deviations of each wild habitat type in each study area. Because each agricultural sample came from a different field, we calculated the overall mean and standard deviation of agricultural plants for each study area. We then used the signatures for each habitat type (agriculture, forest, wetland, and grassland)as the source values in our mixing models. Limiting the number of sources to less than 5 allowed our mixing models to calculate more precise results so we could draw meaningful conclusions from those results. Grouping plant samples by habitat type allowed us to generate source polygons that spanned our adjusted consumer values for valid mixing models, to generate prior estimates from land cover data, and allowed our results to be comparable to other researchers studying habitat use. Using each species as a distinct source would have resulted in too many sources to perform a meaningful diet reconstruction, and if sources were grouped by plant type (i.e. graminoid, forb, woody) or simply wild and agricultural, consumer values fell outside of the source polygon(Phillips et al. 2014).

Because stable isotope ratios generally increase between the food source and the consumer, we corrected for this trophic discrimination by adding a correction factor to source stable isotope ratios (DeNiro and Epstein 1978; DeNiro and Epstein 1981). Published trophic discrimination values for muscle in large mammal herbivores commonly have the problem of inadequate time on the experimental diet to allow for complete turnover. The only published study to measure muscle trophic discrimination in a cervid was in reindeer (*Rangifer tarandus*), where animals were fed the experimental

diet for only 64 days (Halley et al. 2010), far shorter than the time required for complete turnover. Osorio et al. (2011) measured the muscle carbon and nitrogen trophic discrimination of domestic cattle (*Bos tauros*) fed on pasture for a full year, 2.3-2.7 half lives of carbon and nitrogen and corresponding to 80-85% turnover; they estimated carbon trophic discrimination as +3.2±0.8‰ (mean±SD) and nitrogen as+2.8±1.8. For our analyses, we used these values from cattle. For hair, we used trophic discrimination values also measured in cattle of +3.2±0.2‰ for carbon (Sponheimer et al. 2003b) and +2.5±0.5‰ for nitrogen (Sponheimer et al. 2003a). Although they are from a different family, Bovidae, cattle are a useful model for trophic discrimination in cervids because both bovids and cervids are ruminant digesters.

One advantage of a Bayesian approach is the ability to incorporate prior information into our model. We initially assumed each species would feed in each habitat in proportion to its availability, as both are numerous generalist herbivores. Withinthe convex hull of animal sample locations in each study area(the polygon formed by the most extreme locations in each area; Figure 1) we calculated the relative proportions of each habitat to use as our mixing model priors (Table 1). To represent the overall uncertainty in our priors we used a standard deviation of 0.05 for our prior estimate of the agricultural contribution, which would correspond to a 95% confidence interval of 0.40 (Inger et al. 2011) and indicate a low certainty in our priors. To test the sensitivity of our results to our priors we ran our mixing models 3 additional times with uninformative priors (all sources contribute equally to the diets) and with the same prior proportions but with much stricter (sd = 0.025) and much wider (sd= 0.10) standard deviations.

We used the standard ellipse, the bivariate analogue of the univariate standard deviation, of stable isotope ratios as a measure of diet variability because it is less sensitive to outliers than the area of the convex hull, the polygon formed by the most extreme stable isotope ratios of the consumer group(Jackson et al. 2011). To compare the distribution of isotopic signatures we used the Stable Isotope Bayesian Ellipses in R (SIBER) tools (Jackson et al. 2011) in SIAR to create posterior probability distributions of the area of the standard ellipses (i.e., isotopic niche breadth) of muscle and hair for each species in each study area. If increased consumption of agricultural plants decreased diet variability we should see a decrease in standard ellipse area (Figure 2a). Alternatively, incorporation of agricultural foods could just shift the distribution without affecting variability (Figure 2b). Furthermore, as type B generalists we expected deer to have a larger stable isotope standard ellipse in both tissues than type A generalist elk, especially in hair, which represents a shorter time period than muscle. Because differences between individual diets can be masked by changes in individual diets over time, Bearhop et al. (2004) predicted that type B generalists will have more variability in their stable isotope ratios from tissues representing shorter time periods and type A generalists will not. We therefore expected the white-tailed deer would have larger standard ellipse areas for their hair stable isotope ratios than for their muscle, but we would not see a tissue difference in elk.

To verify that changes in animal stable isotope ellipse size across study areas were not due to changes in the underlying differences in distribution of isotopic signatures among plants, we estimated the nitrogen and carbon ranges of our plant samples, and the mean distance to centroid of the plants from each habitat in each study

area (Layman et al. 2007) using SIBER (Jackson et al. 2011) and looked for differences that would confound our observations about animal standard ellipse area. For example, if we found that animal standard ellipse areas were larger in one area than in another, but plant nitrogen range, carbon range and mean distance to centroid were also larger, that would cast doubt on differences in diet causing the observed differences in animal standard ellipse areas.

All of the Bayesian techniques we used generate a series of possible solutions. We then used pairwise comparisons between series to calculate the proportion of solutions in which a prediction is true. This proportion is our P value for that comparison, but rather than using it to test for significance, it gives us the probability that our prediction is true.

Results

We tested the effect of year on deer and elk stable isotope ratios with MANOVA, controlling for species and study area. Year did not affect hair stable isotope ratios ($F_{2,135}$=0.07, p=0.93) and there were no significant interactions involving year (all p≥0.13). Because we had only 1 white-tailed deer muscle sample from our Nipawin study area in 2012 we excluded Nipawin samples from our test of the effect of year on muscle stable isotope ratios. Year did not have a significant effect on muscle stable isotope ratios ($F_{2,131}$=1.48, p=0.23), with no significant interactions involving year (p≥0.13). Therefore, years were combined for subsequent analyses.

White-tailed deer guard hair did not differ from underfur in either carbon (paired t-test, t=-0.94, n=6, p=0.39) or nitrogen (t=2.36, n=6, p=0.065) stable isotope ratios. However, elk guard hair differed from underfur in both $\delta^{13}C$ (t=-3.07, n=10, p=0.013)

and $\delta^{15}N$ (t=-5.62, n=10, p<0.001). Elk guard hair and unsorted samples differed in $\delta^{13}C$ (t=2.97, n=10, p=0.016) but not $\delta^{15}N$ (t=0.77, n=10, p=0.46). To correct for this difference in $\delta^{13}C$ we subtracted the mean difference (0.15‰) from the $\delta^{13}C$ values of unsorted elk hair samples (15 in Manitoba and 9 in Hudson Bay).

In all three study areas, the diets of both deer and elk varied and reflected a mixture of available food sources (Figure 3). Comparing the annual niche breadth of the two species, stable isotope standard ellipses (from muscle) were larger for deer than for elk in the Hudson Bay (p= 0.77) and Manitoba (p=0.99) study areas but did not differ in the Nipawin study area (p=0.42). Similarly, in early fall, standard ellipses (from hair) were larger for deer than for elk in the Hudson Bay (p= 0.84) and Manitoba (p>0.99) study areas but did not differ in the Nipawin study area (p=0.43) (Figure 4). It is possible that elk and white-tailed deer standard ellipses in Nipawin did not differ because the small sample size of elk led to a broad posterior distribution of ellipse area estimates for that species (Figure 5).

We measured stable isotope ratios in 409 plant samples from our three study areas (Appendix 2). Forest and agriculture were the most common habitats in each study area (Table 1). The proportion of agricultural sources in the annual diet of deer (based on muscle stable isotope ratios) varied by study area (Figure 6). Deer in the Nipawin study area, where 75% of the landscape is used for agriculture (Table 1), consumed more agricultural foods (mode 73%) than deer in the Hudson Bay area (mode 44%, p>0.99), where 35% of the landscape is used for agriculture, or in the western Manitoba area (mode 47%, p>0.99), where 42% of the landscape is agricultural, but there was no difference in the amount of agricultural plants consumed by deer in the Hudson Bay and

western Manitoba regions (Hudson Bay greater than western Manitoba p=0.40). We found a similar pattern in annual diet variability (isotopic niche breadth), with deer from Nipawin having smaller standard ellipses than deer from Hudson Bay (p=0.76) or Manitoba (p=0.90), and deer from Hudson Bay having a smaller standard ellipse than deer from Manitoba (p=0.80).

During early fall, white-tailed deer ate more agriculture in Nipawin (mode 73%) than in Manitoba (p>0.99, mode 47%) or Hudson Bay (p>0.99, mode 50%), and ate more agriculture in Hudson Bay than in western Manitoba (p=0.70). Similarly, the niche breadth of white-tailed deer in early fall was lower in Nipawin than in Manitoba (p=0.92) and Hudson Bay (p=0.70), and was lower in Hudson Bay than in Manitoba (p=0.91). Thus, in early fall isotopic niche breadth of deer decreased with increasing consumption of agricultural foods (Figure 6).

The annual diets of elk, reflected in muscle stable isotope ratios, also varied by study area (Figure 6). Elk ate more agricultural plants in Nipawin (mode 75%) than in Manitoba (mode 48%, p>0.99) and Hudson Bay (mode 42%, p=1.00), and in Manitoba than in Hudson Bay (p=0.83). Elk niche breadth (based on muscle) was greater in Nipawin than in Manitoba (p=0.74), but there were no other differences (Hudson Bay greater than Manitoba p=0.58 and Nipawin greater than Hudson Bay 0.59; Figure 6).

Early fall diet of elk, reflected in hair stable isotope ratios, also contained more agricultural foods in Nipawin (mode 75%) than in Hudson Bay (mode 44%, p=1.00) or Manitoba (mode 51%, p=0.99), and in western Manitoba than in Hudson Bay (p=0.86). However, measures of diet variability do not follow the same pattern. The early fall niche

breadth of elk was not lower in Nipawin than in Manitoba ($p=0.19$) or Hudson Bay ($p=0.33$), but was lower in Manitoba than in Hudson Bay ($p=0.70$).

Isotopic variability in plants was greater in Hudson Bay than in Manitoba (mean distance to centroid $p=0.92$, nitrogen range $p=0.93$, carbon range $p=0.76$), but did not differ among other study areas in ways that would interfere with our conclusions about diet variability differences between areas, as the plant isotopic variability in Nipawin was not greater than in Hudson Bay (mean distance to centroid $p=0.09$, nitrogen range $p=0.01$, carbon range $p=0.16$) or Manitoba (mean distance to centroid $p=0.49$, nitrogen range $p=0.13$, carbon range $p=0.40$).

White-tailed deer standard ellipses calculated from hair were larger than those based on muscle for each area (western Manitoba $p=0.95$, Hudson Bay $p=0.85$, Nipawin $p=0.79$), which would be expected since short-term diet variability (reflected in hair) is averaged out over the longer term (in muscle). However, elk stable isotope standard ellipses were not larger for hair than for muscle for the same area (western Manitoba $p=0.64$, Hudson Bay $p=0.68$, Nipawin $p=0.67$), suggesting their individual diets are more similar on longer timescales, with less seasonal variability (Figure 4). Deer in the Hudson Bay region ate more agricultural plants in the early fall than in the year overall ($p=0.87$), but we did not find any other temporal differences in diet ($0.40<p<0.52$).

In early fall, elk ate more from agricultural sources than white-tailed deer in western Manitoba ($p=0.74$) and Nipawin ($p=1.00$), but white-tailed deer ate more in Hudson Bay ($p=0.83$). On an annual timescale, elk ate more from agricultural sources than deer in Nipawin ($p=1.00$) but not in western Manitoba ($p=0.62$) or Hudson Bay ($p=0.33$).

We tested the sensitivity of our conclusions to the priors by running our mixing models again using uninformative priors, strict priors where the prior standard deviation was reduced by half, and vague priors where the prior standard deviation was doubled. The pattern of deer eating the most agricultural food in early fall in Nipawin, followed by Hudson Bay and western Manitoba respectively held for weaker priors, but not for uninformative priors (Table 2).

Discussion

The magnitude of the agricultural subsidy in the diets of elk and white-tailed deer is striking. Agricultural sources made up at least 40% of their diets in both an annual and late fall timescale, and were as high as 80% in the Nipawin area. In early fall elk ate more from agricultural sources than deer in western Manitoba and Nipawin, but deer ate more in Hudson Bay. On an annual time scale, elk from Nipawin also ate more from agricultural sources, although these results have to be interpreted cautiously due to low sample size, but we found no significant species differences in agricultural consumption in western Manitoba and Hudson Bay. Nevertheless, in all three areas, both species, and both time scales, agricultural plants are a large subsidy.

Where the diets of white-tailed deer in our study areas included more agricultural sources, the variability of diets was lower in early fall. For elk, diet variability (niche breadth) was unrelated to the proportion of agricultural sources in the diet. These results suggest that populations of white-tailed deer may respond differently than elk to increased availability of agricultural foods. For white-tailed deer, more individuals may become specialists on agricultural food sources, resulting in an overall increase in

average consumption of crops and a decrease in niche breadth (Figure 2a), whereas in elk, many individuals increase the proportion of agriculture in their individual (generalist) diets (Figure 2b). However, white-tailed deer show less diet diversity where they were eating more of a subsidized resource only in early fall. For deer, the relative importance of the subsidy may be greater in fall, when the nutritional content of browse starts to decline but the nutrition available from agricultural sources is peaking.

Concentrated food sources contribute to the spread of disease in cervid populations, including chronic wasting disease and bovine tuberculosis (Miller et al. 2003; Conner et al. 2008; Sorensen et al. 2013). In the areas we studied, both deer and elk make extensive use of agriculture, a concentrated food source, and the use of this resource subsidy probably contributes to the spread of either disease in its respective areas. Because the diet variability in early fall in deer populations is lower where they consume more agricultural plants, early fall may be a critical time for disease transmission in white-tailed deer. This early fall time period also immediately precedes the rut, when contact rates between white-tailed deer increase (Kjær et al. 2008), suggesting that the entire fall is a time of elevated disease transmission in white-tailed deer. Interestingly, consumption of agricultural plants was highest in both species in the Nipawin area, where prevalence of chronic wasting disease is also highest (Bollinger et al. 2011).

Elk stable isotope standard ellipse sizes were very similar between the two tissues, indicating very little seasonal variation in diet variability among individuals. White-tailed deer hair stable isotope standard ellipses were larger than muscle standard ellipses, showing more diet variation between individuals during the early fall. Because

the time period represented by hair is shorter than that represented by muscle, hair is essentially a smaller sample of the animal's diet and so we would expect more variability in the hair stable isotope signatures even without the underlying diet differences.

Diet variability was greater for white-tailed deer than elk, both during early fall and annually, for the two study areas with sufficient sample sizes for precise estimation of standard ellipse area (Jackson et al. 2011; Figure 5). These results match the predictions of Bearhop et al. (2004) about stable isotope variability in type A generalists (all individuals consume a wide range of resources) and type B generalists (different individuals specialize on different food sources). The type A generalist in our study, elk, had a smaller standard ellipse than the type B generalist, white-tailed deer, in both tissues. The type A generalist had standard ellipses that were the same area for both tissues, while the type B generalist had a larger standard ellipse in the tissue representing the shorter time period. Type B generalists have larger ellipses in tissues representing shorter time periods because the shorter time period tissue is taking a smaller sample of the animal's diet, so there is less opportunity for individual diets to change and average out differences between individuals. Meanwhile, type B generalists have similar standard ellipse areas for all tissue types, because variation between individuals is smaller and it is easier for it to be averaged out over all time scales (Bearhop et al. 2004).

Bearhop et al. (2004) also predicted that species with larger home ranges would show more diet variability than species with smaller home ranges, since they would have a wider variety of sources available within their home range. Our results contradict this prediction, since deer have a smaller home range than elk (Brook and Mclachlan 2006; Edye and Bayne 2008) but showed more diet variability. Although both use a variety of

habitats, elk have stricter habitat requirements than white-tailed deer; elk are essentially type A generalists in their habitat use while deer are type B(Sorensen 2014).Although isotopic differences between habitats can obscure differences in diet when consumers forage between different habitats (Flaherty and Ben-David 2010), our research gets around this concern by measuring consumption from different habitats explicitly, and our diet results reinforce what is known about species differences in habitat use.

Two previous studies have used rumen content analysis to examine the diets of elk in western Manitoba, one of them in comparison with white-tailed deer diets. Garrod et al. (1978) analysed the rumen contents of elk and deer killed by hunters and automobile collisions throughout the year. They found high amounts of barley, an agricultural crop, in the rumens of both elk and deer. In deer, they also found high variability in the amount of agricultural plants in deer rumens, from none to almost entirely barley, again showing a variety of individual diet specializations in white-tailed deer. On the other hand, Mcintosh and Murray (2004) examined rumen contents of elk culled inside Riding Mountain National Park in the winters of 2003 and 2004, and found no evidence of agricultural consumption. This observation is inconsistent with our results, but also comes from a period of the year that is poorly represented in our muscle stable isotope data. Furthermore, the short time period represented by rumen content analysis (Spalinger et al. 1986)combined with the protected area where these rumens were collected suggests that it might not be surprising that their most recent meals did not include resources that would only be available outside of the protected area.

Tissue turnover in muscle is a continuous process and complete turnover takes over a year in large mammalian herbivores (Sponheimer et al. 2006; Bahar et al. 2009).

Both white-tailed deer (DelGiudice and Mech 1992) and elk (Gates and Hudson 1981) have an annual cycle of losing body mass over the winter until spring, and then gaining weight again until the next winter. Black-tailed deer (*Odocoileus hemionus sitkaensis*) lose 10-15% of their protein reserves as part of this annual cycle (Parker et al. 1993), so it is reasonable to assume that some of the mass lost and gained over the course of a year is muscle. This loss and gain accelerates the turnover of stable isotopes in muscle tissue, so while the stable isotope ratios of muscle represent a time period of approximately the past year, the diet during the most recent growing season is overrepresented. In our study, this overrepresented time period corresponds the time period represented by our plant samples, and thus is less of a concern.

When running our mixing model both with uninformative priors and with strict priors, the pattern of white-tailed increasing agricultural consumption with decreasing standard ellipse size disappeared (Table 2). High prior standard deviations indicate a low degree of certainty in our priors, which we considered appropriate given the rather weak source of our prior information. Low certainty in our prior model allows the data we collect (animal and plant stable isotope values) to exert a stronger influence on the results (Parnell et al. 2010). Detecting this pattern only with relatively weak priors shows the value of incorporating prior knowledge into our mixing model, and that our results were not due to overwhelming our data with strong priors.

Darr & Hewitt (2008) measured trophic discrimination in white-tailed deer, but using those values to correct for trophic discrimination would have created some troubling inconsistencies: in all three study areas and in both species, hair stable isotope ratios would have been over 2‰ outside the convex hull of mean plant stable isotope

ratios. We used hair trophic discrimination values measured in cattle hair (Sponheimer et al. 2003b; Sponheimer et al. 2003a) instead of those measured in white-tailed deer by Darr and Hewitt (2008) because the stable isotope ratios of the diets in that study better matched the plants available in our study areas. Darr and Hewitt (2008) fed a diet that included corn (*Zea mays*) as a carbohydrate source, a source of simple carbohydrates that can disrupt the digestive system of ruminants and is not representative of the diet of a wild animal (Wobeser and Runge 1975).

Wild ungulate diets are very frequently studied in isolation, or as a simple comparison between sympatric species (e.g., Garrod et al. 1978, Kirchhoff and Larsen 1998, Mcintosh and Murray 2004). Such studies have provided useful information to wildlife managers, but have led to a great body of literature cataloguing diets for a wide array of species and locations that is very cumbersome for predicting diets in new locations. Few studies have looked at general patterns of consumption by herbivores.

Many stable isotope diet studies of herbivores have had the advantage of dramatic, clear differences in the stable isotope signatures that can be predicted a priori; for example, estimating the contributions of a predominantly C_3 wild habitat and a predominantly C_4 agricultural source (Walter and Leslie 2009) or differences between C_4 grasses and C_3 shrubs to estimate the amount of grazing or browsing in animals' diets (Vogel 1978). Our study areas were too far north for differences in $\delta^{13}C$ between C_3 and C_4 plants to indicate grazing versus browsing reliably, as our study areas contained abundant C_3 grasses and few C_4 grasses (Tieszen et al. 1997; Collatz et al. 1998). Because maize (a C_4 plant) is not a common crop in these areas (Statistics Canada 2011a, Statistics Canada 2011b) we could not use the characteristic differences in $\delta^{13}C$ values

between C_3 and $C_4$to indicate agricultural consumption. Other influences on plant isotopic signatures could include amount of canopy cover, soil moisture, or artificial fertilizers. In our study, the $\delta^{13}C$ value of plants in closed canopy forests should be higher relative to more open habitats such as grassland and agricultural fields, and some wetland habitats (France 1996; Buchmann et al. 1997). We found the opposite pattern, with agriculture the most enriched in ^{13}C, followed by grassland and wetland, with forest the most depleted except in Nipawin, where wetland was more depleted than forest (Figure 3). Increasing soil moisture allows plants to keep their stomata more open, allowing more CO_2 exchange leading to a more depleted $\delta^{13}C$ in wetland habitats (Saurer et al. 1997). Because of artificial nitrogen fertilizer use, we expected agricultural plants to have enriched $\delta^{15}N$ values due to the use of nitrogen fertilizer and for nitrogen-fixing plants to have $\delta^{15}N$of around 0 relative to atmospheric nitrogen (Szpak et al. 2014). In all of our study areas, agricultural plants were more enriched in ^{15}N than plants from wild habitats (Figure 3; Appendix 2).

Management Implications

When carnivores cause livestock damage, management recommendations suggest targeting individuals or groups of individuals causing the damage, rather than reducing the population as a whole (Blejwas et al. 2002). Hegel et al. (2009) suggested a similar approach of targeting control efforts on the small subpopulations of elk responsible for the most damage to crops. Our results suggest that in the areas we studied individual deer specializing in agricultural crops might be selectively targeted to reduce agricultural

damage. Elk, as individual generalists, are less likely to have individual specialists that could be removed.

Controlling disease in wild cervid populations often takes two forms: reducing host population density through increasing hunting pressure, especially on females (Blanchong et al. 2002), and reducing apparent density through removal of concentrated feeding sites (Miller et al. 2003). Agricultural crops can act as both a subsidy, providing 40-80% of the diet of elk and deer in our region and increasing their population sizes, and as a concentrated food source, bringing individuals into close proximity. Successfully controlling agricultural feeding might have the double effect of not only reducing apparent density through removal of concentrated feeding sites, but also reducing overall density by reducing the subsidy. The practical considerations of achieving a dramatic enough reduction in agricultural feeding remain daunting, however (Walter et al. 2010).

We have shown that different patterns of individual diets within a population can result in apparently similar population-level diets, with implications for management of wildlife disease and crop damage. Furthermore, our results also show the value of combining traditional diet reconstruction using stable isotope ratios and isotopic niche metrics. Niche metrics such as standard ellipse size not only allow for hypothesis testing when source stable isotope data are unavailable, but can also allow more refined conclusions about consumer diet when source data are available.

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Table 1 The proportion of land belonging to each habitat type within the convex hull of animal sample locations, as well as the number of plant sampling locations and the number of plant samples from each habitat used to calculate source values.

Study Area		Agriculture	Forest	Wetland	Grassland	Total
Western Manitoba						
	Relative area	0.42	0.47	0.07	0.04	1.00
	Sample locations	31	6	5	5	47
	Samples	42	38	34	49	163
Hudson Bay, SK						
	Relative area	0.35	0.51	0.12	0.02	1.00
	Sample locations	32	6	12	7	57
	Samples	34	29	44	37	144
Nipawin, SK						
	Relative area	0.75	0.21	0.04	-	1.00
	Sample locations	34	4	6	-	44
	Samples	51	11	30	-	92

Table 2 Comparisons of white-tailed deer agricultural consumption in early fall (reflected in hair isotopic signatures) in different study areas under various prior beliefs about the early fall diet of white-tailed deer. Values represent the probability that the comparison is true (Bayesian p-values) under each prior.

Agricultural plant consumption in	**uninformative priors**	**weak priors (sd=0.1)**	**prior (sd=0.05)**	**strong priors (sd=0.025)**
Nipawin > Hudson Bay	0.14	0.65	>0.99	1
Hudson Bay > Manitoba	0.89	0.86	0.70	0.14
Nipawin > Manitoba	0.58	0.88	>0.99	1

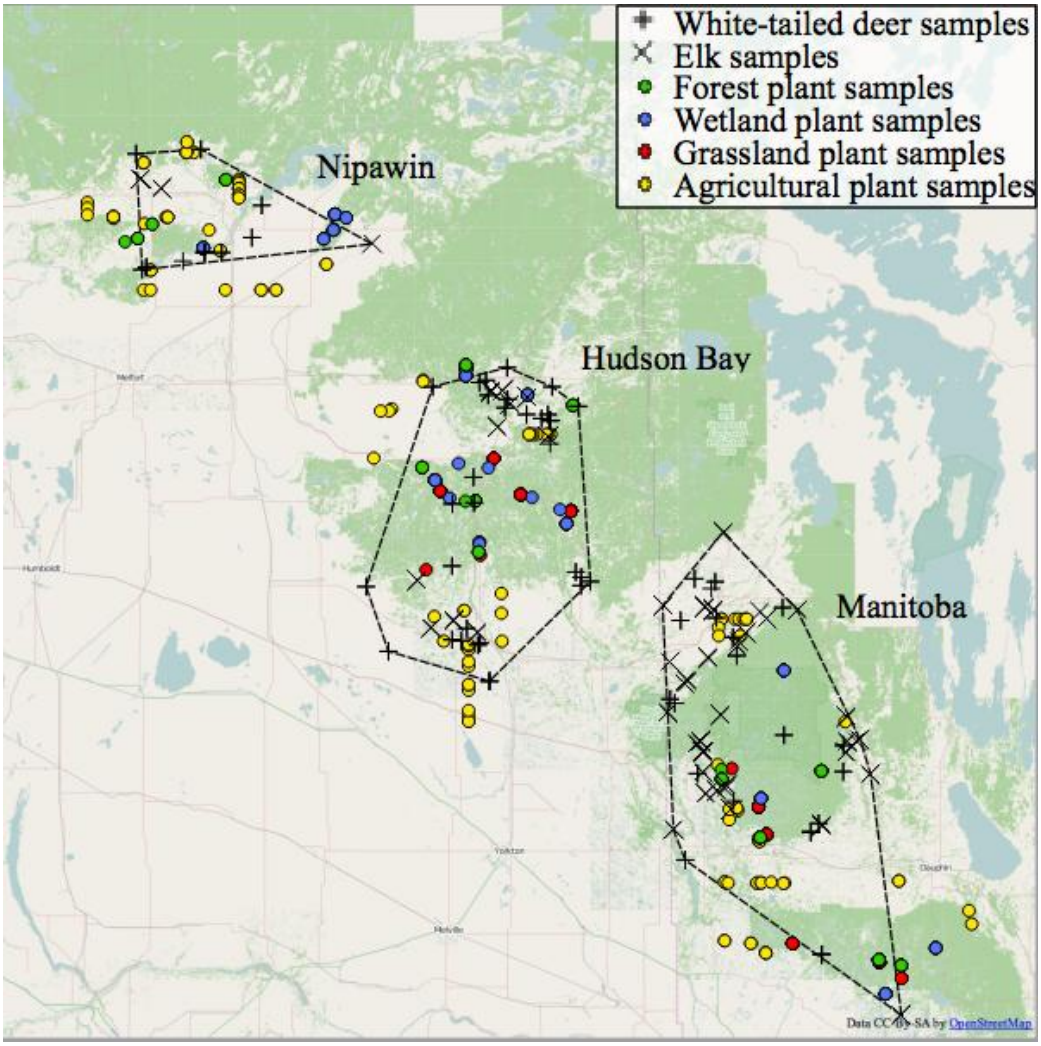
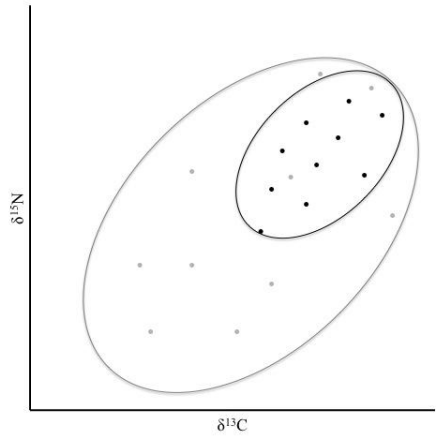


Figure 1 Elk, deer and plant sample locations along with convex hulls of animal sample locations from each study area.

a.



b.

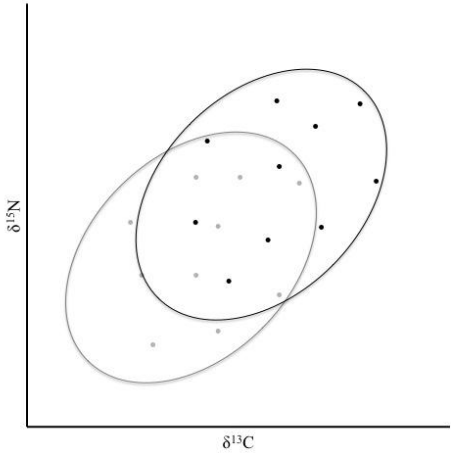


Figure 2 Predicted responses of (a)aspecies that increases agricultural consumption by more individuals specializing on agriculture and (b) a species made up of individual generalists increasing the proportion of agriculture in their diet. Grey points and ellipses represent diets low in agricultural food, and black represents diets higher in agricultural food. For the purpose of these figures, we assume agricultural sources are more enriched in both ^{15}N and ^{13}C.

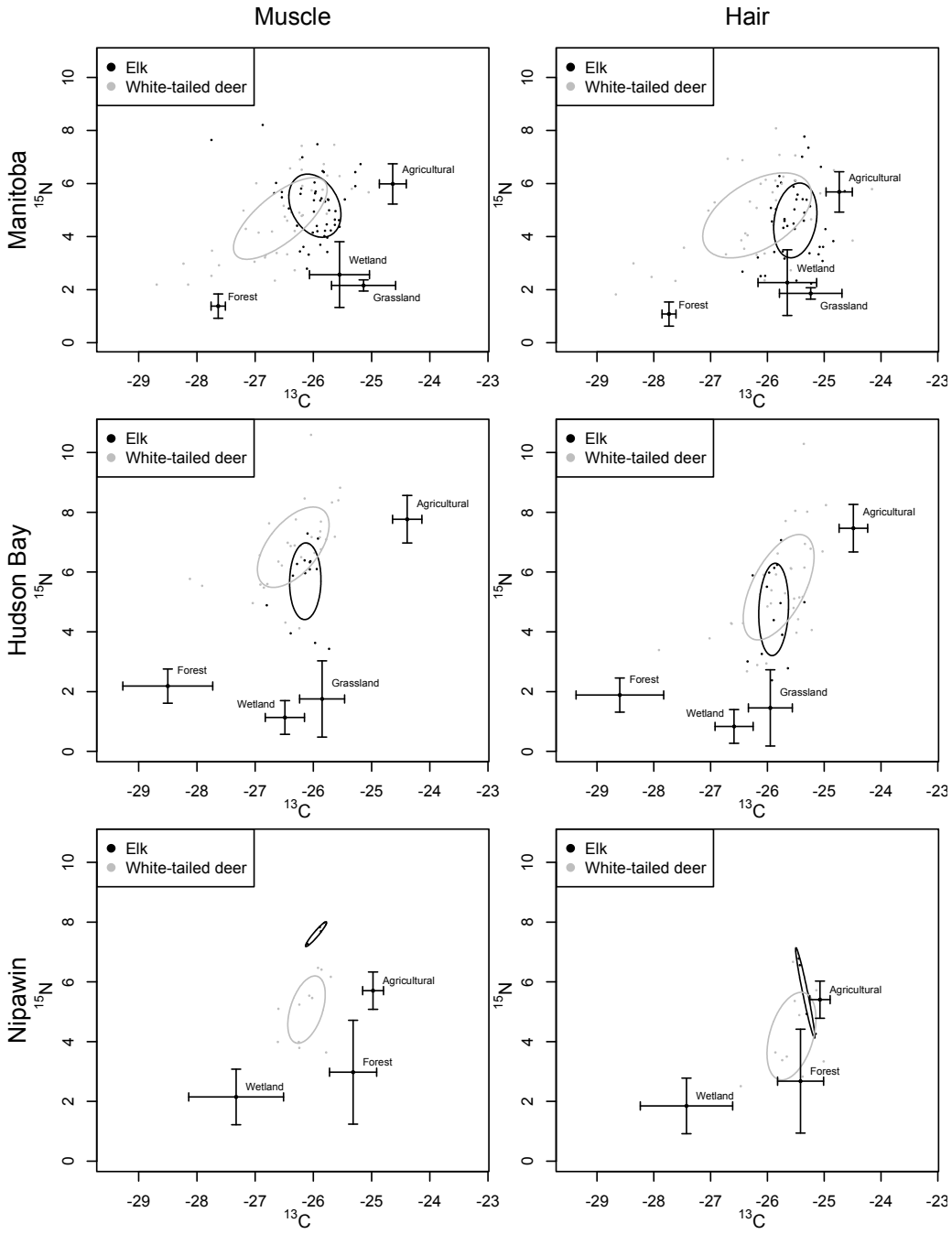


Figure 3 Carbon and nitrogen stable isotope ratios of elk and white-tailed deer hair and muscle with standard ellipses, as well as means and standard errors of plant groups in their diet.

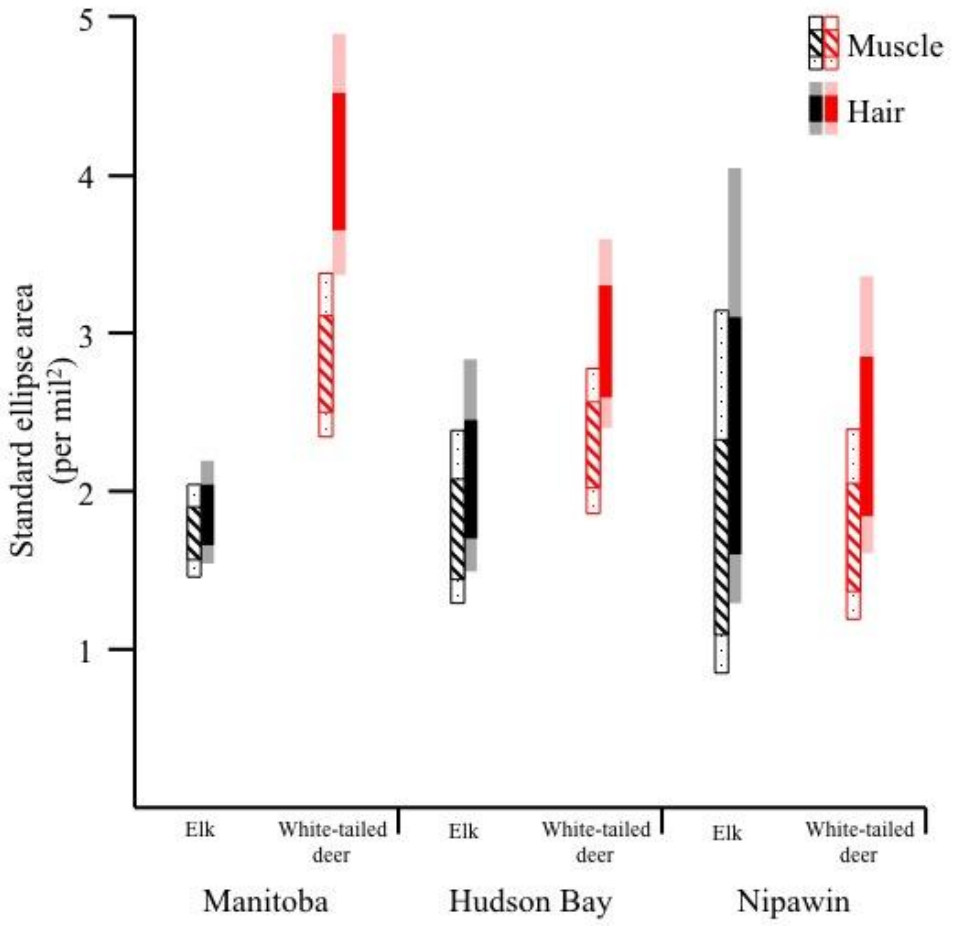


Figure 4 Credibility intervals (50 and 75%) for the standard elliptical areas of the carbon and nitrogen stable isotope ratios of elk (in black) and white-tailed deer (in red) muscle and hair in the three study areas.

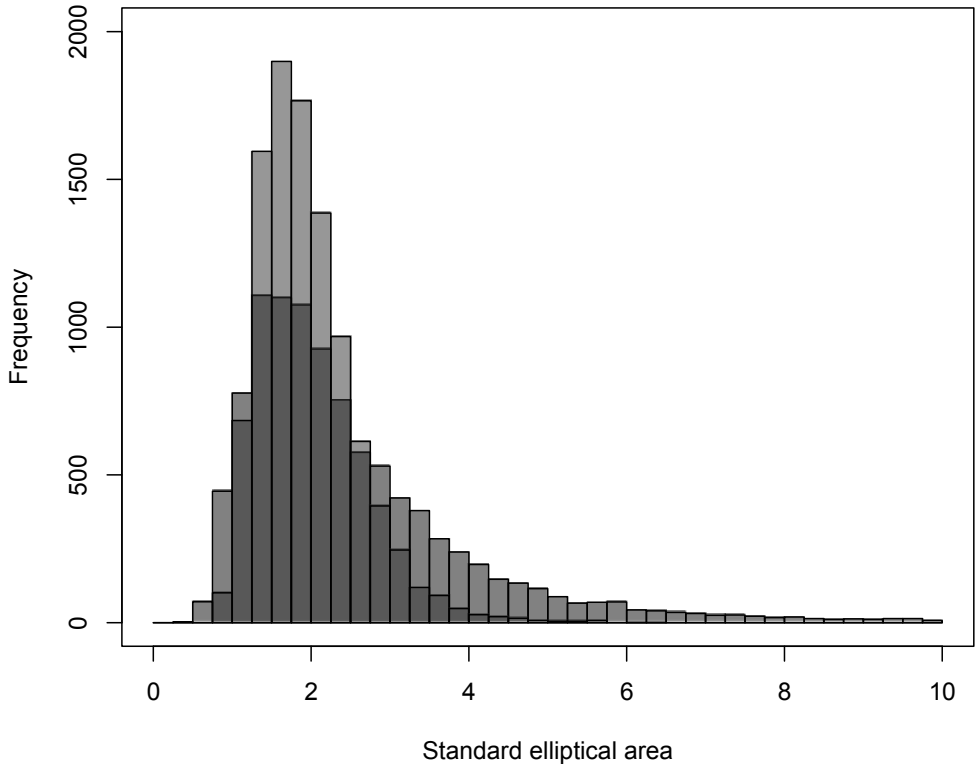


Figure 5 Histogram of the posterior distribution of muscle stable isotope standard elliptical areas for elk (dark grey) and white-tailed deer (light grey) in the Nipawin study area.

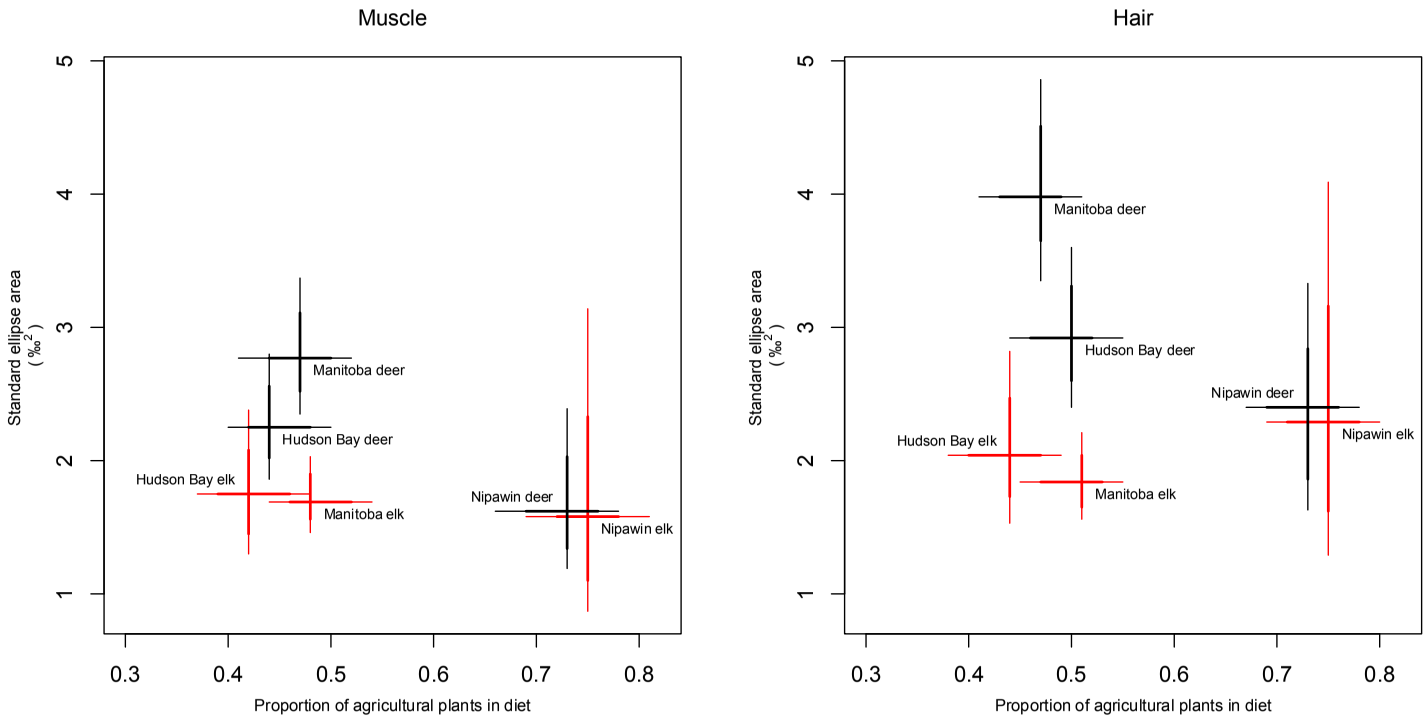


Figure 6 Relationship between isotopic niche breadth and agricultural feeding in the three study areas for white-tailed deer and elk hair and muscle samples. Error bars represent 50% and 75% credibility intervals.

Appendix 1. Variation in diet of elk and deer reflected in stable isotope ratios of hooves

Introduction

The stable isotope ratios of tissues of animal tissues record the stable isotope ratios in their diets when that tissue was formed (Tieszen et al. 1983). Some tissues, such as fur, form during a discrete period and record the diet during that period. Others, such as muscle, blood or liver, are continuously regenerated andrecord a rolling average of diet over the time period leading up to sampling (Dalerum and Angerbjörn 2005). Some tissues grow continuously but are inert after formation; these tissues record a timeline of the animal's diet in their stable isotope ratios. Tissues used like this include baleen (Mitani et al. 2006) and hooves (Barnett 1994; Kielland 2001; Harrison et al. 2007; Walter and Leslie 2009).

We measured the stable isotope ratios of elk and white-tailed deer hooves to examine changes in diet over time. Food availability and quality declines greatly in the winter for these animals, as does their body mass(Gates and Hudson 1981; DelGiudice and Mech 1992) so we expected to see a starvation effect of increased $\delta^{15}N$ during the winter months in at least some animals. We also expected juveniles' nitrogen stable isotope ratios to start out high and then decrease, as they initially acquire all their nutrients from their mother, essentially feeding at a higher trophic level, and as they weaned their diet would shift to the same trophic level as other elk or deer. We also expected the stable isotope ratios of our hoof samples that corresponded with the month of September to be similar to the values from hair from the same animal, since both tissues are keratinous and represent the time period.

Methods

We assumed a growth rate of 8mm per month for juvenile deer and 10mm per month for adult deer (Miller et al. 1986) and estimated that the growth rate for elk would also be 10mm per month, based on data from white-tailed deer (Miller et al. 1986), moose (Kielland 2001), caribou (Barnett 1994) and cattle (Harrison et al. 2007). We took samples from the right claw of the right hind foot for consistency between individuals. Because the rate of hoof wear is higher in the front hooves of males (Bubenik et al. 1978) and we wanted to avoid the possibility of any sex-specific compensatory growth influencing our results. We cleaned the hooves with soap and water.We used the monthly growth rate to calculate the distance from the cuticle for our first samples to be in the month of September, roughly simultaneous with when the hair samples from that individual were growing. Further samples were then taken above (when possible) and below at 1-month (8 or 10 mm) intervals. Samples were 1 month (8 or 10 mm) long and between 2 and 4mm thick and were collected using a coping saw. We washed the monthly samples again using soap and water, and homogenized them using a cryomill. We sent 0.8mg subsamples to the University of Windsor Chemical Tracers Laboratory to measure their carbon and nitrogen stable isotope ratios. We made three comparisons with hoof stable isotope ratios: between hoof samples to examine changes in diet throughout the year; between hair and the hoof sample corresponding to the month of September because these samples represent the same time period; and between muscle and hoof samples because muscle stable isotope ratios represent an average diet over a similar time period to the monthly diets represented by hoof stable isotope ratios.

Results

We obtained 4 white-tailed deer hooves (3 adult males and 1 juvenile female) from the western Manitoba study area and 5 elk hooves (4 adult female and 1 juvenile male) from the Hudson Bay, Saskatchewan study area. Due to this very small and very unbalanced sample we were unable to draw statistically valid conclusions about species, sex, age or location based differences in annual diet variation. Instead, we visually examined the data.The data suggests that neither adult elk (Figure A1.1) nor adult deer (Figure A1.2) consistently showed elevated nitrogen stable isotope ratios during the winter months, and the two juveniles did not show decreasing nitrogen ratios (Figure A1.3). In elk, the hoof $\delta^{13}C$ value from September was 0.5‰ less than the value for hair (matched pairs t-test, $t=-10.63$, $df=4$, $p<0.001$) but there was no significant difference in $\delta^{15}N$ ($t=-1.24$, $df=4$, $p=0.28$).

Discussion

Although we did not have the samples to perform statistical hypothesis testing, there were interesting characteristics to our results. All of the adult female elk showed elevated $\delta^{13}C$ values around the month of May (Figure A1.1), suggesting diet changes in that time. The absence of elevated $\delta^{15}N$ values during the winter months suggests that either a diet change is masking any starvation effect or these elk were finding sufficient food over the winter. The lack of decreasing $\delta^{15}N$ in juveniles is interesting, but with only a single individual from each species it is difficult to draw conclusions. The similarity between elk hoof and muscle $\delta^{15}N$ (Figure A1.1) is interesting, since muscle represents

an average of diet over a similar time period as the hoof, suggesting similar trophic discrimination values between those two tissues.The difference in $\delta^{13}C$ between hoof and hair is useful because it indicates a difference in trophic discrimination values between the two tissues, though it is possible that the difference is also due to temporal mismatch due to inaccurate estimates of hoof growth rate.

Caribou hoof growth rate has high seasonal variation (Barnett 1994). Although we did not account for seasonal variability in growth rate, it likely is a factor in both elk and white-tailed deer. Miller et al. (1986) measured growth rates in captive white-tailed deer; measuring the growth rates in wild animals with their higher activity levels and nutritional stress would capture seasonal variability in growth rate. Accounting for seasonal variability in growth would improve the temporal resolution of diets reconstructed using hoof stable isotope analysis. Further study of using hoof stable isotope values and of the growth rate of those hooves would be fruitful avenues of research.

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Figures

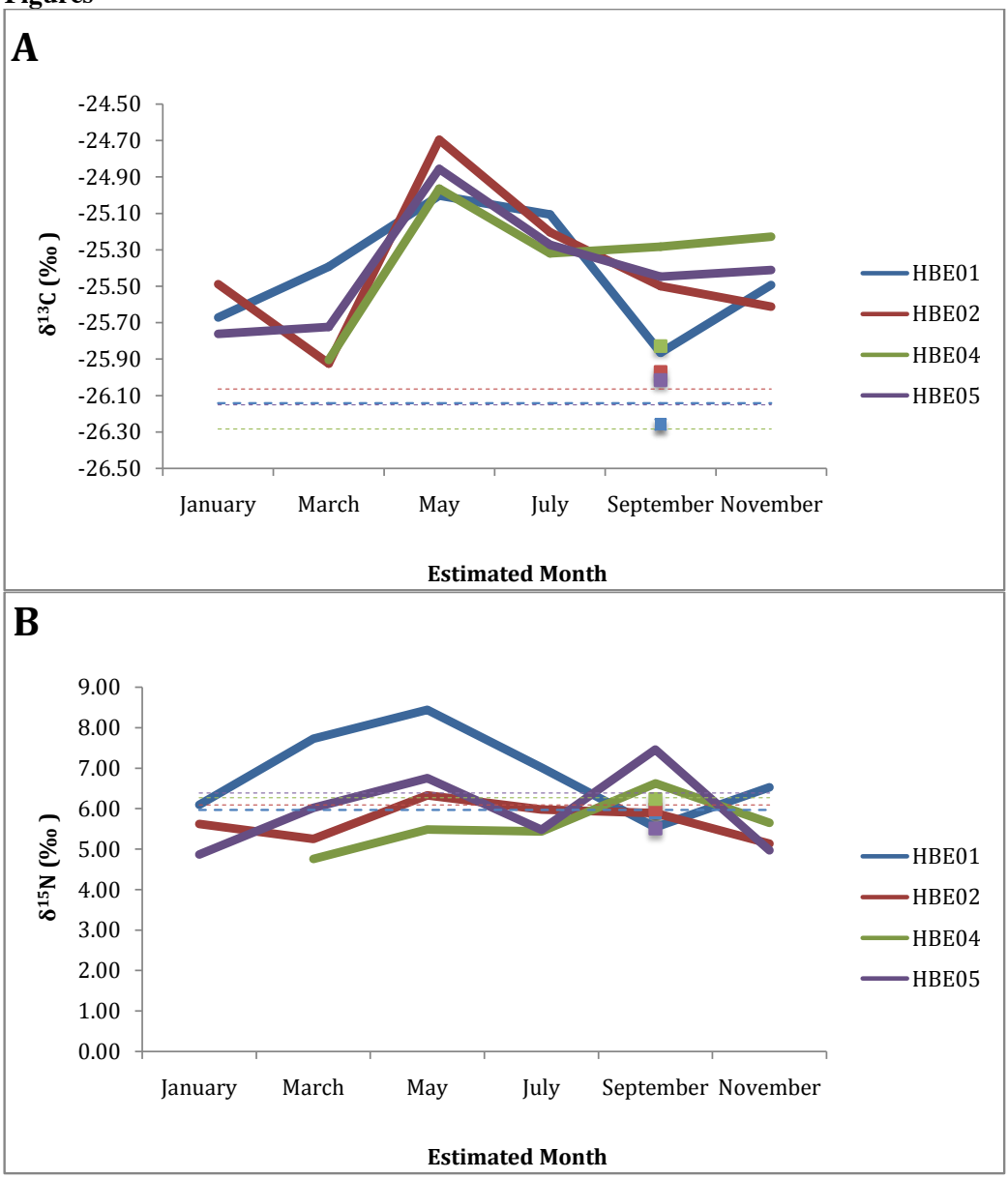

Figure A1.1 Stable isotope ratios of A) carbon and B) nitrogen in hooves (solid lines), muscle (dotted lines) and hair (points) of four adult female elk from near Hudson Bay, Saskatchewan.

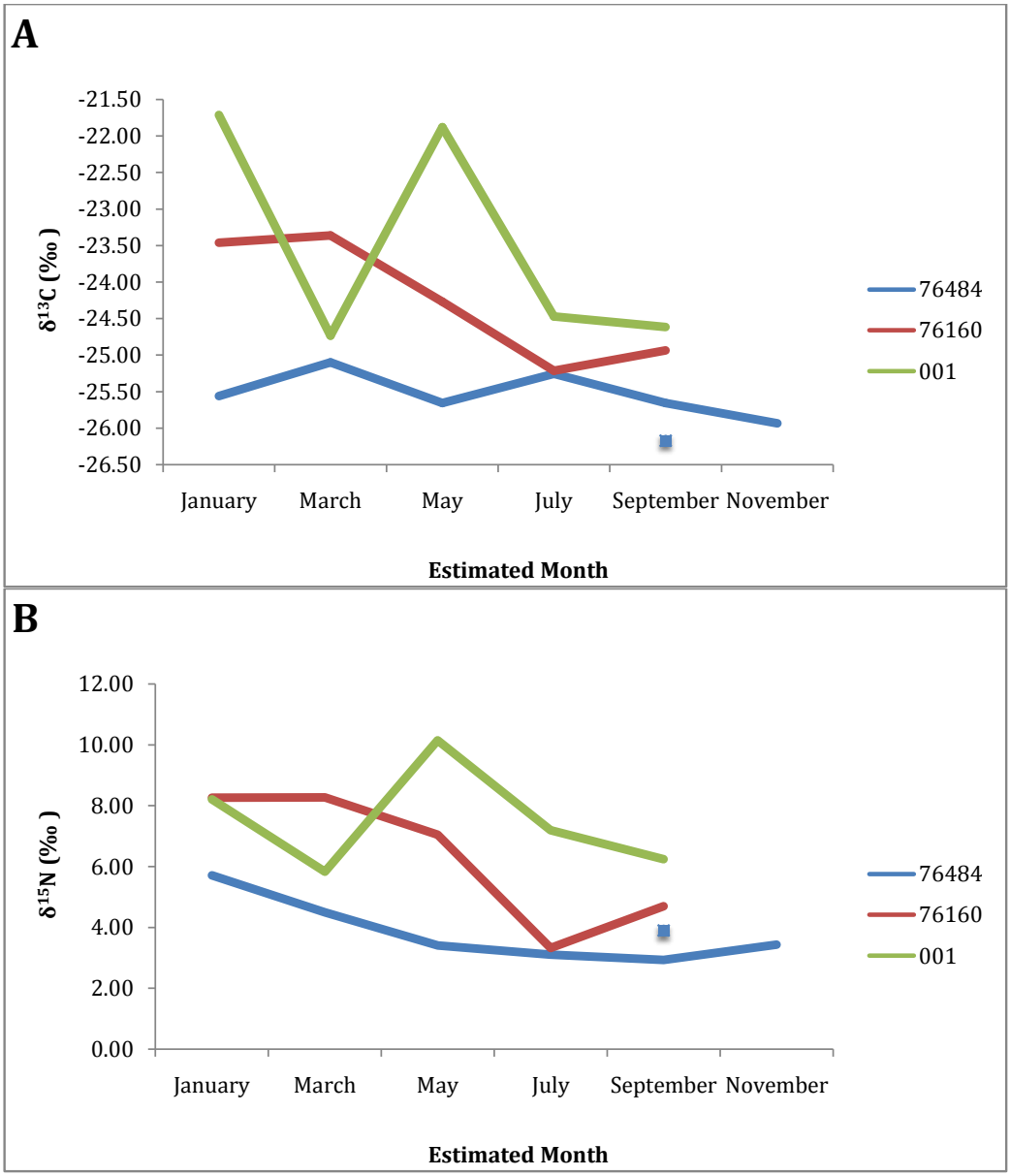

Figure A1.2 Stable isotope ratios A) carbon and B) nitrogen of hooves (solid lines) and hair (single point) from three adult male white-tailed deer in western Manitoba.

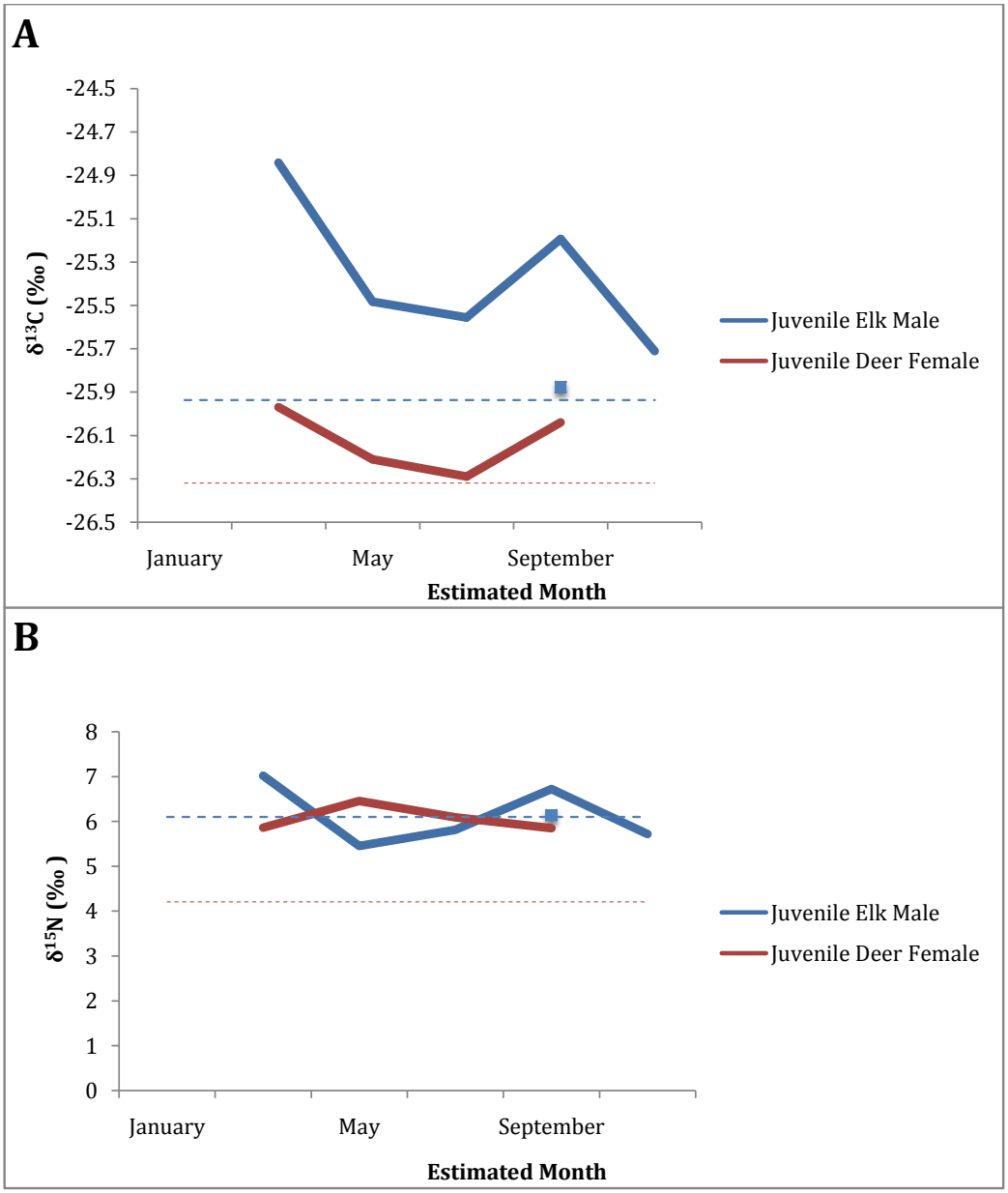

Figure A1.3 Stable isotope ratios of A) carbon and B) nitrogen in hooves (solid lines), muscle (dotted lines) and hair (points) of a juvenile male elk from near Hudson Bay, Saskatchewan and a juvenile female white-tailed deer from western Manitoba.

Appendix 2.Variation in stable isotope ratios among plants

Differences in plant stable isotope ratios could be caused by differences among species, as well as habitat, study area, or growth form. To examine potential influences on plant isotopic signatures we first compared stable isotope ratios of agricultural and wild plants using a 2-way ANOVA to control for study area. Agricultural plants differed significantly from wild plants in $\delta^{13}C$ (ANOVA $F_{1,393}=75.60$, $p<0.001$) and $\delta^{15}N$($F_{1,393}=133.91$, $p<0.001$).Study area significantly affected$\delta^{13}C$ ($F_{2,393}=3.55$, $p=0.030$) but not$\delta^{15}N$ ($F_{2,393}=2.35$, $p=0.10$). The interaction between the agricultural status of a sample and study area significantly affected$\delta^{15}N$ ($F_{2,393}=4.21$, $p=0.016$) but not $\delta^{13}C$ ($F_{2,393}=0.79$, $p=0.45$).Overall, agricultural plants were 1.81‰ more enriched in $\delta^{13}C$ and 4.32‰ more enriched in $\delta^{15}N$, on average.For subsequent analyses we excluded agricultural plants to examine the effects of species, habitat (forest, grassland, or wetland), study area, and growth form (woody, forb, or graminoid) on wild plants.

Because of the large number of species relative to our sample size, we could not test the combined effects of species, habitat, study area, and growth form. Testing species alone, species exerted a significant effect on $\delta^{13}C$ ($F_{84,167}=2.86$, $p<0.001$) and $\delta^{15}N$ ($F_{84,167}=1.47$, $p=0.0183$; Table A2.1). In a test of habitat and growth form, $\delta^{13}C$ values were significantly affected by both habitat($F_{2,265}=15.22$, $p<0.001$; Figure A2.1) and growth form ($F_{2,265}=23.01$,$p<0.001$; Figure A2.2), but the interaction was not significant ($F_{4,265}=2.28$, $p=0.061$).$\delta^{15}N$ values differed among growth forms ($F_{2,265}=6.86$, $p=0.001$) but not habitats ($F_{2,265}=0.80$, $p=0.45$), and their interaction likewise was not significant ($F_{4,265}=1.63$, $p=0.17$). Because we did not collect grassland sample points in the Nipawin study area, we excluded that habitat to test for the combined effects of habitat, growth form and study

area. In this model,stable isotope ratios were affected by growth form (carbon $F_{2,170}$=17.33, p<0.001; nitrogen $F_{2,170}$= 8.61, p <0.001) and the interaction between habitat and study area (carbon $F_{2,170}$=28.42, p<0.001; nitrogen $F_{2,170}$=3.73, p=0.026).Stable isotope ratios were not affected by habitat (carbon $F_{1,170}$=3.91, p=0.067; nitrogen $F_{1,170}$=0.15, p=0.70), study area (carbon $F_{2,170}$=1.15, p=0.32; nitrogen $F_{2,170}$=1.54 p=0.22), the interaction between study area and growth form (carbon $F_{2,170}$=1.15, p=0.32; nitrogen $F_{2,170}$=1.54 p=0.22), the interaction between habitat and growth form (carbon $F_{2,170}$=0.67, p=0.51; nitrogen $F_{2,170}$=1.31 p=0.27) or the interaction between all three main effects (carbon $F_{4,170}$=1.23, p=0.30; nitrogen $F_{4,170}$=1.17 p=0.32). The interaction between study area and habitat is due to forest and wetland having opposite $\delta^{13}C$ values relative to each other in Nipawin compared to their $\delta^{13}C$ values in the other two study areas, and the variation of wetland $\delta^{15}N$ values between study areas (Figure A2.1).

Table A2.1 Carbon and nitrogen stable isotope ratios and concentrations of all plant samples used for diet reconstruction. Also shown are the habitats each sample was collected in: agricultural (A), forest (F), grassland (G), or wetland (W). Growth form is listed for wild plants (not agricultural): woody shrubs and trees (W), forbs (F) and graminoids (G). Latitude and longitude reflect the location where each sample was collected. Samples identified as hay were collected from hay bales.

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Western Manitoba								
Achillia millefolium	-30.91	44.65	1.45	1.09	G	F	50.87930	100.85332
Achillia millefolium	-30.22	43.68	-1.80	1.26	W	F	50.86301	100.04064
Agrimonia striata	-28.37	40.80	2.57	4.64	W	F	50.69816	100.32537
Agropyron trachycaulum	-29.38	39.85	-0.46	1.70	G	G	50.81156	100.35923
Agrostis scabra	-29.93	44.50	-1.09	1.42	F	G	51.49301	100.68957
Alnus rugosa	-28.70	50.70	-1.45	1.92	F	W	50.82090	100.36314
Alnus rugosa	-31.71	46.66	-1.39	2.94	F	W	51.49301	100.68957
Alnus rugosa	-26.01	47.64	-1.77	2.10	W	W	50.86301	100.04064
Amelanchier alnifolia	-30.38	48.87	-1.62	2.85	F	W	50.82090	100.36314
Amelanchier alnifolia	-28.49	48.81	0.00	1.66	G	W	50.81156	100.35923
Amelanchier alnifolia	-30.60	47.53	-1.01	1.29	G	W	50.81156	100.35923
Amelanchier alnifolia	-28.97	50.41	-1.45	1.32	W	W	50.82056	100.36376
Aralia nudicaulis	-32.51	40.00	-1.71	2.07	F	F	51.25786	101.03620
Betula occidentalis	-28.97	52.18	-2.50	1.86	W	W	51.84710	100.90259
Bromus inermis	-28.44	47.34	-0.42	1.46	W	G	50.82056	100.36376
Bromus ssp.	-26.15	45.52	-1.69	1.53	W	G	50.86301	100.04064
Calamagrostis canadensis	-30.56	45.50	-2.41	1.16	F	G	51.46439	101.25526
Calamagrostis canadensis	-26.52	38.48	0.56	1.29	G	G	51.36617	101.04611
Carex spp.	-25.39	44.12	-1.92	1.15	G	G	50.75441	100.23454
Carex spp.	-30.34	45.82	3.34	1.84	W	G	51.84710	100.90259
Cirsium arvense	-29.16	43.74	1.70	3.28	F	F	50.80045	100.23643

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Western Manitoba (cont.)								
Cirsium arvense	-29.33	41.17	0.28	1.67	W	F	51.39629	101.03227
Cornus stolonifera	-31.51	41.48	-2.74	1.49	F	W	50.82090	100.36314
Corydalis auren	-30.83	35.80	9.22	2.67	W	F	50.69816	100.32537
Corylus cornuta	-28.62	48.22	-3.74	1.89	F	W	51.46439	101.25526
Corylus cornuta	-28.69	47.78	0.90	2.60	G	W	51.26818	101.00046
Corylus cornuta	-30.83	45.12	-2.58	1.90	G	W	50.81156	100.35923
Corylus cornuta	-28.75	45.82	-1.04	2.91	W	W	50.69816	100.32537
Diervilla lonicera	-30.36	33.10	-1.07	1.19	F	W	50.82090	100.36314
Dracocephalum parviflorum	-28.36	45.63	-1.50	1.48	G	F	50.75441	100.23454
Eurybia conspicua	-34.22	41.83	-1.00	3.11	G	F	51.26818	101.00046
Eurybia conspicua	-29.56	44.46	-3.19	1.52	G	F	50.75441	100.23454
Festuca spp.	-35.68	42.41	0.77	3.23	F	G	50.80045	100.23643
Festuca spp.	-28.81	46.05	-2.06	1.18	G	G	51.36617	101.04611
Festuca spp.	-28.91	40.37	-2.06	1.05	G	G	50.87930	100.85332
Festuca spp.	-26.87	47.76	-0.50	1.45	G	G	51.50170	101.19832
Fragaria vesca	-32.68	45.44	-2.96	2.26	F	F	50.82090	100.36314
Fragaria virginiana	-33.89	44.36	-0.20	2.66	F	F	51.25786	101.03620
Fragaria virginiana	-35.88	42.95	0.20	2.94	F	F	50.80045	100.23643
Fragaria virginiana	-30.58	44.53	-4.34	1.06	F	F	51.46439	101.25526
Fragaria virginiana	-28.90	44.96	-1.33	2.11	G	F	51.36617	101.04611
Fragaria virginiana	-27.56	45.10	-0.86	1.81	G	F	50.87930	100.85332
Fragaria virginiana	-30.92	45.79	0.80	2.03	G	F	50.81156	100.35923
Fragaria virginiana	-28.38	42.74	-2.02	2.03	W	F	50.82056	100.36376
Galium boreale	-31.39	43.96	2.47	2.36	F	F	50.80045	100.23643
Galium boreale	-29.20	45.54	-2.21	1.49	G	F	50.87930	100.85332
Galium trifidum	-32.64	44.77	-2.05	1.83	F	F	51.49301	100.68957

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Western Manitoba (cont.)								
Galium triflorum	-34.08	40.00	-2.53	1.30	F	F	50.82090	100.36314
Lathyrus ochroleucus	-25.10	46.27	0.03	3.12	G	F	51.36617	101.04611
Lathyrus ochroleucus	-27.43	46.52	-0.56	2.55	G	F	50.87930	100.85332
Lathyrus ochroleucus	-31.57	44.07	0.60	3.34	G	F	51.26818	101.00046
Lathyrus ochroleucus	-28.19	44.10	-0.15	3.08	G	F	50.81156	100.35923
Lathyrus ochroleucus	-27.37	45.42	-1.42	2.65	W	F	50.82056	100.36376
Lathyrus ochroleucus	-30.02	45.09	5.43	4.12	W	F	50.69816	100.32537
Ledum groenlandicum	-28.61	53.89	-5.42	1.37	W	W	51.84710	100.90259
Lycopus uniflorus	-33.30	49.28	-3.56	1.75	F	F	51.49301	100.68957
Maianthemum trifolium	-29.77	46.04	-5.17	4.39	W	F	51.84710	100.90259
Oryzopsis asperifolia	-31.08	43.48	0.54	1.95	F	G	51.25786	101.03620
Petasites palmatus	-31.98	45.18	-1.52	1.32	F	F	51.46439	101.25526
Petasites palmatus	-26.19	42.73	1.09	1.79	G	F	51.36617	101.04611
Phleum pratense	-28.75	44.67	0.35	1.05	W	G	51.39629	101.03227
Picea glauca	-29.76	50.53	-3.49	1.06	F	W	50.82090	100.36314
Picea glauca	-26.88	50.24	-2.61	1.01	F	W	51.46439	101.25526
Picea glauca	-27.27	51.77	-3.43	0.94	W	W	50.82056	100.36376
Picea mariana	-27.82	51.01	2.58	1.63	F	W	50.80045	100.23643
Picea mariana	-29.06	52.40	-5.71	1.05	F	W	51.49301	100.68957
Picea mariana	-26.57	50.17	-2.55	0.99	G	W	50.87930	100.85332
Picea mariana	-28.35	51.74	0.00	1.05	G	W	50.75441	100.23454
Picea mariana	-28.21	52.24	-1.65	0.79	G	W	50.81156	100.35923
Picea mariana	-27.53	51.38	-0.28	1.05	W	W	50.86301	100.04064
Picea mariana	-30.27	51.30	-4.60	0.60	W	W	51.84710	100.90259
Populus balsamifera	-26.93	49.21	0.71	2.68	F	W	51.25786	101.03620
Populus balsamifera	-30.12	50.71	-1.76	1.57	F	W	51.46439	101.25526

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Western Manitoba (cont.)								
Populus balsamifera	-28.54	49.41	-1.10	2.34	G	W	50.87930	100.85332
Populus balsamifera	-26.19	51.87	0.12	2.58	G	W	51.26818	101.00046
Populus balsamifera	-27.98	49.49	2.93	1.97	W	W	51.39629	101.03227
Populus balsamifera	-27.36	48.95	-2.32	1.49	W	W	50.82056	100.36376
Populus tremuloides	-27.72	51.68	-0.96	2.32	F	W	51.25786	101.03620
Populus tremuloides	-28.20	49.36	1.35	1.77	G	W	51.36617	101.04611
Populus tremuloides	-28.97	49.13	-0.50	1.75	G	W	50.87930	100.85332
Populus tremuloides	-27.47	50.43	-1.19	2.32	G	W	51.26818	101.00046
Rosa acicularis	-30.14	43.14	0.22	2.65	F	W	51.25786	101.03620
Rosa acicularis	-30.16	25.01	-0.34	1.02	F	W	50.82090	100.36314
Rosa acicularis	-28.27	49.71	0.98	2.02	G	W	51.36617	101.04611
Rosa acicularis	-27.44	46.55	-0.25	2.01	G	W	50.87930	100.85332
Rosa acicularis	-30.57	44.70	-0.77	2.70	G	W	51.26818	101.00046
Rosa acicularis	-26.78	46.78	-0.79	1.29	G	W	50.75441	100.23454
Rosa acicularis	-28.85	46.46	-0.19	2.10	W	W	50.82056	100.36376
Rosa acicularis	-28.60	45.09	0.56	2.63	W	W	50.69816	100.32537
Rubus idaeus	-27.74	47.00	1.64	3.02	F	W	50.80045	100.23643
Rubus idaeus	-29.58	47.16	-0.81	3.45	G	W	51.26818	101.00046
Rubus idaeus	-29.39	46.37	-1.05	1.93	G	W	50.81156	100.35923
Rubus idaeus	-28.43	46.89	-3.42	2.01	W	W	50.82056	100.36376
Salix scouleriana	-26.61	49.19	-2.05	2.08	G	W	51.36617	101.04611
Salix scouleriana	-27.86	45.58	-3.16	1.81	G	W	50.87930	100.85332
Salix scouleriana	-27.55	49.75	-2.12	1.47	W	W	50.82056	100.36376
Salix spp.	-28.14	50.89	-2.00	1.93	F	W	51.49301	100.68957
Salix spp.	-26.79	46.83	1.45	1.58	G	W	50.75441	100.23454
Salix spp.	-27.60	50.07	3.03	2.22	W	W	51.39629	101.03227

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Western Manitoba (cont.)								
Shepherdia canadensis	-28.73	48.37	-0.62	2.41	G	W	50.81156	100.35923
Sonchus arvensis	-30.56	44.43	-1.35	2.12	F	F	51.49782	101.25785
Symphyotrichum ciliolatum	-29.45	43.40	-3.16	2.04	G	F	50.87930	100.85332
Symphyotrichum ciliolatum	-28.29	48.35	-3.53	1.70	W	F	50.82056	100.36376
Symphyotrichum puniceum	-33.81	46.44	-3.87	2.20	F	F	51.49301	100.68957
Symphyotrichum puniceum	-32.58	46.07	-2.75	2.04	F	F	50.82090	100.36314
Symphyotrichum puniceum	-30.51	44.63	-0.27	1.77	G	F	50.81156	100.35923
Symphyotrichum puniceum	-30.90	43.13	0.24	2.66	W	F	51.39629	101.03227
Taraxacum officinale	-28.84	40.57	-0.60	2.21	G	F	51.36617	101.04611
Taraxacum officinale	-31.29	45.02	2.58	4.10	W	F	50.69816	100.32537
Unidentified	-35.50	48.06	-0.75	3.24	F	F	51.25786	101.03620
Unidentified	-33.25	43.62	-1.11	1.89	F	F	51.46439	101.25526
Unidentified	-28.63	47.99	-0.69	1.64	G	F	50.75441	100.23454
Unidentified	-28.66	44.66	-2.27	1.29	G	F	50.75441	100.23454
Unidentified C_3 grass	-30.10	44.51	-1.16	1.49	F	G	50.82090	100.36314
Unidentified C_3 grass	-33.90	41.30	0.26	1.89	G	G	51.26818	101.00046
Unidentified C_3 grass	-29.56	43.84	-0.42	2.00	G	G	50.81156	100.35923
Unidentified C_3 grass	-26.76	41.60	-0.52	0.75	W	G	50.86301	100.04064
Unidentified C_3 grass	-28.29	44.93	-1.74	1.35	W	G	50.82056	100.36376
Unidentified C_3 grass	-30.82	42.55	7.01	2.64	W	G	50.69816	100.32537
Viola canadense	-32.13	39.51	2.06	2.33	G	F	51.26818	101.00046
Viola renifolia	-32.56	43.61	-4.14	0.78	W	F	51.84710	100.90259
Alfalfa (*Medicago sativa*)	-27.37	42.76	-0.29	3.85	A		51.09993	101.23851
Alfalfa (*Medicago sativa*)	-26.80	51.80	5.37	1.99	A		51.66735	100.55372
Alfalfa (*Medicago sativa*)	-27.51	41.94	1.16	4.31	A		52.02703	101.15890
Alfalfa (*Medicago sativa*)	-28.82	43.86	-0.33	5.20	A		51.09408	100.90574

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Western Manitoba (cont.)								
Alfalfa (*Medicago sativa*)	-27.58	48.19	0.01	3.98	A		51.35205	101.16622
Alfalfa (*Medicago sativa*)	-29.06	44.90	0.82	4.06	A		51.32039	101.21295
Alfalfa (*Medicago sativa*)	-28.05	44.76	-0.45	4.44	A		51.35741	101.21290
Alfalfa (*Medicago sativa*)	-28.44	43.57	-0.02	3.71	A		51.36196	101.17074
Alfalfa (*Medicago sativa*)	-27.52	43.97	-1.05	2.74	A		50.88916	101.23919
Alfalfa (*Medicago sativa*)	-29.41	43.02	-0.76	3.31	A		50.87946	101.09011
Alfalfa (*Medicago sativa*)	-28.71	42.60	0.29	3.46	A		50.84510	101.00578
Alfalfa (*Medicago sativa*)	-28.29	45.78	6.40	3.20	A		51.09573	100.89876
hay	-26.88	45.86	1.65	1.47	A		51.51471	101.27899
hay	-29.57	45.81	2.14	0.78	A		51.09609	101.03095
hay	-27.92	46.27	-2.30	0.78	A		51.36196	101.17074
hay	-26.49	48.87	2.16	0.42	A		50.84510	101.00578
hay	-27.38	45.91	-0.10	0.38	A		50.84510	101.00578
hay	-29.34	82.66	-2.00	0.58	A		50.99647	99.85235
Oilseed (*Brassica* spp.)	-27.52	54.07	1.28	1.47	A		52.02706	101.18214
Oilseed (*Brassica* spp.)	-25.89	49.12	2.08	2.22	A		52.02709	101.25682
Oilseed (*Brassica* spp.)	-27.59	43.55	20.09	1.06	A		51.96841	101.27202
Oilseed (*Brassica* spp.)	-29.77	45.12	5.17	3.25	A		52.02699	101.11453
Oilseed (*Brassica* spp.)	-27.40	45.86	2.20	0.43	A		51.09852	101.23811
Oilseed (*Brassica* spp.)	-25.65	43.51	5.99	1.53	A		51.09556	101.21951
Oilseed (*Brassica* spp.)	-25.91	44.66	19.19	1.78	A		51.09576	101.05546
Oilseed (*Brassica* spp.)	-30.74	45.34	5.51	0.59	A		51.10252	100.25061
Oilseed (*Brassica* spp.)	-26.11	50.58	6.26	2.12	A		51.24304	101.04212
Oilseed (*Brassica* spp.)	-26.54	56.93	10.34	1.99	A		50.87946	101.09011
Unidentified grain	-29.09	46.21	3.26	0.30	A		51.96857	101.15033
Unidentified grain	-28.65	48.04	10.21	0.28	A		51.99794	101.27372

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Western Manitoba (cont.)								
Unidentified grain	-29.13	46.20	2.72	0.24	A		52.02696	101.13040
Unidentified grain	-27.38	42.13	1.57	1.60	A		52.02699	101.11453
Unidentified grain	-27.96	90.07	-0.61	0.40	A		51.10252	100.25061
Unidentified grain	-30.39	42.52	1.69	1.25	A		51.24304	101.04212
Unidentified grain	-29.01	47.24	2.62	0.22	A		51.25562	101.04708
Unidentified grain	-29.97	43.41	0.39	0.39	A		50.88916	101.23919
Unidentified grain	-28.80	45.74	5.57	0.36	A		50.94867	99.83634
Wheat (*Triticum* spp.)	-26.05	40.93	2.74	1.23	A		52.02709	101.25682
Wheat (*Triticum* spp.)	-24.60	45.57	8.49	1.69	A		51.09576	101.05546
Wheat (*Triticum* spp.)	-28.02	44.53	0.12	0.64	A		51.09609	101.03095
Wheat (*Triticum* spp.)	-24.55	47.95	7.30	2.12	A		51.09811	100.97501
Hudson Bay								
Achillia millefolium	-30.01	45.32	1.47	2.70	G	F	52.47201	102.85354
Amelanchier alnifolia	-30.88	49.67	2.26	2.75	G	W	52.40410	102.11163
Amelanchier alnifolia	-32.02	51.16	0.40	2.43	G	W	52.40192	102.11200
Amelanchier alnifolia	-30.86	33.90	-0.22	1.21	G	W	52.45983	102.39587
Amelanchier alnifolia	-28.68	52.69	0.02	2.06	W	W	52.35886	102.13622
Amelanchier alnifolia	-28.77	54.58	0.20	2.32	W	W	52.86887	102.70765
Anemone nemoras	-31.91	44.90	-2.70	1.89	F	F	52.55315	102.95549
Arctostaphylos uva-ursi	-32.45	52.14	-3.91	1.00	W	F	52.89089	102.70643
Betula papyrifera	-29.99	52.82	-0.08	1.75	G	W	52.45983	102.39587
Bromus inermis	-28.55	44.05	-1.34	0.89	W	G	52.50923	102.88289
Chamaedaphne calycuta	-26.99	45.86	2.25	2.86	W	W	52.80395	102.35750
Cirsium spp.	-30.66	44.37	-2.34	1.43	W	F	52.50923	102.88289
Cornus canadensis	-31.27	41.06	1.85	1.44	F	F	52.43776	102.65321

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Hudson Bay (cont.)								
Cornus canadensis	-32.52	43.29	-14.00	2.29	F	F	52.90583	102.70715
Cornus canadensis	-30.58	46.81	-0.19	1.29	W	F	52.89089	102.70643
Corylus cornuta	-31.01	47.29	-0.43	2.44	F	W	52.43776	102.65321
Corylus cornuta	-31.11	43.41	-0.77	2.14	F	W	52.26050	102.63488
Corylus cornuta	-28.81	55.19	-5.13	1.95	F	W	52.90583	102.70715
Corylus cornuta	-29.85	44.51	-3.17	2.14	F	W	52.55315	102.95549
Corylus cornuta	-30.90	44.90	-0.82	2.40	G	W	52.45983	102.39587
Corylus cornuta	-28.17	47.71	-4.02	2.31	W	W	52.50923	102.88289
Diervilla lonicera	-29.21	46.92	-1.17	2.48	G	W	52.45983	102.39587
Festuca spp.	-28.55	47.19	-0.34	0.59	G	G	52.40192	102.11200
Fragaria spp.	-32.56	43.05	-1.18	2.93	W	F	52.56713	102.74892
Fragaria vesca	-33.15	48.84	1.14	2.23	F	F	52.90583	102.70715
Fragaria vesca	-27.99	48.88	-0.32	2.04	G	F	52.58464	102.54895
Fragaria virginiana	-30.49	46.81	0.97	2.70	G	F	52.40410	102.11163
Fragaria virginiana	-29.61	46.29	-2.80	2.27	W	F	52.50923	102.88289
Fragaria virginiana	-28.86	50.05	-1.37	2.63	W	F	52.35886	102.13622
Galium boreale	-32.15	43.57	-0.16	2.03	F	F	52.43776	102.65321
Galium spp.	-30.11	42.13	2.03	1.93	G	F	52.58464	102.54895
Geum aleopicum	-34.06	43.07	-3.15	2.14	G	F	52.45983	102.39587
Geum rivale	-30.52	45.69	-3.94	1.17	W	F	52.50923	102.88289
Lathyrus ochroleucus	-30.83	46.11	2.15	4.64	G	F	52.40410	102.11163
Lathyrus ochroleucus	-29.20	47.86	2.12	2.89	G	F	52.40192	102.11200
Lathyrus ochroleucus	-29.32	26.46	0.96	1.74	W	F	52.50923	102.88289
Lathyrus spp.	-29.62	46.16	0.30	5.63	W	F	52.86887	102.70765
Maianthemum canadense	-30.57	46.81	1.52	1.72	F	F	52.26050	102.63488
Picea glauca	-30.13	49.20	-2.12	0.93	F	W	52.90583	102.70715

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Hudson Bay (cont.)								
Picea glauca	-26.11	53.77	-4.34	0.84	W	W	52.86887	102.70765
Poa spp.	-31.05	46.11	-0.83	0.80	W	G	52.35886	102.13622
Populus tremuloides	-29.57	48.01	-1.87	2.13	F	W	52.55315	102.95549
Populus tremuloides	-27.89	49.44	2.29	1.97	G	W	52.47201	102.85354
Populus tremuloides	-29.00	47.91	-2.18	1.77	W	W	52.50923	102.88289
Populus tremuloides	-27.10	50.84	-4.94	1.77	W	W	52.86887	102.70765
Rosa acicularis	-31.40	46.10	0.59	1.99	F	W	52.26050	102.63488
Rosa acicularis	-30.37	44.91	-0.38	1.98	F	W	52.90583	102.70715
Rosa acicularis	-31.39	50.25	-0.27	2.39	F	W	52.55315	102.95549
Rosa acicularis	-29.85	38.56	0.65	2.49	G	W	52.40410	102.11163
Rosa acicularis	-28.26	48.90	0.87	2.67	G	W	52.40192	102.11200
Rosa acicularis	-29.45	43.85	1.24	1.14	G	W	52.58464	102.54895
Rosa acicularis	-28.92	45.17	2.41	2.18	G	W	52.47201	102.85354
Rosa acicularis	-29.21	47.35	-0.96	1.44	W	W	52.40759	102.17307
Rosa acicularis	-29.65	47.15	-1.67	1.53	W	W	52.50923	102.88289
Rosa acicularis	-30.09	47.62	-0.68	1.80	W	W	52.89089	102.70643
Rosa acicularis	-28.63	54.25	-6.02	1.05	W	W	52.45004	102.33233
Rosa acicularis	-27.18	48.65	-1.15	1.70	W	W	52.86887	102.70765
Rubus idaeus	-28.38	48.40	-2.98	2.72	F	W	52.76728	102.09957
Rubus pubescens	-30.53	41.41	2.62	1.53	F	W	52.26050	102.63488
Rubus pubescens	-31.62	46.57	0.09	2.02	F	W	52.90583	102.70715
Rubus pubescens	-31.24	45.47	0.24	1.41	F	W	52.55315	102.95549
Salix discolor	-28.79	51.53	0.14	2.00	W	W	52.89089	102.70643
Salix monticola	-28.92	46.82	-0.42	2.50	F	W	52.76728	102.09957
Salix spp.	-30.65	49.90	-1.07	1.65	F	W	52.55315	102.95549
Salix spp.	-29.07	47.72	-0.33	3.28	G	W	52.40410	102.11163

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Hudson Bay (cont.)								
Salix spp.	-27.27	49.41	2.87	2.30	G	W	52.58464	102.54895
Salix spp.	-28.45	48.97	0.22	2.49	G	W	52.45983	102.39587
Salix spp.	-28.16	46.91	-2.49	2.02	W	W	52.50923	102.88289
Solidago canadensis	-30.71	33.02	1.90	1.83	G	F	52.58464	102.54895
Sonchus arvensis	-32.03	45.03	1.67	2.84	G	F	52.40410	102.11163
Symphyotrichum boreale	-29.58	46.18	2.08	1.88	W	F	52.35886	102.13622
Taraxacum officinale	-30.02	43.53	3.23	2.96	G	F	52.47201	102.85354
Taraxacum officinale	-31.47	41.42	-0.72	2.45	W	F	52.35886	102.13622
Trifolium hybridum	-31.57	38.66	-1.55	2.68	G	F	52.47201	102.85354
Trifolium hybridum	-30.95	42.47	0.48	2.72	W	F	52.35886	102.13622
Unidentified	-35.29	43.00	-1.71	2.52	F	F	52.76728	102.09957
Unidentified	-30.35	46.82	0.24	3.64	F	F	52.76728	102.09957
Unidentified	-35.55	33.82	-0.48	2.03	F	F	52.43642	102.70995
Unidentified	-29.14	45.74	-1.06	2.29	G	F	52.40192	102.11200
Unidentified	-32.14	41.03	0.97	2.48	G	F	52.45983	102.39587
Unidentified	-33.82	42.20	-1.16	1.56	G	F	52.45983	102.39587
Unidentified	-31.35	45.97	-4.28	2.14	W	F	52.80395	102.35750
Unidentified	-28.92	43.78	-3.02	1.84	W	F	52.80395	102.35750
Unidentified	-29.56	46.81	-2.07	0.97	W	F	52.55167	102.58019
Unidentified	-31.02	45.84	-2.42	1.88	W	F	52.44761	102.79881
Unidentified	-27.73	74.49	-7.05	2.18	G	W	52.24876	102.62561
Unidentified	-29.29	56.65	-4.53	1.01	G	W	52.19880	102.93319
Unidentified	-29.56	53.36	-4.36	0.94	W	W	52.29489	102.63004
Unidentified	-29.22	50.88	0.20	2.25	W	W	52.29489	102.63004
Unidentified	-30.26	48.47	2.42	2.45	W	W	52.28860	102.63087
Unidentified C_3 grass	-27.91	44.36	5.54	1.71	F	G	52.76728	102.09957

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Hudson Bay (cont.)								
Unidentified C_3 grass	-32.28	44.63	1.70	2.37	F	G	52.26050	102.63488
Unidentified C_3 grass	-32.28	44.31	0.02	1.96	F	G	52.90583	102.70715
Unidentified C_3 grass	-30.94	43.23	0.75	1.65	F	G	52.55315	102.95549
Unidentified C_3 grass	-30.55	44.03	0.59	2.16	G	G	52.40410	102.11163
Unidentified C_3 grass	-28.88	44.34	-0.05	1.68	G	G	52.40192	102.11200
Unidentified C_3 grass	-30.17	43.71	4.39	2.07	G	G	52.45983	102.39587
Unidentified C_3 grass	-26.91	45.90	-0.41	1.28	G	G	52.47201	102.85354
Unidentified C_3 grass	-28.20	45.49	0.84	2.10	G	G	52.47201	102.85354
Unidentified C_3 grass	-27.89	47.31	-5.82	1.45	W	G	52.80395	102.35750
Unidentified C_3 grass	-27.46	46.04	1.10	1.08	W	G	52.50923	102.88289
Unidentified C_3 grass	-29.99	48.28	-1.58	0.85	W	G	52.89089	102.70643
Unidentified C_3 grass	-30.03	31.93	-0.25	0.76	W	G	52.35886	102.13622
Unidentified C_3 grass	-29.00	46.19	-4.38	1.36	W	G	52.86887	102.70765
Unidentified C_3 grass	-28.01	46.07	-1.73	1.18	W	G	52.86887	102.70765
Unidentified C_4 grass	-13.79	44.45	2.60	1.08	G	G	52.40410	102.11163
Vaccinium myrtilliodes	-30.36	50.09	1.78	1.46	W	W	52.89089	102.70643
Vaccinium myrtilliodes	-29.83	50.94	-1.68	1.68	W	W	52.86887	102.70765
Viburnum opulus var. *americanum*	-28.70	50.23	-0.62	2.83	F	W	52.43776	102.65321
Viola rugulosa	-33.50	39.31	-1.27	1.85	F	F	52.43776	102.65321
Viola spp.	-34.88	38.76	-3.44	1.20	F	F	52.55315	102.95549
Viola spp.	-30.53	44.19	-2.75	1.81	W	F	52.86887	102.70765
Alfalfa (*Medicago sativa*)	-27.12	47.93	0.79	3.96	A		51.77758	102.69181
Alfalfa (*Medicago sativa*)	-28.35	44.05	0.77	3.63	A		51.92111	102.69176
Alfalfa (*Medicago sativa*)	-28.92	35.98	1.22	2.02	A		52.03555	102.88670
Alfalfa (*Medicago sativa*)	-28.08	43.65	2.89	4.14	A		52.11601	102.50598

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Hudson Bay (cont.)								
Alfalfa (*Medicago sativa*)	-30.87	33.86	2.18	3.86	A		52.05635	102.71681
Alfalfa (*Medicago sativa*)	-29.80	45.62	2.36	4.29	A		52.66771	102.34863
hay	-26.95	45.07	-2.10	1.22	A		51.92111	102.69176
hay	-29.69	45.19	5.09	0.77	A		51.93827	102.69174
hay	-28.31	47.91	-0.31	1.43	A		52.05635	102.71681
hay	-28.49	44.83	1.75	0.63	A		52.66771	102.34863
Oat (*Avena sativa*)	-26.34	46.39	3.02	1.69	A		51.66829	102.69194
Oat (*Avena sativa*)	-26.14	46.19	3.14	1.43	A		51.87802	102.69181
Oat (*Avena sativa*)	-28.23	44.25	4.89	0.91	A		51.94970	102.83356
Oat (*Avena sativa*)	-27.78	44.51	4.71	1.05	A		51.94915	102.50284
Oat (*Avena sativa*)	-29.91	46.58	2.05	1.01	A		52.66768	102.32596
Oat (*Avena sativa*)	-28.12	44.91	2.99	1.12	A		52.66771	102.33978
Oilseed (*Brassica* spp.)	-26.52	52.41	9.73	2.16	A		51.68461	102.69190
Oilseed (*Brassica* spp.)	-25.07	51.81	11.60	2.08	A		51.66829	102.69194
Oilseed (*Brassica* spp.)	-28.25	46.21	15.80	1.08	A		51.79707	102.69180
Oilseed (*Brassica* spp.)	-27.70	49.65	17.38	1.26	A		51.93326	102.69172
Oilseed (*Brassica* spp.)	-27.75	48.60	13.59	1.46	A		52.04694	102.50589
Oilseed (*Brassica* spp.)	-25.77	50.99	5.86	2.22	A		52.66769	102.22546
Oilseed (*Brassica* spp.)	-25.89	54.41	3.33	1.96	A		52.66776	102.24223
Oilseed (*Brassica* spp.)	-25.93	51.14	7.06	1.87	A		52.75491	103.12839
Oilseed (*Brassica* spp.)	-26.15	42.81	14.13	2.42	A		52.74734	103.19144
Unidentified grain	-28.40	43.85	1.12	0.26	A		51.70636	102.69183
Unidentified grain	-28.51	46.27	2.80	0.29	A		51.79707	102.69180
Unidentified grain	-27.59	48.41	7.92	0.28	A		51.86245	102.69180
Unidentified grain	-29.77	46.45	8.73	0.96	A		52.66769	102.25095
Unidentified grain	-29.62	22.99	4.60	0.17	A		52.84874	102.94989

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Hudson Bay (cont.)								
Wheat (*Triticum* spp.)	-26.72	44.32	2.18	1.24	A		52.66768	102.30438
Wheat (*Triticum* spp.)	-26.40	43.87	3.00	1.34	A		52.85336	102.94998
Wheat (*Triticum* spp.)	-27.19	46.14	4.94	1.22	A		52.74801	103.14341
Wheat (*Triticum* spp.)	-24.54	42.64	3.77	1.65	A		52.58542	103.23028
Nipawin								
Agrostis scabra	-28.89	46.29	3.49	0.57	F	G	53.33711	104.57004
Amelanchier alnifolia	-31.27	49.29	-1.04	0.87	W	W	53.41892	103.45066
Betula spp.	-30.95	50.16	-3.15	1.95	W	W	53.41892	103.45066
Betula spp.	-29.92	50.04	-2.59	1.16	W	W	53.40667	103.38642
Cornus canadensis	-30.50	44.13	-1.12	1.13	W	F	53.41892	103.45066
Corylus cornuta	-31.52	47.30	-0.42	1.93	W	W	53.30394	104.19792
Dasiphora fruticosa	-32.28	49.43	0.88	1.50	W	W	53.41892	103.45066
Dasiphora fruticosa	-30.82	49.73	-1.10	1.43	W	W	53.40667	103.38642
Fraxinus pennsylvanica	-32.67	46.98	0.45	2.13	W	W	53.30394	104.19792
Galium triflorum	-34.81	38.98	-3.24	3.39	W	F	53.33532	103.51442
Galium triflorum	-34.20	41.38	-1.00	2.33	W	F	53.30394	104.19792
Juncus spp.	-26.78	50.18	4.51	1.03	W	G	53.36526	103.45917
Maianthemum canadense	-26.96	53.71	-4.26	1.48	F	F	53.53546	104.07013
Petasites saggitatus	-29.07	45.09	1.66	1.57	W	F	53.36526	103.45917
Phalaris arundinacea	-26.92	48.48	3.96	1.35	F	G	53.38510	104.48695
Pinus banksiana	-29.67	54.70	-2.15	1.33	F	W	53.32538	104.64167
Poa pratensis	-27.68	44.08	5.04	1.02	F	G	53.33711	104.57004
Populus tremuloides	-27.68	50.47	-0.62	2.02	F	W	53.33711	104.57004
Populus tremuloides	-29.86	94.68	-6.01	1.23	W	W	53.40667	103.38642
Rosa acicularis	-30.33	45.29	-0.87	2.43	W	W	53.40667	103.38642

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Nipawin (cont.)								
Rosa acicularis	-34.17	47.10	1.10	2.53	W	W	53.30394	104.19792
Rubus arcticus ssp. *acaulis*	-30.70	45.32	-3.12	1.54	W	W	53.40667	103.38642
Rubus idaeus	-32.04	39.41	0.26	2.80	W	W	53.33532	103.51442
Rubus idaeus	-31.94	48.81	1.81	3.27	W	W	53.30394	104.19792
Rubus pubescens	-31.11	46.71	-0.17	1.41	W	W	53.41892	103.45066
Rubus pubescens	-31.60	46.29	-0.40	2.41	W	W	53.30394	104.19792
Rubus pubescens	-32.14	46.64	1.24	2.56	W	W	53.30394	104.19792
Salix petiolaris	-29.08	51.29	0.93	2.08	F	W	53.33711	104.57004
Salix pyrifolia	-30.93	39.89	-0.69	1.65	W	W	53.33532	103.51442
Shepherdia canadensis	-29.98	46.86	-1.55	1.08	W	W	53.40667	103.38642
Solidago simplex	-32.61	42.59	0.38	3.32	W	F	53.33532	103.51442
Symphyotrichum spp.	-30.35	47.66	0.04	0.88	F	F	53.53546	104.07013
Unidentified	-28.63	40.49	-3.18	1.30	F	F	53.53546	104.07013
Unidentified	-28.59	51.10	-4.34	1.77	W	W	53.30547	104.19759
Unidentified	-27.47	50.13	2.05	0.84	W	W	53.36526	103.45917
Unidentified C_3 grass	-28.97	39.61	-5.87	0.99	F	G	53.53546	104.07013
Unidentified C_3 grass	-28.56	47.21	3.98	1.73	F	G	53.38510	104.48695
Unidentified C_3 grass	-31.48	41.56	3.44	1.11	W	G	53.41892	103.45066
Unidentified C_3 grass	-31.94	46.35	3.94	1.14	W	G	53.40667	103.38642
Unidentified C_3 grass	-33.95	44.49	2.56	2.68	W	G	53.30394	104.19792
Unidentified C_3 grass	-28.78	45.04	1.42	1.31	W	G	53.36526	103.45917
Alfalfa (*Medicago sativa*)	-27.50	46.69	0.94	3.94	A		53.62784	104.29347
Alfalfa (*Medicago sativa*)	-29.44	45.86	-0.78	4.86	A		53.41665	104.85547
Alfalfa (*Medicago sativa*)	-28.66	43.71	-0.57	3.14	A		53.24940	103.49960
hay	-27.36	44.89	0.50	1.12	A		53.22895	104.49513
hay	-26.95	43.24	0.33	0.89	A		53.22895	104.49513

	Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Nipawin (cont.)									
	hay	-26.94	44.94	1.36	0.80	A		53.62784	104.29347
	hay	-28.16	45.83	0.62	2.95	A		53.41026	104.70804
	hay	-28.50	42.16	1.78	3.14	A		53.41026	104.70804
	hay	-27.47	47.73	-0.61	0.90	A		53.48523	103.99564
	hay	-27.76	48.62	-1.60	0.82	A			
	hay	-28.79	46.22	2.26	0.93	A			
	Oat (*Avena sativa*)	-27.75	47.25	0.59	0.99	A		53.36549	104.16467
	Oat (*Avena sativa*)	-28.69	46.60	1.79	1.35	A		53.62727	104.25196
	Oat (*Avena sativa*)	-27.96	45.29	3.06	1.47	A		53.62784	104.29347
	Oat (*Avena sativa*)	-28.61	46.63	4.46	1.17	A		53.30457	104.19744
	Oat (*Avena sativa*)	-26.44	46.09	4.56	1.39	A		53.66245	104.29032
	Oat (*Avena sativa*)	-28.56	43.77	0.85	0.66	A		53.41026	104.70804
	Oat (*Avena sativa*)	-28.23	42.76	4.96	0.87	A		53.59280	104.53603
	Oat (*Avena sativa*)	-28.43	44.04	3.17	1.09	A		53.40898	104.39904
	Oat (*Avena sativa*)	-25.44	45.15	-0.12	2.39	A		53.16186	103.86949
	Oat (*Avena sativa*)	-27.68	46.31	0.77	1.21	A			
	Oilseed (*Brassica* spp.)	-29.47	53.64	0.26	2.18	A		53.29673	104.10193
	Oilseed (*Brassica* spp.)	-29.72	48.27	-0.22	0.28	A		53.62784	104.29347
	Oilseed (*Brassica* spp.)	-29.70	44.97	2.32	0.75	A		53.66245	104.29032
	Oilseed (*Brassica* spp.)	-27.04	47.03	-0.47	1.10	A		53.40483	104.70802
	Oilseed (*Brassica* spp.)	-25.84	54.50	2.51	1.83	A		53.50556	103.99562
	Oilseed (*Brassica* spp.)	-29.40	44.91	3.67	0.75	A		53.50556	103.99562
	Oilseed (*Brassica* spp.)	-26.59	51.36	-0.70	1.39	A		53.48523	103.99564
	Oilseed (*Brassica* spp.)	-27.31	50.99	1.09	1.19	A		53.47398	103.99564
	Oilseed (*Brassica* spp.)	-28.43	43.72	4.72	0.92	A		53.59280	104.53603
	Oilseed (*Brassica* spp.)	-28.84	44.93	7.35	0.62	A		53.43990	104.85545

Species	$\delta^{13}C$ (‰)	%C	$\delta^{15}N$ (‰)	%N	Habitat	Growth form	Lat (°N)	Long (°W)
Nipawin (cont.)								
Oilseed (*Brassica* spp.)	-29.69	47.07	6.90	0.35	A		53.40898	104.39904
Oilseed (*Brassica* spp.)	-29.96	44.12	5.45	0.47	A		53.16176	104.53661
Oilseed (*Brassica* spp.)	-27.26	47.34	27.23	1.27	A		53.16188	104.07215
Oilseed (*Brassica* spp.)	-29.66	43.03	8.18	0.85	A		53.16190	103.78484
Rye (*Secale cereal*)	-30.82	47.10	7.27	3.08	A		53.30457	104.19744
Rye (*Secale cereal*)	-29.93	48.18	6.91	0.69	A		53.30457	104.19744
Unidentified grain	-28.59	45.22	5.03	0.92	A		53.29326	104.09998
Unidentified grain	-30.13	47.79	0.77	0.38	A		53.53704	103.99556
Unidentified grain	-27.93	49.22	1.67	0.34	A		53.52368	103.99556
Unidentified grain	-30.39	47.61	6.51	0.40	A		53.50556	103.99562
Unidentified grain	-27.97	44.77	0.33	0.55	A		53.47398	103.99564
Unidentified grain	-28.44	48.43	0.42	0.23	A		53.59280	104.53603
Unidentified grain	-27.46	47.73	0.43	0.24	A		53.45835	104.85540
Unidentified grain	-28.24	44.29	6.83	0.45	A		53.40895	104.40904
Unidentified grain	-29.13	49.78	0.48	0.22	A		53.16180	104.49661
Unidentified grain	-30.04	43.94	6.11	0.54	A		53.16186	103.86949
Unidentified grain	-27.43	44.36	8.17	0.53	A		53.16190	103.78484
Unidentified grain	-29.39	48.33	0.90	0.20	A		53.24940	103.49960
Wheat (*Triticum* spp.)	-26.47	43.53	1.00	0.97	A		53.38709	104.53086

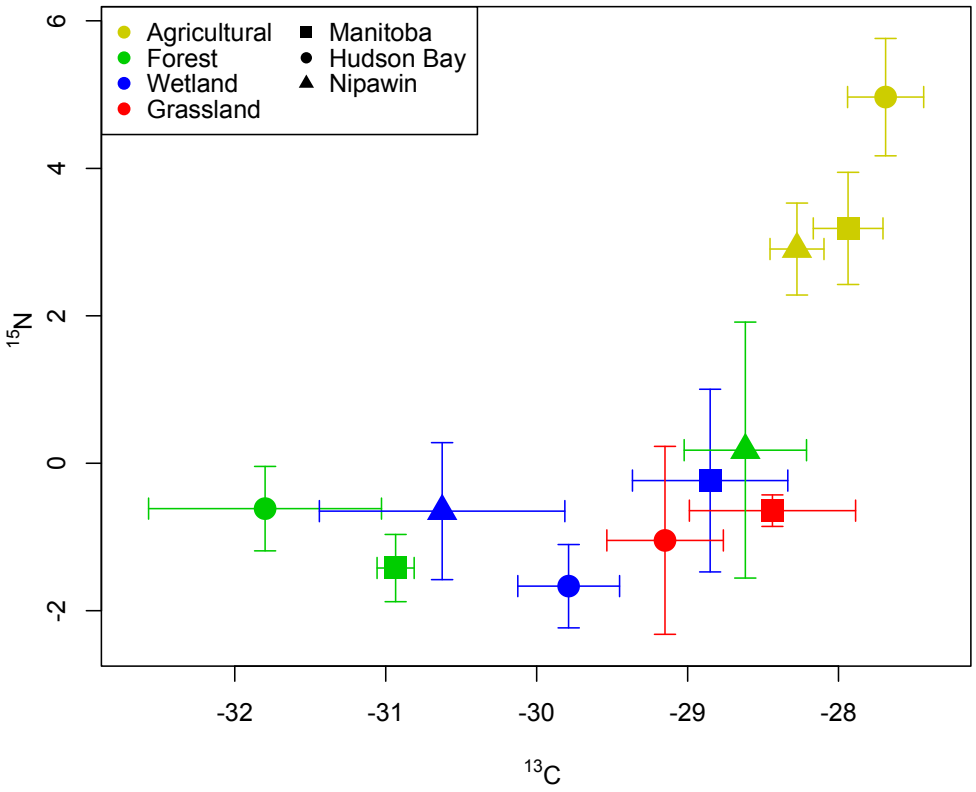

Figure A2.1 Means and standard errors of carbon and nitrogen stable isotope ratios of plants from agricultural, forest, wetland, and grassland habitats in the western Manitoba, Hudson Bay, and Nipawin study areas.

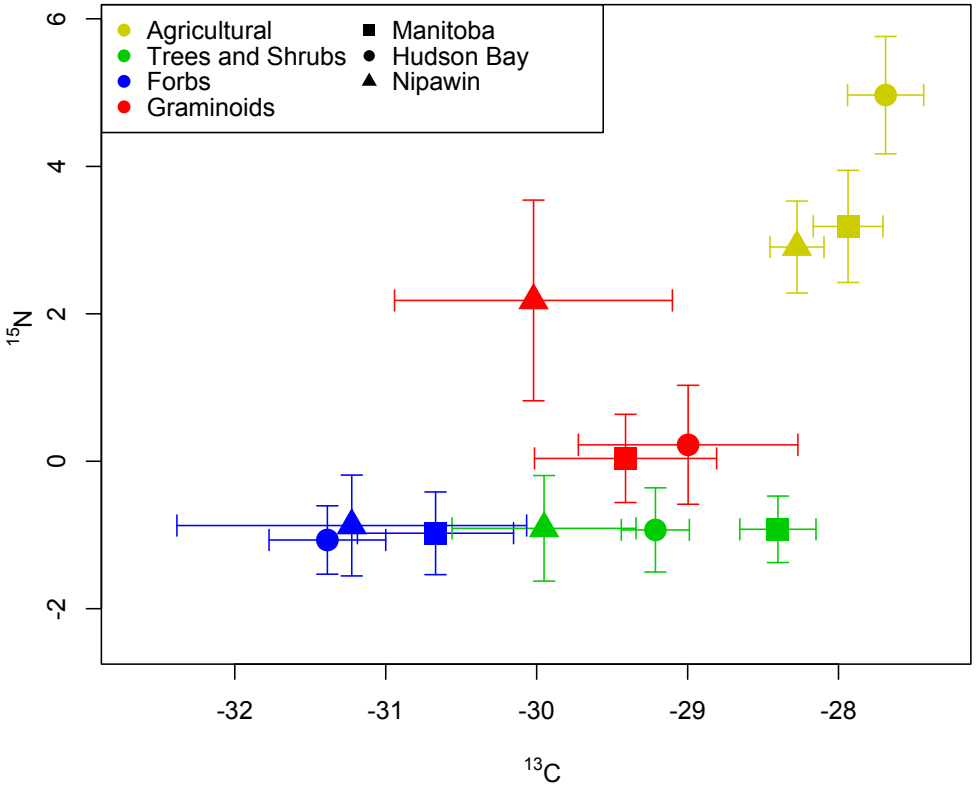

Figure A2.2 Means and standard errors of carbon and nitrogen stable isotope ratios of agricultural plants with those of trees and shrubs, forbs and graminoids from the western Manitoba, Hudson Bay, and Nipawin study areas.