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Landscape Variation in the Diet and Productivity of Reindeer in Alaska Based on Stable Isotope Analyses

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Abstract

Productivity of a managed grazing system is dependent upon both the grazing strategy of ungulates and decisions made by humans. Herds of domestic reindeer (*Rangifer tarandus tarandus*) graze on discrete ranges of the Seward Peninsula, Alaska with variable production rates. We show that the ^{15}N natural abundance of reindeer forages vary significantly and the $\delta^{15}N$ value of collagen deposited in antler bone from spring until ossification was significantly correlated with the $\delta^{15}N$ signature of the diet. Calf weight in June was related to isotopic signatures in antler and soft tissue of adult females, and was inversely correlated with the absolute differential between summer and winter serum $\delta^{15}N$ values. This observation suggests that female reindeer with smaller calves had catabolized more body protein during winter than females in adjacent herds. Moreover, in herds with smaller calves, female reindeer consumed proportionately more shrubs in early spring resulting in a strong relationship between $\delta^{15}N$ signatures of antler collagen deposited in May and calf weight. These data suggest female reindeer catabolizing relatively more body protein during winter may attempt to compensate by increasing consumption of high-protein catkins and leaf buds of shrubs during May. Herders with relatively smaller calves in their herds may be able to improve protein balance of reproductive females and thus increase calf productivity by increasing access to shrub habitats during spring.

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Introduction

Productivity of a managed grazing system is dependent upon decisions made by both humans and the grazing animal. Choosing where and when to feed across a variable landscape occurs at a number of scales (Senft et al., 1987; Bailey et al., 1996) where large-scale landscape decisions like defining home and regional ranges are generally made by humans, whereas small-scale decisions like patch and bite selections are made by the grazing animal. A better understanding of the strategies taken by grazing ungulates will help humans to make better landscape-wide decisions because choices made at the larger scales will constrain the choices available to grazers at smaller scales.

Domestic reindeer (*Rangifer tarandus tarandus*) are managed in extremely heterogeneous tundra environments across the circumpolar north (Nellemann and Thomsen, 1994; Marell and Edenius, 2006). The vascular plant growing season of tundra environments is also very short so the spatial-temporal availability of high quality forage is limited. Reindeer appear to forage selectively on species that contain high concentrations of protein during the growing season (Klein, 1970; Nieminen and Heiskari, 1989; Staaland and Saebö, 1993; Finstad, 2008) because growth of both hard (bone, hair) and soft tissue (muscle, organs) is at a maximum. Comparatively small differences in the proportion of nutrients in forage can markedly influence weight gain in reindeer (McEwan and Whitehead, 1970; White, 1983). Thus, proper seasonal placement of reindeer on a highly heterogeneous nutritional landscape is very critical for animal productivity (Klein, 1970; Pulliainen, 1971; Skogland, 1978; Staaland and Saebö, 1993; Finstad, 2008)

Domestic reindeer were introduced to the Seward Peninsula; Alaska, during the late 1890s and currently are one of the primary livestock under production in Alaska (Stern et al., 1980; Finstad et al., 2006). Reindeer on the Seward Peninsula exhibit fast growth rates (0.43 kg day^{-1} for male, 0.37 kg day^{-1} for female calves) during summer and achieve a high body mass (98 kg for females in winter) and high reproductive rates (up to 39% yearling females lactating) compared to other circumpolar *Rangifer* populations (Prichard et al., 1999; Finstad and Prichard, 2000).

Forage availability (energy) is often considered the primary constraint of production for free-ranging ungulates, but this may not be the case for reindeer on the Seward Peninsula. Stocking densities of reindeer from the late 1980s to present have been relatively low (Finstad et al., 2002, 2006), and range inventories (Natural Resource Conservation Service, 1998) indicated an abundance of lichen, a primary summer and winter energy-rich forage. Indigenous caribou (*Rangifer tarandus grantii*) were not present on the Seward Peninsula in significant numbers at the time of this study to graze competitively with reindeer. Although growth and body weights of calves and adults were comparatively high across the Seward Peninsula there were differences among discrete populations of reindeer that are likely related to variation in forage quality (protein) during spring and summer (Finstad and Prichard, 2000; Finstad, 2008). Recent studies have also demonstrated the importance of diet in influencing protein allocation, protein balance, and reproduction in *Rangifer* (Barboza and Parker, 2008; Parker et al., 2009). In a recent study, Finstad (2008) found that diets of reindeer were not related to the habitat composition of ranges on the Seward Peninsula, Alaska. Instead,

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diet composition was likely related to the nutritional characteristics of individual plant growth forms.

Since many northern plant growth forms have distinctive $\delta^{15}N$ signatures (Schulze et al., 1994; Nadelhoffer et al., 1996; Kielland et al., 1998), N assimilated into various tissues of reindeer may provide insight into the environmental sources of N that are related to animal production (Gannes et al., 1997). Identification of forages that are drivers of production in reindeer populations may help herders to seasonally distribute animals on the landscape.

Hard tissue, like collagen in bone, is inert and can be used to estimate diet long after the animal has died and the soft tissue decomposed (Schell et al., 1989). For example, differences in isotopic signature of sequential hoof layers of reindeer and caribou represent annual changes in diet composition (Barnett, 1994). Antlers of reindeer and caribou are shed during the winter and regrow during the summer months when nutrient availability is high. Nitrogen in collagen is laid down during the synthesis of cartilage as antlers are formed. In reindeer, cartilage formed during antler synthesis is vascularized so it does not undergo erosion by invading blood vessels as happens in cartilage of long bones (Rönning et al., 1990). As a result, $\delta^{15}N$ signatures in sequential antler layers should temporally reflect dietary N during the growth period. Each successive layer of deposited nitrogen in antler bone may have a distinct isotopic signature indicating source (plant growth form) of protein from the environment. Since circulating N is used for synthesis of protein found in both hard and soft tissue alike, the isotopic signature of soft tissue at any one time should correspond to the N signature of collagen in sequential layers of hard tissues like hooves (Barnett, 1994) and bone in antlers.

The degree of isotope enrichment of body tissue has also been used to estimate body condition of animals (Hobson et al., 1993). Tissues of animals under nutritional stress that are catabolizing body protein show a progressive enrichment of body tissue compared to animals on diets meeting maintenance requirements (Hobson et al., 1993). In *Rangifer,* the lighter nitrogen in the waste product urea is recycled and used in place of dietary protein; therefore animal lean tissue becomes more enriched as recycled urea is used as the source of metabolic N instead of the diet (Barboza and Parker, 2006). Consequently, reindeer in negative N balance may demonstrate stronger ^{15}N enrichment of tissue than animals of better nutritional status.

Although there have been previous studies using isotopes to track N flux through ecosystems (Deniro and Epstein, 1981; Peterson and Fry, 1987; Kielland, 2001a), we know of no studies tracking flux of N through a grazing system that can be manipulated by humans to increase food production. Here we present data on $\delta^{15}N$ in both forage plants and reindeer tissue across the Seward Peninsula, Alaska. We hypothesized that variation in diet selection would be reflected in $\delta^{15}N$ signatures of reindeer tissues, which in turn may be correlated with herd productivity.

The objectives of this study were to (1) measure the $\delta^{15}N$ signatures of plant growth forms consumed by reindeer across ranges of the Seward Peninsula; (2) examine the relationship between seasonal diet composition and $\delta^{15}N$ signatures of feces, antler, and soft tissue of reindeer; and (3) measure variation of $\delta^{15}N$ signatures of reindeer tissues across herds and examine the relationship between these parameter and an index of animal production (calf weights). Samples were also collected from hunter-harvested caribou from the Western Arctic Herd (WAH) and from caribou and reindeer housed at the University of Alaska (UAF) Large Animal Research Station (LARS), for comparison of isotopic signatures of tissue from animals with sources of dietary N other than the Seward Peninsula.

Study Sites

The state and federal public lands of the Seward Peninsula have been segregated into discrete allotments where individuals are given exclusive reindeer grazing permits. This study was conducted on five reindeer grazing allotments (hereafter called ranges) extending from White Mountain (64°43′N, 163°28′W) to Shishmaref (66°14′N, 166°07′W), each with its own distinctive mix of vegetation communities (Fig. 1), (Swanson et al., 1985; Finstad, 2008). The cold Bering Sea influences climate with persistent winds in winter and cool wet weather in summer. Generally, there is an increasing ratio of graminoids to deciduous shrubs comprising the northern ranges than those in the southern Seward Peninsula (Swanson et al., 1985; Finstad and Kielland, 2005).

The Weyiouanna range consists of wet and dry tundra where graminoids, especially sedges, *Eriophorum*s spp. and *Carex aquatilis* dominate with riparian willows found in relatively small drainages (Fig. 1). The Olanna range consists of wet tundra merging with dry tundra on lower slopes of hills and mountains while upper slopes are bald limestone and lava beds. Local weather is influenced by onshore winds with cold persistent winds in winter with cool wet, foggy summers (Fig. 1). The Noyakuk range is dominated by deciduous shrubs in the floodplain surrounding the Imruk basin, a large brackish lake in the southern portion of the range and vast areas of tussock tundra extending northward to the windswept Kougarok Mountains (Fig. 1). The Davis range consists of the coastal plains near Nome where grasses dominate to the more mountainous area to the north where woody shrubs predominate (Fig. 1). The majority of the range is rolling valleys containing rivers, streams, and lowlands that support deciduous shrubs, while upland areas contain mostly lichen and graminoid species. The climate is transitional with cool, wet summers along coastal areas, but much drier and warmer inland. The Gray range is the demarcation of tree line in western Alaska so communities of predominantly deciduous shrubs are interspersed with coniferous trees (Fig. 1). The Fish River Delta is a large expanse of tidal marshes, wet sedge meadows and shrub lands. Upland slopes of dry and upland tundra surround this delta. The climate is maritime, but uplands buffer the maritime winds and precipitation so spring and summers are warm and dry which is indicated by the presence of spruce forests that are absent from the surrounding coastal areas.

Study Animals

All animal use procedures were reviewed and approved by the University of Alaska Institutional Animal Care and Use Committee, protocol 96-02.

Domestic reindeer demonstrate strong site fidelity and are relatively sedentary, so their movements and foraging activities are confined to relatively small areas (± 20 km) within the designated ranges (Oleson, 2005). Seward Peninsula reindeer herders practice an extensive management system where reindeer are allowed to free-range for much of the year, but are herded and held at specific locations throughout the year for calving or conservation of grazing areas. Recently, there has been an interest and a shift to more intensive range management to increase the productivity and economic output of their operations, particularly meat production (Finstad et al., 2006).

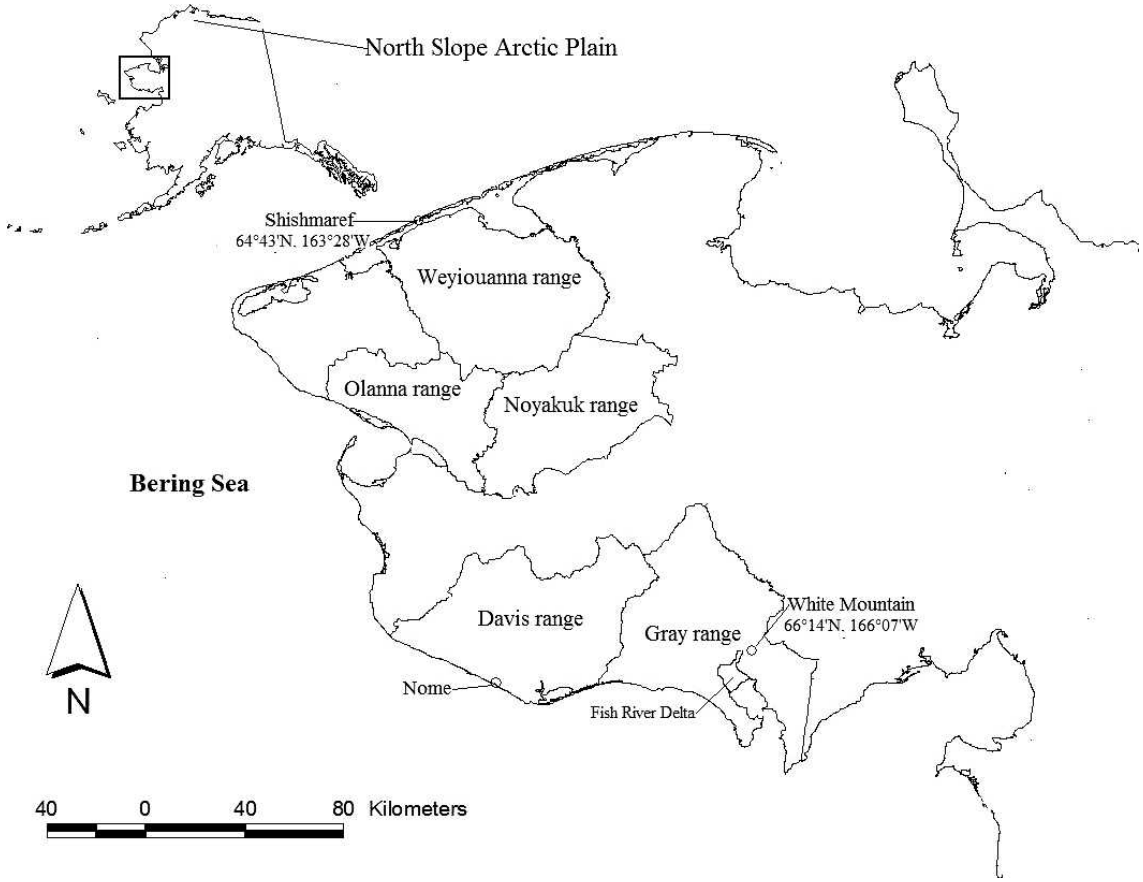

FIGURE 1. Reindeer ranges of the Seward Peninsula, Alaska where study was conducted. [please add latitude and longitude and resubmit this figure]

Herd recruitment rates were high during the time of this study, likely due to good nutrition and low predation rates. Wolves (*Canis lupus*) were generally absent from the Seward Peninsula, wolverine (*Gulo gulo*) numbers were low because of active trapping and hunting, and herders watched over animals during calving to minimize grizzly bear (*Ursus arctos horribilis*) predation of neonates at the time of this study. Indices of winter severity (cumulative wind × cumulative snow depth) were similar and around average for the winters of 1996–1997 (Finstad, 2008). Climatic events (Weladji et al., 2002; Rattenbury et al., 2009) and insect harassment (Mörschel and Klein, 1997) are known to influence *Rangifer* production, but we assumed these ubiquitous effects were constant across herds during the course of the study.

Caribou of the WAH calve on the arctic plain of the North Slope of Alaska during June (Fig. 1). The North Slope Arctic Plain is dominated by graminoids in wet sedge meadow communities (White et al., 1975). Caribou in this herd typically migrate much greater distances (100–500 km) compared to reindeer.

Samples were collected from archived antlers cast from reindeer and caribou at LARS. The LARS research station comprises 54 hectares of which approximately 50% is pasture consisting of smooth bromegrass (Bromus inermis). Caribou and domestic reindeer were fed a consistent diet of commercial pelleted ration, (Quality Texture™; QTX), and pasture throughout the antler growing season.

Methods

Ten- to twenty-gram samples of reindeer forage plants were collected once a week, May through August 1996 and May through August 1997 as part of another study (Finstad, 2008) on four replicate sites on the Davis range, five on the Gray range, three on the Olanna range, and one site on the Weyiouanna range during June 1996. Differences in number of sampling sites were due to logistical difficulties caused by extreme remoteness and severe weather. The samples included deciduous shrubs: *Salix, Betula, and Vaccinium* spp.; graminoids: *Carex,* and *Eriophorum* spp., *Arctophila fulva,* and *Calamagrostis canadensis*; forbs: *Artemisia arctica, Petasites frigidus, Equisetum* spp., *Hedysarum alpinum, Hippuris vulgaris, Epilobium* spp., *Ranunculus* spp., *Pedicularis* spp.; and lichens: *Cetraria cucullata, C. islandica, Cladina mitis/arbuscula,* and *Cladina rangiferina.* All samples were dried for 48 hours at 60 °C and then ground in a Wiley™ mill using a 1 mm screen.

We report ^{15}N natural abundance using the conventional delta notation

$$\delta^{15}\mathrm{N} = \left(\left[{}^{15}\mathrm{N}/{}^{14}\mathrm{N}\ \text{sample}/{}^{15}\mathrm{N}/{}^{14}\mathrm{N}\ \text{standard}\right] - 1\right) \times 1000), \qquad (1)$$

where the standard reference is atmospheric N (Peterson and Fry, 1987). Natural abundance of ^{15}N of all plant, antler, serum, red blood cells, muscle, urine, and fecal samples were assayed with a Europa Scientific 20–20 Continuous-flow Isotope Ratio Mass Spectrometer at the Alaska Stable Isotope Facility, University of Alaska Fairbanks. Accuracy of standard assays for peptone from meat (P7750, Sigma, Milwaukee, Wisconsin) were within 0.5‰.

The diet composition of reindeer across herds was estimated by fecal microhistological analysis. Radio-collars had been placed on adult female reindeer in each herd to support other research projects and to aid in range management. Groups of reindeer were located seasonally, either by aerial radio-tracking or by consulting with the

TABLE 1

Mean (±SE) percentage of plant growth form found in digestibility corrected seasonal diets of Seward Peninsula reindeer estimated by microhistological analysis of pooled fecal samples. Data taken from Finstad (2008).

Range	season	willow	shrub	grass	sedge	*Equisetum*	forb	lichen	moss	rhizome
Davis	spring	4.1 ± 0.6	10.2 ± 1.3	4.4 ± 0.9	9.5 ± 0.9	3.5 ± 0.1	1.6 ± 0.4	56.2 ± 2.1	10.4 ± 1.1	0.3 ± 0.2
	n/p	36/n.s.	36/**	36/n.s.	36/n.s.	36/**	36/n.s.	36/*	36/n.s.	36/n.s.
	June	19.5 ± 3.0	3.7 ± 1.0	4.2 ± 0.8	9.6 ± 1.4	6.7 ± 1.9	2.7 ± 1.0	49.0 ± 3.2	4.4 ± 0.7	0.0 ± 0.0
	n/p	21/*	21/n.s.	21/n.s.	21/**	21/*	21/n.s.	21/*	21/**	21/n.s.
	July	12.5 ± 1.9	2.4 ± 0.6	2.3 ± 0.8	11.8 ± 1.9	3.2 ± 1.0	3.4 ± 0.6	62.3 ± 3.4	2.1 ± 0.4	0.0 ± 0.0
	n/p	23/n.s.	23/n.s.	23/n.s.	23/**	23/*	23/n.s.	23/**	23/**	23/n.s.
	fall	3.8 ± 1.4	2.7 ± 0.9	1.2 ± 0.5	6.7 ± 4.7	0.0 ± 0.0	1.7 ± 0.6	81.3 ± 3.5	2.7 ± 1.5	0.0 ± 0.0
	n/p	6/n.s.	6/n.s.	6/n.s.	6/n.s.	6/*	6/n.s.	6/*	6/n.s.	6/n.s.
	winter	4.0 ± 1.5	2.3± 0.7	4.6 ± 1.4	10.7 ± 1.1	1.2 ± 0.7	0.9 ± 0.1	71.8 ± 3.0	5.4 ± 1.9	0.0 ± 0.0
	n/p	4/n.s.	4/n.s.	4/n.s.	4/n.s.	4/n.s.	4/**	4/n.s.	4/n.s.	4/n.s.
Gray	spring	2.4 ± 0.7	2.6 ± 0.7	2.5 ± 0.6	8.6 ± 1.4	4.3 ± 2.2	2.4 ± 2.0	65.1 ± 2.3	8.6 ± 1.3	3.5 ± 1.6
	n/p	29/n.s.	29/**	29/n.s.	29/n.s.	29/**	29/n.s.	29/*	29/n.s.	29/n.s.
	June	26.6 ± 3.2	1.7 ± 1.1	7.3 ± 1.6	25.1 ± 3.0	0.9 ± 0.4	0.8 ± 0.9	36.8 ± 5.5	0.6 ± 0.2	0.2 ± 0.1
	n/p	23/*	23/n.s.	23/n.s.	23/**	23/*	23/n.s.	23/*	23/**	23/n.s.
	July	30.5 ± 4.8	1.2 ± 0.8	8.5 ± 1.9	31.8 ± 3.9	1.2 ± 0.7	1.8 ± 0.9	24.1 ± 7.2	0.6 ± 0.9	0.3 ± 0.3
	n/p	15/n.s.	15/n.s.	15/n.s.	15/**	15/*	15/n.s.	15/**	15/**	15/n.s.
	fall	1.4 ± 0.7	3.9 ± 0.8	4.3 ± 0.4	8.1 ± 1.4	5.7 ± 1.4	2.3 ± 1.1	68.7 ± 2.3	3.6 ± 0.5	1.0 ± 0.3
	n/p	24/n.s.	24/n.s.	24/n.s.	24/n.s.	24/*	24/n.s.	24/*	24/n.s.	24/n.s.
	winter	0.8 ± 0.3	3.8 ± 0.9	2.9 ± 1.0	9.6 ± 1.9	0.2 ± 0.1	0.16 ± 0.3	71.9 ± 3.6	9.4 ± 2.3	1.3 ± 0.8
	n/p	18/n.s.	18/n.s.	18/n.s.	18/n.s.	18/n.s.	18/**	18/n.s.	18/n.s.	18/n.s.
Noyakuk	spring	2.4 ± 0.5	5.5 ± 1.2	2.5 ± 1.4	7.8 ± 2.7	4.4 ± 1.9	1.3 ± 0.7	68.8 ± 4.4	7.3 ± 2.0	0.0 ± 0.0
	n/p	7/n.s.	7/*	7/n.s.	7/n.s.	7/**	7/n.s.	7/*	7/n.s.	7/n.s.
	June	41.4 ± 9.6	4.7 ± 4.7	2.6 ± 0.6	7.8 ± 3.8	0.0 ± 0.0	1.2 ± 1.2	38.9 ± 14.4	3.4 ± 3.4	0.0 ± 0.0
	n/p	2/*	2/n.s.	2/n.s.	2/**	2/*	2/n.s.	2/*	2/**	2/n.s.
	winter	5.4 ± 1.6	7.3 ± 0.9	1.2 ± 0.6	3.6 ± 2.2	0.0 ± 0.0	2.8 ± 1.0	76.6 ± 3.1	3.1 ± 0.7	0.0 ± 0.0
	n/p	4/n.s.	4/n.s.	4/n.s.	4/n.s.	4/n.s.	4/**	4/n.s.	4/n.s.	4/n.s.
Olanna	spring	4.2 ± 1.2	1.9 ± 0.6	3.3 ± 0.7	8.8 ± 1.6	14.2 ± 5.1	1.0 ± 0.5	56.0 ± 5.1	8.2 ± 1.6	2.5 ± 1.0
	n/p	9/n.s.	9/*	9/n.s.	9/n.s.	9/**	9/n.s.	9/*	9/n.s.	9/n.s.
	June	13.9 ± 3.1	1.6 ± 0.8	6.3 ± 2.2	11.6 ± 2.1	8.5 ± 2.3	0.6 ± 0.3	49.4 ± 3.2	4.8 ± 0.6	3.3 ± 2.6
	n/p	9/*	9/n.s.	9/n.s.	9/**	9/*	9/n.s.	9/*	9/**	9/n.s.
	July	17.0 ± 2.7	3.9 ± 2.2	1.4 ± 0.6	12.1 ± 3.9	7.2 ± 1.8	3.0 ± 1.0	48.8 ± 5.0	5.9 ± 1.2	0.8 ± 0.6
	n/p	9/n.s.	9/n.s.	9/n.s.	9/**	9/*	9/n.s.	9/**	9/**	9/n.s.
	winter	0.0	7.7	0.6	2.5	0.0	0.0	76.0	13.3	0.0
	n/p	1/n.s.	1/n.s.	1/n.s.	1/n.s.	1/n.s.	1/**	1/n.s.	1/n.s.	1/n.s.
Weyiouanna	June	40.1 ± 3.4	2.7 ± 0.9	4.7 ± 0.9	12.0 ± 3.3	4.4 ± 1.4	2.3 ± 1.3	31.4 ± 4.5	1.8 ± 0.5	0.0 ± 0.0
	n/p	9/*	9/n.s.	9/n.s.	9/**	9/*	9/n.s.	9/*	9/**	9/n.s.

Comparison of seasonal column means across ranges; n = sample size,* = $p < 0.05$; ** = $p < 0.01$; n.s. = not significant.

reindeer herder. Ground crews traveled to reindeer group locations and collected fresh fecal pellets. Each sample was a composite of 5–10 fecal pellets from 8–10 distinct pellet groups. Composite samples were used to estimate overall diet of the herd rather than individual reindeer. The samples were sent to the Wildlife Habitat Laboratory, Washington State University, for diet composition analysis at Level A, 100 views (Table 1). Results were partitioned into spring (March–May), June, July, and winter (December–February) time periods. There is variation in digestibility of the different plant growth forms eaten by reindeer which will influence the proportion of undigested plant cell fragments found in the feces. The diet composition data was corrected for digestibility of the different plant growth forms found on the Seward Peninsula using digestibilities taken from Finstad (2008). Sub-samples of the fecal collections were analyzed for natural abundance of ^{15}N.

We wished to explore the premise that the isotopic value of an animal's feces reflects the relative contributions of different food items to its diet. This premise relies on the assumption that a linear relationship exists where the composition of the feces equals the weighted proportion of a food item's contribution to the diet (adjusted for digestibility) times its isotopic value (Coates et al., 1991). Since N concentrations and δ^{15} N signatures are similar among species of forage on the Seward Peninsula, an estimate of the δ^{15}N signature of the feces based on the δ^{15} N input of growth forms in the diet can be estimated by the equation:

$$\delta^{15}\text{N feces} = \sum\left[\frac{\%\text{ growth form in diet} \times [\text{N}]}{\sum \%\text{ growth form in diet} \times [\text{N}]} \times \delta^{15}\text{ N of growth form}\right], \quad (2)$$

where growth forms were shrubs, graminoids, forbs, lichen, and mosses.

Mosses were not collected from the Seward Peninsula ranges, but appeared in the microhistological fecal analysis, hence N concentrations and δ^{15}N values were taken from Kielland (1997, 2001a).

Although velvet antlers were harvested by the reindeer herders in these herds during summer handlings, the animals were dispersed over large and rugged ranges and a number of reindeer escaped gathering and herding. These animals retain a full set of antlers through the winter months until casting in the spring. Cast antlers from adult females were collected from calving grounds during May from the Davis (Nome), and Gray (White Mountain) ranges on the Seward Peninsula, Alaska.

Hard antlers were cut off immediately above the corona with a hack saw from slaughtered adult females at the Noyakuk,

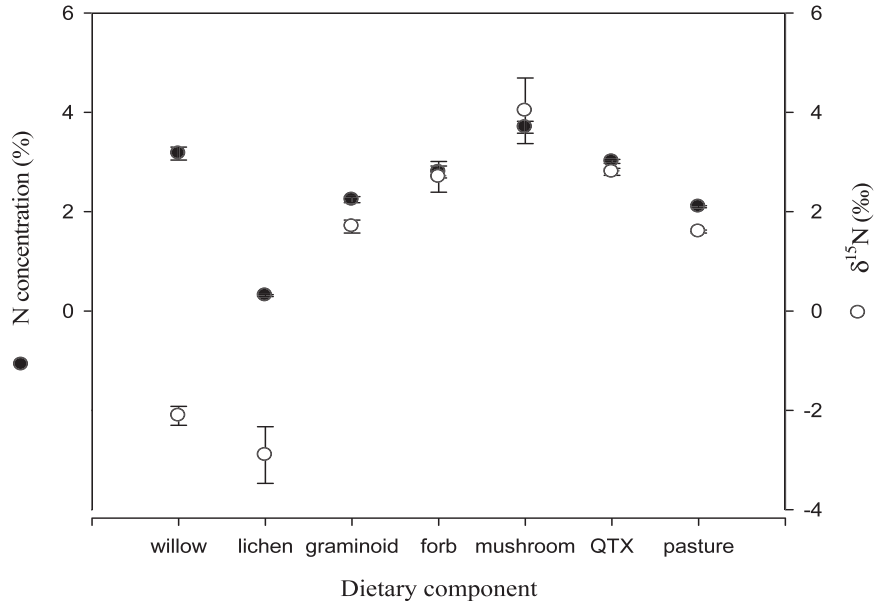

FIGURE 2. Mean (±SE) N concentration (%) and $\delta^{15}N$ values (‰) of dietary components eaten by free-ranging reindeer on the Seward Peninsula and by reindeer and caribou at the University of Alaska Large Animal Research Station (LARS) (commercial pellets and pasture). (*n* = willow (93), lichen (11), graminoid (150), forb (62), mushroom (3), QTX (Quality Texture, a commercial pelleted ration) (5), and pasture (5)).

Olanna, and Weyiouanna midwinter reindeer handlings. Antlers were removed in the same manner from 10 WAH caribou (2 adult females, 6 yearling males, and 2 two-year-old caribou males) killed by hunters in the Fish River Flats near White Mountain, Alaska. Ages of harvested animals were estimated by experienced local hunters from body size and antler conformation. Cast antlers were collected from known age reindeer and caribou located at LARS. Composition of cut and cast antlers is assumed to be stable and comparable since mineral deposition is halted after the velvet is shed earlier in the year. All antlers were scrubbed with a stiff nylon brush and rinsed with distilled water to remove any residual blood, velvet, or other organic material and allowed to dry.

Five grams of core trabecular bone (AC) was collected by drilling an 8 mm × 60 mm hole centered in the base parallel to the axis of the antler with a handheld electric drill using a stainless steel masonry bit. The filings were collected in a plastic 100 mm × 100 mm plastic weigh boat. A 5-gram sample of peripheral compact bone (AP) was also collected near the base of the antler. A stainless steel burring bit mounted on a hand held drill was used to grind off 1 mm of surface bone from 20–60 mm above the base of the antler. The filings were collected in a plastic 100 mm × 100 mm plastic weigh boat. All samples were ground in a Wiley™ mill using a 20 mesh screen.

Subsamples of serum and red blood cells were partitioned from blood samples collected from lactating adult females during early summer (June) at Davis, Gray, and Olanna handlings. Blood was collected from parturient adult females in all herds during mid-winter along with feces, and muscle tissue from slaughtered adult pregnant Noyakuk females, as well as from hunter-killed WAH caribou. Serum, red blood cells, muscle tissue, and urine were dried at 60 °C for 48 to 72 hours in stainless steel vessels.

In this study, June 1996 and 1997 calf weights were used as an indicator of reproductive capacity and productivity as used in other *Rangifer* studies (Reimers et al., 1983; Reimers, 1997). Heavier calves going into winter have a greater survival rate (Haukioja and Salovaara, 1978; Cook et al., 2004) which improves recruitment and population dynamics (Gaillard et al., 1998). All reindeer in each herd were located from the air and herded into a corral system by helicopter during the latter part of June for censusing, ear tagging, veterinary care, and husbandry. All calves herded into the corral during the June handling were weighed on a Tru-test™ livestock scale to the nearest 0.5 kg. If the corralling and weighing did not occur on the same day across herds, then the calf weights were adjusted by the daily rate of gain of calves to standardize the date of weighing to 25 June (Finstad, 2008).

To meet the assumption of normality, all proportional data was transformed using the arcsine of the square root prior to statistical analysis. Transformed and untransformed data were checked for assumptions of normality and homogeneity of error variance. Analysis of Variance (ANOVA) was used to compare differences in AC, AP, feces, muscle tissue, serum, and RBC $\delta^{15}N$ values (effects) due to range (factors). A general linear model (GLM) procedure using Systat 8.0 (1998) was used to evaluate the effects of differences in the proportions of plant growth forms in the diet on fecal, antler, soft tissue $\delta^{15}N$ concentrations, and June calf weight across herds. (Systat 8.0). For all statistical tests, $p \leq 0.05$ was deemed significant.

Results

Diet composition results were reported according to plant growth form. Nitrogen concentrations and $\delta^{15}N$ values varied little among species within a plant growth form (mean ± 1.0%), so these results were pooled according to plant growth form for comparative analysis with diet composition results. Nitrogen concentrations and $\delta^{15}N$ values of different growth forms eaten by free-ranging reindeer of the Seward Peninsula varied significantly (ANOVA; $F_{(4,329)}$ 34.7, $p < 0.001$); ($F_{(4,329)}$ 95.6, $p < 0.001$); (Fig. 2). Nitrogen concentration was highest in mushrooms (3.6% ± 0.1) and foliage of willows (3.2% ± 0.1), followed by forbs (2.8% ± 0.1), then graminoids (2.2% ± 0.1), with lichens containing very low concentrations (0.3% ± 0.0). We found depleted $\delta^{15}N$ signatures in the foliar tissue of willows (−2.1‰ ± 0.2) and lichens (−2.3‰ ± 0.5), whereas forbs (2.7‰ ± 0.3), graminoids (1.7‰ ± 0.1), and mushrooms (4.0‰ ± 0.6) were relatively enriched in ^{15}N. Nitrogen concentrations and $\delta^{15}N$ values of the QTX fed to reindeer and caribou at LARS were 3.0% ± 0.1 and 2.8‰ ± 0.1 (Fig. 2), respectively. The N concentrations and $\delta^{15}N$ values of the LARS pasture grass was 2.8% ± 0.1 and 1.6‰ ± 0.0, respectively (Fig. 2).

Prediction of the isotopic signature of feces by the input of $\delta^{15}N$ of each forage class in the seasonal diet (estimated by

TABLE 2

Nitrogen concentrations (mean ± SE) of feces and tissue from five reindeer ranges and WAH caribou on the Seward Peninsula, Alaska, and captive reindeer and caribou at the University of Alaska Large Animal Research Station (LARS). AC = antler core, AP = antler periosteum, RBC = red blood cells.

	percentage (%) Nitrogen							
	winter						summer	
Range	AC	AP	muscle	serum	RBC	fecal	serum	fecal
Davis	7.1 ± 0.13	8.1 ± 0.2		13.0 ± 0.1			13.8 ± 0.1	3.2 ± 0.1
n/p	15/**	12/**		8/**			6/**	14/**
Gray	7.2 ± 0.19	8.7 ± 0.3		13.4 ± 0.1			13.3 ± 0.1	3.1 ± 0.0
n/p	13/**	5/**		11/**			13/**	7/**
Noyakuk	6.8 ± 0.2	7.9 ± 0.3	13.2 ± 0.3	13.0 ± 0.1	15.3 ± 0.1	2.0 ± 0.0		
n/p	21/**	21/**	4/n.s.	11/**	14/*	5/n.s.		
Olanna	7.0 ± 0.3	6.8 ± 0.2		13.7 ± 0.1	15.7 ± 0.0		13.1 ± 0.1	2.7 ± 0.1
n/p	11/**	8/**		21/**	3/*		22/**	6/**
Weyiouanna	7.0 ± 0.3	7.6 ± 0.2		12.8 ± 0.4	15.4 ± 0.1			
n/p	7/**	7/**		8/**	9/*			
WAH	8.0 ± 0.4	9.1 ± 0.5	13.1 ± 0.1	12.4 ± 0.2	15.4 ± 0.0	1.9 ± 0.1		
n/p	9/**	8/**	7/n.s.	6/**	6/*	9/n.s.		
LARS	5.9 ± 0.2	6.9 ± 0.3						
n/p	21/**	16/**						

Comparison of column means; *n/p*, n = sample size, * = $p < 0.05$; ** = $p < 0.01$; n.s. = not significant.

Equation 2) was significant ($p = 0.004$), although R^2 was relatively low 0.24. The prediction equation was:

$$\delta^{15}\text{N feces} = 42.7(\delta^{15}\text{N willows}) - 54.3(\delta^{15}\text{N graminoids}) - 34.1(\delta^{15}\text{N forbs}) + 32.7(\delta^{15}\text{N lichens}) + 91.2(\delta^{15}\text{N mosses}) + 92.4. \quad (3)$$

The concentration of N (Table 2) and δ^{15}N signatures (Table 3) of reindeer and caribou tissues varied significantly across ranges. Values for δ^{15}N varied from −3.1‰ ± 0.8 in urine to above 3.0‰ ± 0.1 in the AP layer and muscle tissue (Fig. 3).

Nitrogen concentration of antlers from penned animals at LARS was significantly lower in both AC (5.9 ± 0.2%) and AP (6.9 ± 0.3%) layers than antlers from Seward Peninsula reindeer and WAH caribou (Table 2). AC δ^{15}N values were significantly and inversely related to AC N concentrations ($n = 62$; $p < 0.01$; $R^2 = 0.20$). The differential in δ^{15}N values of AC to AP layers varied among Seward Peninsula reindeer herds and WAH caribou, whereas there was no difference in isotopic signature between antler layers of captive animals from LARS (Fig. 4; Table 3). AC δ^{15}N values were significantly and inversely related to proportions of shrubs in May diets across ranges ($n = 62$; $p = 0.005$; $R^2 = 0.13$), (Fig. 5).

Serum δ^{15}N values varied significantly across ranges both in summer and winter (Table 3), and all serum was more enriched in winter than in summer, but there was considerable variation among herds (Fig. 6).

Whereas 25 June calf weight varied significantly interannually among herds ($F_{(4,2764)}$ 384.0; $p > 0.0001$), there was relatively little

TABLE 3

δ^{15}N values (mean ± SE) of feces and tissue from five reindeer ranges and Western Arctic Herd (WAH) caribou on the Seward Peninsula, Alaska, and captive reindeer and caribou at the University of Alaska Large Animal Research Station (LARS). AC = antler core, AP = antler periosteum, RBC = red blood cells.

	δ^{15} Nitrogen							
	winter						summer	
Range	AC	AP	muscle	serum	RBC	fecal	serum	fecal
Davis	−0.6 ± 0.2	0.3 ± 0.1		1.2 ± 0.2			−0.5 ± 0.1	−1.7 ± 0.2
n/p	14/**	11/**		8/**			6/**	14/**
Gray	0.5 ± 0.1	0.7 ± 0.2		1.4 ± 0.1			1.0 ± 0.2	−0.6 ± 0.1
n/p	13/**	5/**		11/**			13/**	7/**
Noyakuk	1.01 ± 0.2	2.5 ± 0.2	3.1 ± 0.1	2.1 ± 0.1	1.9 ± 0.1	−1.0 ± 0.1		
n/p	21/**	21/**	4/**	11/**	14/**	4/n.s.		
Olanna	1.9 ± 0.2	3.3 ± 0.2		2.4 ± 0.1	2.2 ± 0.1		1.4 ± 0.1	−0.02 ± 0.3
n/p	11/**	8/**		21/**	3/**		22/**	6/**
Weyiouanna	2.4 ± 0.2	3.0 ± 0.3		2.1 ± 0.2	2.3 ± 0.1			
n/p	7/**	7/**		7/**	9/**			
WAH	1.0 ± 0.2	1.6 ± 0.2	2.0 ± 0.2	1.9 ± 0.2	1.5 ± 0.1	−0.8 ± 0.2		
n/p	9/**	8/**	9/**	6/**	6/**	9/n.s.		
LARS	5.7 ± 0.1	5.8 ± 0.1						
n/p	21/**	16/**						

Comparison of column means; n/p, *n* = sample size, * = $p < 0.05$, ** = $p < 0.01$, n.s. = not significant.

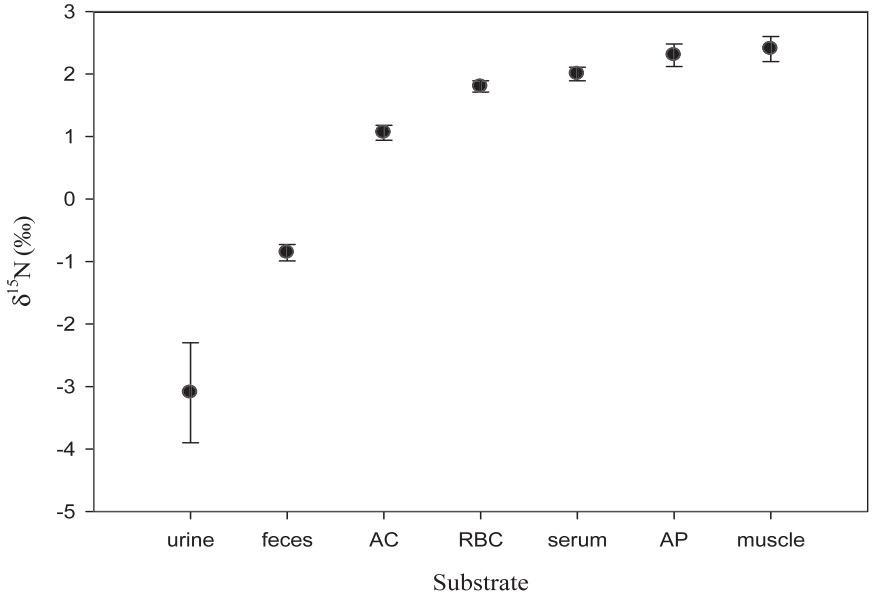

FIGURE 3. Mean (±SE) $\delta^{15}N$ values of reindeer and caribou tissue on the Seward Peninsula during winter. AC = antler core; RBC = red blood cells; AP = antler periphery. (*n* = urine (3), feces (41), AC (97), RBC (32), serum (65), AP (77), muscle (11)).

interannual variation of 25 June calf weight within a herd (Table 4). Summer serum ($n = 41$; $p < 0.01$; $R^2 = 0.40$), and AC $\delta^{15}N$ ($n = 62$; $p < 0.01$, $R^2 = 0.3$) values were significantly and positively related to June calf weight of the following year, but serum $\delta^{15}N$ explained more of the variation. Winter serum $\delta^{15}N$ ($n = 58$; $p = 0.02$; $R^2 = 0.1$) and AP $\delta^{15}N$ ($n = 62$; $p < 0.01$; $R^2 = 0.33$) values also were significantly and positively related to herd mean calf weight of the following year. The percentage of shrubs in the May diet was significantly and inversely related to mean calf weight the previous June ($n = 2771$; $p < 0.001$; $R^2 = 0.3$).

Discussion

Nitrogen from diverse plant growth forms with distinct isotopic signature was deposited in tissues in a manner that reflects temporal-spatial patterns of grazing that in turn are associated with variation in animal productivity amongst Seward Peninsula reindeer herds.

It has been suggested that arctic plants in the same habitat absorb N from different pools with significant differences in $\delta^{15}N$ signatures (Nadelhoffer et al., 1996; Michelsen et al., 1996; Kielland, 1997). Evergreen and deciduous shrubs are typically much more depleted in ^{15}N than graminoids and forbs (Schulze et al., 1994; Nadelhoffer et al., 1996; Valentine et al., 2006; Yano et al., 2010). The differences in $\delta^{15}N$ values of plant growth forms found on the Seward Peninsula may be attributed to different rooting depths tapping N pools associated with soil horizon (Gebauer and Schulze, 1991), mycorrhizal association (Michelson et al., 1996; Hobbie and Hobbie, 2006), or form of N absorbed (Kielland and Chapin, 1992; Kielland, 1997; Yano et al., 2010).

Although diet determines the overall isotopic signature of tissues of animals, considerable variation among different tissues exists. Bone, because of its metabolic longevity, usually is the most enriched tissue of the body (Schoeninger and DeNiro, 1984). However; N metabolism in antler bone is different than skeletal bone. N deposited as collagen in antler cartilage is not replaced

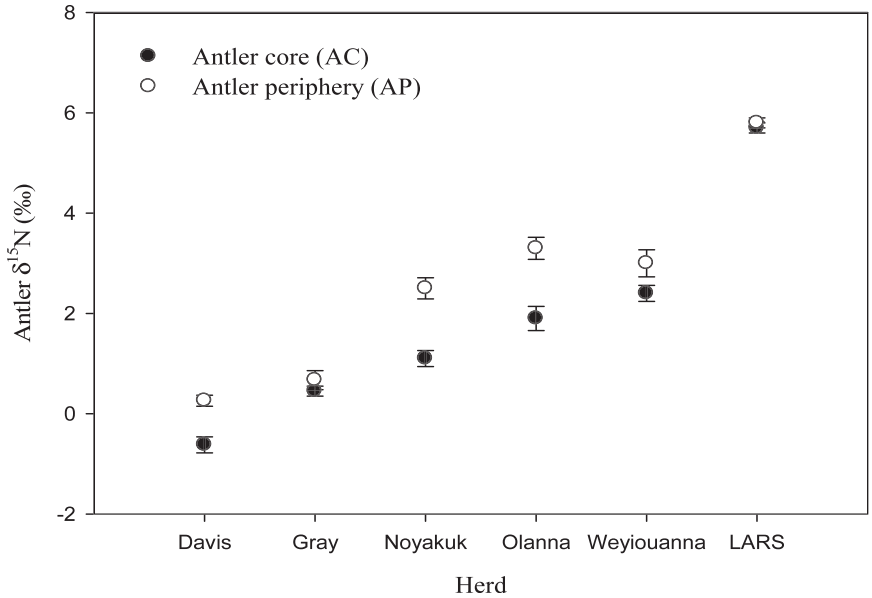

FIGURE 4. Mean (±SE) $\delta^{15}N$ values of samples taken from the core and periphery of antlers collected from reindeer herds across the Seward Peninsula and LARS. (*n* for each group can be found in Table 3).

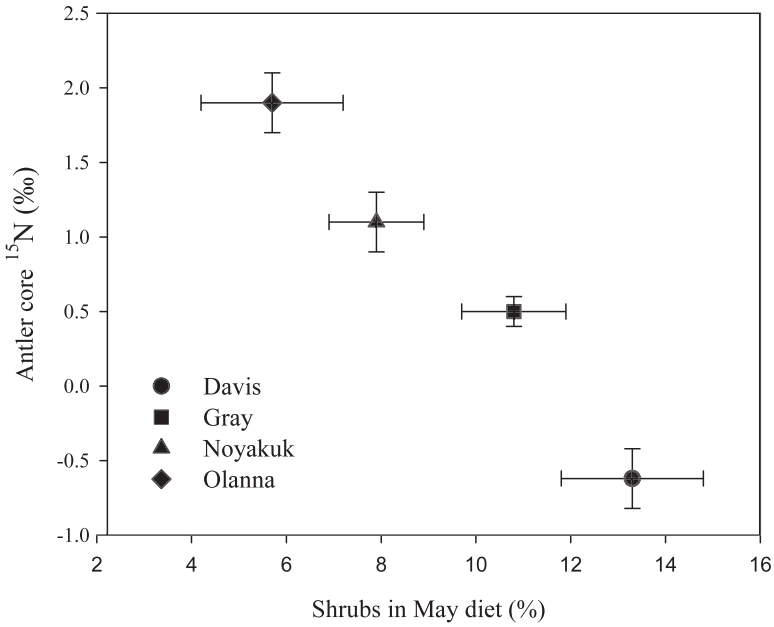

FIGURE 5. Relationship between percentage of shrubs in the May diet and the δ^{15}N signature of bone taken from the antler core (AC) across reindeer herds of the Seward Peninsula, Alaska. Means (±SE).

later during bone synthesis, but instead is embedded in the inert matrix of the antler (Rönning et al., 1990). A shortened metabolic pathway of deposited antler nitrogen relative to skeletal nitrogen may explain why antler δ^{15}N values were more depleted than soft tissues (Fig. 3).

Turnover experiments have demonstrated that diet-switching influences δ^{15}N values of body tissue (Peterson and Fry, 1987). For example, seasonal variations in proportions of forage consumed (woody shrubs in winter vs. forbs and aquatic vegetation in summer) are reflected in fluctuating δ^{15}N hoof values in moose (Kielland, 2001b). Analysis of δ^{15}N in rumen and hooves in Alaskan caribou show correlated enrichments during early spring and autumn when forbs and graminoids predominate in the diet compared to depleted summer values when caribou are grazing on a higher proportion of deciduous shrubs (Barnett, 1994). In this study, δ^{15}N enrichment of reindeer antlers and soft tissue deposited throughout the growing season corresponded to the shift in diet from predominately deciduous shrubs to graminoids (Fig. 4; Table 1). Both caribou and reindeer diets shifted from shrub-based in spring to graminoid-based later in summer (Table 1). Antler peripheral bone was enriched in ^{15}N compared to AC in all free-ranging reindeer and caribou, whereas captive LARS reindeer exhibited negligible variation, consistent with a uniform diet throughout the year. These data suggest that layers of collagen deposited during the antler growing season provide an index of the proportions of different plant growth forms in the diet at the time the collagen was being deposited. Although AP was biologically inert months before blood was collected in winter, the δ^{15}N values of AP and winter serum should be correlated. Deposition of N in lean tissue and organs is greatly reduced in animals having reached body condition thresholds during fall (Chan-McLeod et al., 1994); hence δ^{15}N of lean tissues should remain relatively stable throughout fall and winter as a result of this metabolic inactivity. The correlation between the isotopic signature of soft tissue and antler collagen suggest that AC and AP δ^{15}N signatures can be used to estimate source of N (plant growth form) in spring and summer diets of reindeer that are assimilated into lean tissue.

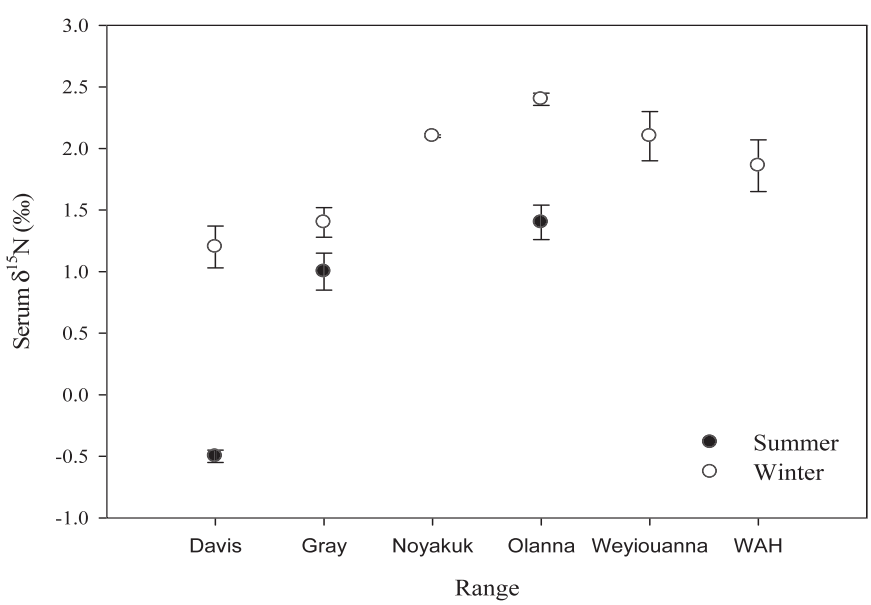

FIGURE 6. Mean (±SE) serum δ^{15}N values during summer and winter from Seward Peninsula reindeer and the Western Arctic Herd (WAH) caribou. (*n* for each group can be found in Table 3).

TABLE 4

Mean (±SE) 25 June calf weight (kg) and sample size for reindeer herds across the Seward Peninsula, Alaska.

Davis		Gray		Noyakuk		Olanna		Weyiouanna	
1996	1997	1996	1997	1996	1997	1996	1997	1996	1997
27.5 ± 0.1	27.6 ± 0.2	34.0 ± 0.2	34.0 ± 0.4	32.4 ± 0.3	31.9 ± 0.5	31.4 ± 0.3	32.7 ± 0.6	31.4 ± 0.3	32.6 ± 0.3
451	361	371	156	393	62	180	150	411	236

We have also shown that fecal $\delta^{15}N$ was significantly related to the proportional intake of forage growth forms consumed throughout the spring and summer. However, it could only predict about 20% of the variation in dietary $\delta^{15}N$. Proteins in forage have various solubilities and digestibilities that will likely "steer" N into different metabolic pathways (Van Soest, 1994). Isotopic composition of ruminant tissue is generally enriched by 3 to 6‰ relative to the diet (Steele and Daniel, 1978; Halley et al., 2010). This enrichment occurs during the many metabolic processes that fractionate stable isotopes after consumption by animals. Transamination of amino acids favors the lighter isotope resulting in lighter end products and enrichment for the substrate amino acids (Macko et al., 1986). Thus, depending upon the pathways and transamination reactions involved, individual amino acids can differ greatly from the source material from which they were derived (Macko et al., 1987). This is especially true in ruminants where protein undergoes a variety of deamination and transamination reactions before being digested and absorbed in the small intestine. Bacterial protein in the rumen undergoes a much different metabolic route than protein contained in ruminal protozoa, further muddling enrichment pathways (Van Soest, 1994).

Concomitant with reduced food intake during winter (Tyler et al., 1999), reindeer conserve body protein by recycling urea. They will also break down lean tissue to meet metabolic energy demands when dietary intake of N is lower than maintenance requirements (Parker et al., 2005). This process could increase ^{15}N fractionation as the animal continues to remain in a negative N balance. Reindeer in a negative N balance would thus be expected to have more enriched $\delta^{15}N$ tissue values than animals in neutral or positive N balance (Hobson et al., 1993). Pregnant females, in particular, are most vulnerable to N deficits in late winter because of demands for fetal growth. Female *Rangifer* in poor winter body condition typically have smaller calves (Reimers, 1997). Moreover, an increase in mass loss of the female during winter often results in reduced milk production and calf growth (Rognmo et al., 1983). Consequently, female reindeer exhibiting relatively enriched $\delta^{15}N$ tissue values should be expected to have lighter calves. Our results on calf weights and serum $\delta^{15}N$ in parturient female reindeer do not support this attractive, parsimonious hypothesis. Across 5 reindeer herds we failed to detect a significant inverse relationship between winter serum $\delta^{15}N$ of parturient females and calf weight the following June, but instead found a positive, although weak relationship: calf weight (kg) = 30.1 + winter serum δ^{15} N(1.03); ($n = 58$, $p = 0.02$, $R^2 = 0.1$). Indeed, the herd with the lowest calf weight (Davis) had the most depleted $\delta^{15}N$ tissue values (Table 4, Table 3).

Reindeer catabolizing a larger proportion of their body protein during winter will be expected to have both greater seasonal tissue $\delta^{15}N$ differentials and less body protein to contribute to fetal development and lactation. We found that a fourfold increase in serum $\delta^{15}N$ differential ($|\delta^{15}N$ winter $- \delta^{15}N$ summer$|$; Fig. 6) corresponded to a nearly 20% reduction in mean June calf weight (Table 3), ($n = 64$, $p < 0.001$, $R^2 = 0.66$). These data suggest that the relative difference between summer and winter serum $\delta^{15}N$ signatures is positively correlated with the degree of protein catabolization in female reindeer during winter and negatively correlated to mean calf weights the following June.

The proportion of shrubs in the diet during May (when antlers first start to grow) was highly and positively correlated with AC $\delta^{15}N$ values. Even though gain during spring in female reindeer is inversely correlated with initial weight (Fauchald et al., 2004), lighter females may not reach a similar body mass in autumn as animals starting in good spring body condition (Gjøstein et al., 2004). Hence, one would expect females with lower protein reserves in spring to increase the proportion of protein in their diets to support lactation and to regain lean mass. Leaves of most shrubs, graminoids, and forbs on the Seward Peninsula do not emerge until June (Finstad, 2008), but many shrubs are translocating N to stems and leaf buds before emergence which results in higher protein concentrations (Chapin et al., 1980). Leaves and catkins of forage shrubs on the Seward Peninsula contain high concentrations of protein, but relatively little digestible energy (Finstad, 2008). Catkins, stems, and leaf buds of shrubs began appearing in diets of Seward Peninsula reindeer during May, whereas proportions were found to be inversely correlated with June calf weight the previous year (Tables 2 and 4).

Protein depots of female reindeer appear to be critical for reproduction. Female reindeer appear to invest proportionally more body than dietary protein in fetal growth (capital breeders) compared to caribou (income breeders) (Barboza and Parker, 2008). Also, protein requirements increase 110–130% to support lactation (Barboza and Parker, 2008). Reindeer in a more negative protein balance may be compensating by selecting for a more protein-rich diet earlier in the spring as suggested by our results. However, this strategy would likely come at an energetic cost to foraging reindeer. Deep drifts caused by blowing snow bury deciduous shrubs, particularly riparian habitats on the Seward Peninsula, which persist well into late spring. Reindeer would likely expend considerable energy struggling through deep, soft, wet snow to access habitats with protein-rich, but energy deficient forages during May (Fancy and White, 1985). Reindeer generally avoid areas where snow impedes access to food (Skogland, 1978), but reindeer herders could increase accessibility and reduce the energetic cost of foraging by establishing trails into shrub habitats during late spring with the use of snowmobiles.

Tissues from herds that are isotopically depleted in May remain depleted even though the diet becomes much more enriched later in summer and fall (Fig. 5; Table 1). Forages contain a variety of anti-herbivory compounds that influence the digestibility and the cycling of N through the digestive system of ruminants (Robbins et al., 1987). Binding of condensed tannins (CT) with proteins can reduce the degradation of forage proteins in the rumen. Undegraded proteins enter the abomasum where they are hydrolyzed and absorbed by the small intestine (Min et al., 2003). These "escaped" amino acids most likely will have a $\delta^{15}N$ signature more similar to the diet than amino acids originating from microbial protein. Newly emerging leaves of shrubs contain CT, which explains the lower digestibility of newly

emerged shrub leaves on the Seward Peninsula (Finstad, 2008). A moderate concentration of CT in the diet of ruminants has been shown to improve animal production, presumably because CT reduces rumen protein degradation (Min et al., 2003). Reindeer fed isonitrogenous diets showed significantly higher feed conversion efficiency on a low rumen-degradable protein ration (Finstad et al., 2007). These studies and our data suggest that female reindeer on inferior ranges may be compensating by consuming protein-rich forages with low levels of CT earlier in the spring to promote a more complete amino acid profile of digesta reaching the small intestine. This in turn may support higher N assimilation rates in lean tissue. This may also explain why AC N concentrations were significantly and inversely related to AC $\delta^{15}N$. The interaction of a less fractionated protein in the diet and high N assimilation rates of lean tissue, shrubs in spring diets may leave a $\delta^{15}N$ legacy in the tissues of reindeer and caribou.

The climate of northern environments is expected to change dramatically which will likely influence composition of plant communities, thus the nutritional landscape of the Seward Peninsula. Our study suggests reindeer herders can use cast antlers (or soft tissues) as a bio-indicator of the seasonal diet of reindeer. Long-term changes in $\delta^{15}N$ values of antler layers may represent dietary shifts caused by newly emerging vegetation communities. Historical calving and seasonal use areas may no longer provide the protein-rich forages to support the high productivity of reindeer herds on the Seward Peninsula. Herders now may be able to detect and react to climate-induced vegetation changes by evaluating new grazing areas by following the flux of protein (N) through their reindeer herds.

Although our study proposes that $\delta^{15}N$ values of cast antlers are the product of unique nutritional landscapes across the Seward Peninsula, it remains to be seen if this technique can be used in other *Rangifer* populations. Discrete herds of reindeer on the Seward Peninsula forage in relatively small, unique habitats, which contain abundant protein-rich forages with distinct $\delta^{15}N$ signatures, and they abruptly shift diets during the year (Oleson, 2005; Finstad, 2008). Other *Rangifer* populations may consume forage with less distinct $\delta^{15}N$ signatures over much larger areas with a greater diversity of habitats. This may decrease the resolution in which we can match sources of N in the environment to soft and hard tissues in *Rangifer*.

In conclusion, we argue that values of $\delta^{15}N$ in cast antlers may be used to track fluxes of N through a grazing ecosystem that can be manipulated by humans. We showed that $\delta^{15}N$ signatures of plant growth forms consumed by reindeer across the Seward Peninsula varied significantly with shrubs and lichens being much more depleted in ^{15}N than graminoids and forbs. Reindeer began consuming shrubs during and after snowmelt and shifted to an isotopically more enriched diet of graminoids later in summer. The abundance of ^{15}N in layers of antler bone as were soft tissue were significantly correlated with that of the seasonal diet; supporting our hypothesis that antler may be used as a bio-indicator of seasonal diet.

June calf weights were inversely related to the isotopic differential in seasonal serum values across Seward Peninsula reindeer herds, suggesting increased catabolism of body protein during winter by parturient females negatively influenced growth of their calves.

AC $\delta^{15}N$ values among herds were positively correlated to the proportion of shrubs in the May diet, and AP $\delta^{15}N$ values were enriched in all herds likely due to an increased proportion of graminoids and forbs later in the summer diet. Reindeer in herds with lighter June calves consumed proportionately more shrubs the following May, presumably to compensate for lower protein reserves. In herds with greater serum isotope differentials and lower calf weights, herders may be able to increase protein balance of reproductive females by improving access to areas with protein-rich shrubs during spring.

Acknowledgments

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