Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology

David R. Klein[1]

[1] Alaska Cooperative Wildlife Research Unit, University of Alaska. Fairbanks, Alaska 99775, U.S.A. (This research unit is cooperatively supported by the U.S. Fish and Wildlife Service, the University of Alaska, and the Alaska Department of Fish and Game).

Abstract: Plant parts used as forage by caribou and reindeer *(Rangifer tarandus)* have been collected in conjunction with studies of foraging dynamics, nutrition, growth, and population ecology of this arctic ungulate over the course of several years in Alaska and other circumpolar areas. These samples were subjected to proximal analyses for percent nitrogen, phosphorus, sodium, carbohydrate, cell wall (NDF), acid detergent fiber (ADF), lignin, cellulose, and residual ash, and treated to determine *in vitro* and nylon bag dry matter digestibility (DMD). Among winter vascular plant forage only carbohydrates showed a positive correlation with digestibility, wheras in summer nitrogen, phosphorus, and in some cases sodium, also are positively correlated with digestibility. Forage from shrubs and forbs in early summer had higher nitrogen and carbohydrate levels than later in the season, wheras graminoids show an increase in these levels during the first few weeks of growth. Floral parts during anthesis showed higher nitrogen, phosphorus, and carbohydrate levels and higher digestibility than corresponding leaf material. The annual dietary cycle is the product of adjustment of the physiological cycle to seasonal fluctuation in forage quality and quantity.

Key words: *Rangifer tarandus,* forage quality, plant phenology, proximate analysis

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Introduction

It is generally accepted that forage type, phenology, and season are primary factors influencing the quality of forage available to ungulates. Forage used by reindeer and caribou is also believed to be under these influences, however, generalizations extrapolated from investigations on other species may be misleading. For example, the emphasis on nitrogen content of winter browse for North American deer as an index of quality does not have relevance to assessment of quality of the lichen-dominated winter diet of caribou and reindeer.

The foraging pattern or strategy of caribou and reindeer throughout the year is under the control of the physiological-metabolic demands of the animal and the quality and quantity of forage available. All of these factors undergo annual fluctuations that are tied to the extreme solar cycle of northern latitudes. This investigation examines variations occurring in vascular plant forage of caribou and reindeer and the correlations existing among the nutritional components of the forage.

Methods

Forage samples were collected during 1975 - 1980 in connection with studies of foraging dynamics and habitat selection of caribou, reindeer, and muskoxen, through the Alaska Cooperative Wildlife Research Unit (Thing, 1977; Wright,1979; Boertje, 1981; Robus, 1981; Kuropat,1984). All samples collected were known to be used by caribou and reindeer. These samples were subjected to proximal analyses for percent nitrogen, phosphorus, sodium, carbohydrate, cell walls (NDF), acid detergent fiber (ADF), lignin, cellulose, and residual ash at the Plant and Soil Analysis Laboratory, Palmer, Alaska. Many of the samples were also treated to determine *in vitro* and nylon bag dry matter digestibility (DMD) using a fistulated reindeer as a source of innoculum and for the nylon bag studies. This work was done at the Institute of Arctic Biology, University of Alaska Fairbanks. The following individuals assisted in the collections and analyses of forage samples reported here: Rodney Boertje, John Bryant, Karma Krelle, Peggy Kuropat, Martha Robus, Dan Roby, Hans Staaland, Henning Thing, and John Wright. Dan Roby provided assistance for data analysis.

Forage samples were grouped in the analyses of data according to the following categories (plant nomenclature is from Hultén 1974):

Winter:

Evergreen (Oct.-Apr.):	*Ledum palustre, Dryas integrifolia, Empetrum nigrum, Vaccinium vitis-idaea*
Early winter green: (Oct. & Nov.)	*Carex aquatilis/stans, Hippuris vulgaris, Stellaria longipes, Equisetum variegatum*
Early winter other: (Oct. & Nov.)	*Eriophorum vaginatum, Carex* spp., *Potentilla palustris, Salix pulchra* (leaves)
Mid-late winter green: (Dec.-Apr.)	*Pyrola grandiflora, Carex aquatilis/stans, Equisetum scirpoides*
Dead/dry (Oct.-Apr.):	*Eriophorum vaginatum, Carex.* spp., *Salix pulchra* (leaves), *Calamagrostis* sp., *Poa glauca*

Summer:

New growth-leaves (June)	Leaves of *Salix* spp., *Betula nana* and numerous forbs
New growth including flowers (June)	Leaves, terminal growing tips of twigs, and floral parts of *Salix* spp. and *Betula nana*, as well as leaves and floral parts of numerous forbs
New growth-flowers (June)	Floral parts of *Salix* spp. and forbs
Evergreen leaves: (June-July)	*Ledum palustre, Vaccinium vitis-idaea, Dryas integrifolia*
Graminoids (June-July)	*Eriophorum vaginatum, Carex aquatilis/stans, C. Bigellowii, Arctophila fulva*

Additional species represented in the grouped analysis data:

Shrubs:	*Salix pulchra, S. alaxensis, S. glauca, S. lanata, S. reticulata*
Graminoids:	*Carex aquatilis, C. Bigelowii, Eriophorum vagi-*

natum, *Arctophila fulva*, *Poa glauca*, *Festuca altaica*, *Hierochloe alpina*, *Calamagrostis* sp.

Forbs: *Epilobium latifolium*, *E. angustifolium*, *Artemesia arctica*, *A. tilesii*, *Pedicularis kanei*, *P. sudetica*, *P. langsdorfii*, *Lupinus arcticus*, *Oxytropis viscida*, *Hedysarum alpinum*, *Ranunculus glacialis*, *Anenome parviflora*, *Oxyria digyna*, *Rumex arcticus*, *Arctostaphylos alpina*, *Petasites frigidus*, *Boykinia richardsonii*, *Geum glaciale*, *Stellaria longipes*, *Sanguisorba officinalis*

Results and discussion

Considerable variation exists in the quality of natural forage available to caribou and reindeer. This variation is associated with plant species, plant part, plant phenology, and season (Table 1).

The generally accepted correlation between nitrogen (i.e. crude protein = N x 6.25) and forage quality is based on the assumption that nitrogen is usually the limiting nutrient in ruminant forage. This assumption has some validity for growing, lactating, or other animals that may be in a dynamic physiological state, which is coincident with the summer growth period of forage plants. During winter, however, when northern ruminants enter a growth plateau, protein requirements are greatly reduced over summer and metabolizable energy becomes the dominant component sought in forace consumed (White et al.,1981). Thus lichens, low in nitrogen and high in available energy and digestibility, become a major component of the winter diet of caribou and reindeer when available (Karaev, 1968, Holleman et al., 1979; Helle, 1981). Among winter vascular plant forage analyzed in this study only carbohydrates showed a positive correlation with digestibility (Table 2). This is in contrast to summer forage in which nitrogen, phosphorus, and in some cases sodium also show positive correlations with digestibility. Although nitrogen levels in winter forage are low by summer standards, vascular plants averaging in excess of 1.5 percent nitrogen may be able to provide the nitrogen required by reindeer and caribou to meet their relatively low metabolic requirements for nitrogen in winter. In addition, nitrogen available from vascular plants in winter probably also provides a necessary supplement to the lichen-dominated diet to enable optimal development of the rumen microorganism complex essential for efficient digestion of lichens. Although nitrogen levels of vascular plant forage in winter are low in contrast to summer, there are exceptions, such as *Hippuris vulgaris* and the aquatic vegetation incorporated in muskrat pushups (Table 1). Both of these are exploited as forage by caribou in early winter before snow conditions limit their availability.

In summer it is generally believed that forage plants in early stages of growth have higher nitrogen and carbohydrate levels and are therefore of higher quality than similar plants later in the growth period (Klein,1970). This generalization should be qualified, however. Whereas new growth vegetation from deciduous shrubs and forbs generally has higher nitrogen and carbohydrate levels than is the case later in the season (June vs. July), this does not appear to be true of perennial graminoids (grasses and sedges)(Fig. 1). Nitrogen and carbohydrate levels appear to increase in graminoids, in contrast to shrubs and forbs during the first month of growth, which seems counter intuitive in view of the close correlation between digestibility and these nutrients in other forage types. An inverse correlation between gross energy content and digestibility, however, also has been

Table 1. Composition and digestebility of vascular plant forage types available to *Rangifer tara*

Forage type	(n)	Proximal and detergent analyse:			
		N[1]	P	Na	CHO
		x̄ ± SD	x̄ ± SD	x̄ ± SD	x̄ ± SD
WINTER					
Evergreen	9	1.35 ± 0.34	0.18 ± 0.07	0.89 ± 0.23	6.01 ± 8
Early winter green	12	1.53 ± 0.40	0.17 ± 0.05	0.71 ± 0.33	5.10 ± 5
Early winter other	10	1.11 ± 0.50	0.14 ± 0.04	0.70 ± 0.39	4.53 ± 3
Mid-late winter green	12	1.84 ± 0.58	0.20 ± 0.08	0.47 ± 0.55	11.46 ± 5
Dead/dry	15	1.17 ± 0.39	0.14 ± 0.03	0.92 ± 0.59	3.29 ± 3
Hippuris vulgaris (10/6 & 11/16)	2	2.27 ± 0.42	0.22 ± 0.03	0.74 ± 0.87	12.50 ± 14
Muskrat pushup (11/16)	1	3.18	0.38	1.19	4.53
SUMMER					
New growth - leaves	25	3.45 ± 1.02	0.38 ± 0.13	0.63 ± 0.24	5.51 ± 2
New growth inc. flowers	35	3.36 ± 1.23	0.44 ± 0.19	0.74 ± 0.36	4.34 ± 1
New growth - flowers	30	3.58 ± 1.05	053 ± 0.14	0.73 ± 0.36	7.93 ± 3
Evergreen leaves	12	1.53 ± 0.40	0.17 ± 0.05	0.71 ± 0.33	5.10 ± 5
Graminoids - June	25	2.34 ± 0.82	0.34 ± 0.15	0.67 ± 0.23	4.62 ± 2
Graminoids - July	6	4.19 ± 0.67	0.40 ± 0.12	0.76 ± 0.09	7.95 ± 1
Forbs - June	23	3.69 ± 1.31	0.51 ± 0.19	0.82 ± 0.31	8.37 ± 4
Forbs - July	5	2.98 ± 1.43	0.41 ± 0.13	0.76 ± 0.47	6.02 ± 4
Shrubs June	15	4.10 ± 0.86	0.56 ± 0.17	0.79 ± 0.47	3.12 ± 1
Shrubs July	8	3.52 ± 0.89	0.36 ± 0.12	0.73 ± 0.24	4.99 ± 1
Willow - new growth	6	4.29 ± 0.64	0.60 ± 0.13	0.97 ± 0.67	2.77 ± 0
Willow - leaves only	11	3.28 ± 0.55	0.36 ± 0.12	0.58 ± 0.30	5.41 ± 1
Sedge - new growth: leaves, culms, flowers	10	2.34 ± 0.82	0.27 ± 0.09	0.78 ± 0.18	4.13 ± 1
Sedge - new growth leaves	6	3.38 ± 1.45	0.32 ± 0.11	0.62 ± 0.18	5.97 ± 2
Pedicularis Kanei -- new growth	4	4.15 ± 0.72	0.55 ± 0.15	0.97 ± 0.42	9.55 ± 3
Betula nana - new growth	4	4.63 ± 0.55	0.49 ± 0.02	0.81 ± 0.17	3.28 ± 1.
Eriophorum vaginatum	18	2.48 ± 0.89	0.39 ± 0.16	0.63 ± 0.29	5.21 ± 3.
E. vaginatum - flowers	7	2.96 ± 0.56	0.52 ± 0.04	0.71 ± 0.18	6.59 ± 2.
Carex aquatilis/stans	6	2.46 ± 1.03	0.27 ± 0.09	0.55 ± 0.43	9.27 ± 4.
Carex Bigelowii	5	2.28 ± 0.95	0.22 ± 0.07	0.68 ± 0.13	4.44 ± 2.
Arctophila fulva	5	2.37 ± 1.60	0.29 ± 0.19	0.93 ± 0.13	11.28 ± 8.
Dryas intergrifolia	3	2.32 ± 0.38	0.28 ± 0.04	0.36 ± 0.31	6.75 ± 5.

[1] N=nitrogen, P=phosporus, Na=sodium, CHO=carbohydrates, NDF=neutral detergent fil

hroughout their circumpolar distribution. Sample size is indicated by (n).

					Digestibility		
NDF	ADF	LIG	CELL	ASH	In Vitro	Nylon Bag	(n)
± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	
± 17.7	39.2 ± 9.9	13.7 ± 8.7	23.5 ± 6.4	1.94 ± 2.08	42.5 ± 14.2	57.6 ± 28.3	4
± 19.3	38.5 ± 9.4	15.0 ± 6.7	20.2 ± 7.5	3.38 ± 6.09	36.7 ± 3.1	40.4 ± 15.4	5
± 14.9	29.8 ± 14.9	7.4 ± 4.9	20.0 ± 12.4	2.43 ± 6.82	30.8 ± 8.2	53.4 ± 24.9	9
± 12.6	33.1 ± 6.6	5.8 ± 3.8	23.5 ± 6.4	3.78 ± 6.37	52.7 ± 13.5	59.6 ± 10.3	11
± 15.2	33.8 ± 14.1	7.9 ± 5.1	24.6 ± 10.9	1.25 ± 2.69	28.8 ± 8.1	51.0 ± 26.5	11
± 11.6	31.6 ± 17.6	12.0 ± 5.6	19.0 ± 12.2	0.55 ± 0.07	43.1	67.8 ± 2.8	2
	40.8	9.3	13.3	18.23	39.1	47.4	1
3 ± 15.5	25.4 ± 6.7	6.7 ± 2.8	17.7 ± 5.6	0.97 ± 1.75	53.5 ± 16.5	56.8 ± 14.2	25
2 ± 23.0	25.8 ± 9.7	6.7 ± 3.7	18.5 ± 7.9	0.56 ± 1.10	53.8 ± 16.1	55.2 ± 13.7	33
7 ± 18.6	21.7 ± 5.9	5.3 ± 2.6	16.2 ± 4.3	0.38 ± 0.48	70.7 ± 14.3	65.3 ± 13.5	26
4 ± 19.3	38.5 ± 9.4	15.0 ± 6.7	20.2 ± 7.5	3.38 ± 6.09	36.7 ± 3.1	40.4 ± 15.4	5
0 ± 7.1	29.1 ± 8.0	5.1 ± 2.1	23.8 ± 5.9	0.42 ± 0.49	57.9 ± 20.3	59.0 ± 14.8	19
5 ± 5.6	21.4 ± 6.9	3.4 ± 1.9	17.6 ± 6.4	0.43 ± 0.54	65.4 ± 21.2	68.6 ± 8.0	6
0 ± 7.2	20.3 ± 6.4	5.8 ± 3.4	14.2 ± 4.6	0.33 ± 0.39	70.8 ± 14.9	66.8 ± 10.5	22
3 ± 13.2	22.6 ± 10.0	5.8 ± 2.4	14.3 ± 5.6	2.56 ± 3.59	63.7 ± 2.9	67.6 ± 10.9	4
7 ± 10.6	28.6 ± 9.5	9.3 ± 4.2	17.9 ± 5.1	1.43 ± 2.98	46.6 ± 9.7	49.4 ± 12.7	15
2 ± 6.5	22.1 ± 3.7	6.7 ± 2.2	14.7 ± 4.0	0.66 ± 0.67	48.5 ± 7.2	53.9 ± 11.6	8
5 ± 10.5	23.2 ± 8.8	7.7 ± 4.0	14.5 ± 4.4	1.10 ± 2.26	46.0 ± 6.8	53.3 ± 10.7	6
5 ± 6.8	24.5 ± 4.8	7.5 ± 2.4	16.3 ± 3.7	0.63 ± 0.61	51.0 ± 6.8	55.5 ± 11.6	11
5 ± 4.8	31.6 ± 5.0	5.3 ± 1.6	26.1 ± 3.7	0.20 ± 0.25	52.8 ± 15.0	53.2 ± 11.3	10
6 ± 8.7	28.8 ± 7.7	5.0 ± 3.0	23.3 ± 4.9	0.57 ± 0.57	46.2 ± 21.9	57.1 ± 19.6	6
9 ± 8.9	20.8 ± 5.2	6.0 ± 3.0	14.6 ± 3.8	0.15 ± 0.19	80.1 ± 3.7	60.2 ± 6.9	4
3 ± 11.9	23.5 ± 6.7	8.6 ± 3.3	14.8 ± 4.6	0.10 ± 0.14	42.8 ± 3.5	45.6 ± 5.9	4
6 ± 7.7	28.0 ± 9.7	4.9 ± 2.6	23.0 ± 7.1	0.34 ± 0.41	58.8 ± 20.6	62.5 ± 13.3	15
2 ± 8.6	19.4 ± 4.9	3.5 ± 2.4	16.4 ± 2.8	0.34 ± 0.30	80.1 ± 11.2	72.7 ± 6.2	6
9 ± 3.6	29.6 ± 2.4	3.7 ± 1.7	25.2 ± 2.9	0.67 ± 0.55	60.5 ± 17.1	60.5 ± 13.6	6
1 ± 4.3	32.1 ± 3.8	6.2 ± 1.8	25.5 ± 1.8	0.42 ± 0.45	41.7 ± 17.5	44.0 ± 15.5	5
3 ± 18.4	23.5 ± 10.8	3.7 ± 0.8	19.6 ± 10.7	0.32 ± 0.36	60.2 ± 24.8	68.1 ± 14.0	5
6 ± 6.0	35.2 ± 6.3	12.2 ± 6.7	21.4 ± 3.0	1.57 ± 1.52	42.5 ± 8.9	49.5 ± 8.4	3

F=acid detergent fiber, LIG=lignin, CELL=cellulose

Table 2. Correlation (Pearson's product-moment) between digestibility (IV = *in vitro* and NB = nylon bag) and chemical composition of forages grouped by season, phenology, and forage type. Positive and negative correlations with p values <0.05 are shown.

	N[1]		P		Na		CHO		NDF		ADF		Lignin		Cellu-lose		Ash	
Forage Type	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB	IV	NB
Winter																		
Early winter green					-		+	+		-	-							
All forage minus lichens					-		+	+			-	-	-	-		-		
Summer																		
New growth - leaves		+		+			+	+		-	-	-	-	-	-	-		
New growth - flowers					+		+	+			-	-	-	-	-	-	-	-
All growing forage	+	+	+	+			+	+	-		-	-	-	-	-	-		
Graminoids	+	+	+	+	+		+	+	-	-	-	-	-	-	-	-		
Forbs	+		+		+					-	-	-	-	-				-
Shrubs							+	+					-	-			-	-
All forage	+	+	+	+			+	+	-	-	-	-	-	-	-	-		-

N = nitrogen, P = phosphorus, NA = sodium, CHO = carbohydrates, NDF = neutral detergent fiber, ADF = acid detergent fiber.

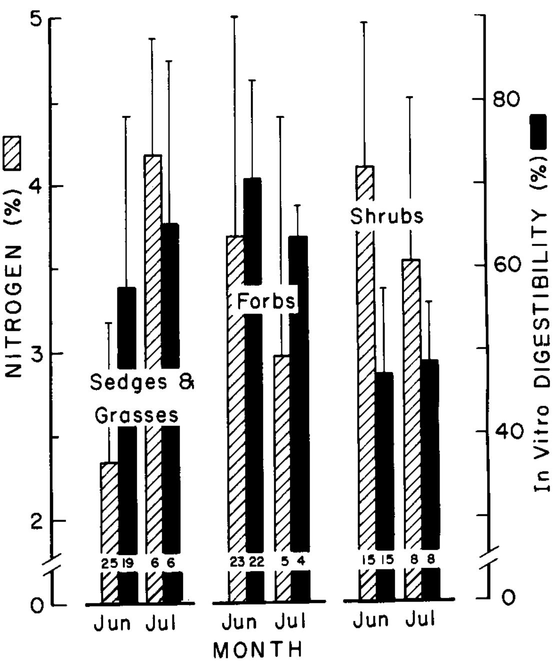

Fig. 1. Differences in quality of major forage types in the Arctic at initiation of plant growth (June) and during peak growth (July) as reflected in nitrogen content and in digestibility. Histograms represent means with inclusive sample sizes, plus one standard deviation.

observed among forage species eaten by other herbivores associated with secondary chemicals apparently employed by the plants as defense against herbivory (Bryant and Kuropat, 1980). Deciduous shrubs have been shown to have high plasticity in the production and mobilization of secondary chemicals that inhibit digestion (Bryant et al., 1983).

Floral parts during anthesis, as a general rule, have higher nitrogen, phosphorus and carbohydrate levels than corresponding leaf material and also have higher digestibility levels (Table 1). This would justify the selective foraging for floral parts that has been observed among caribou and reindeer, often at the expense of optimization of biomass ingestion.

Analyses of forage types presented herein allow refinement of generalization about optimal foraging strategies of caribou and reindeer. The annual physiological cycle of caribou and reindeer has apparently evolved to follow the annual cycle in forage quality and quantity, therefore, the annual dietary cycle reflects this relationship. Figure 2 provides a simplified mo-

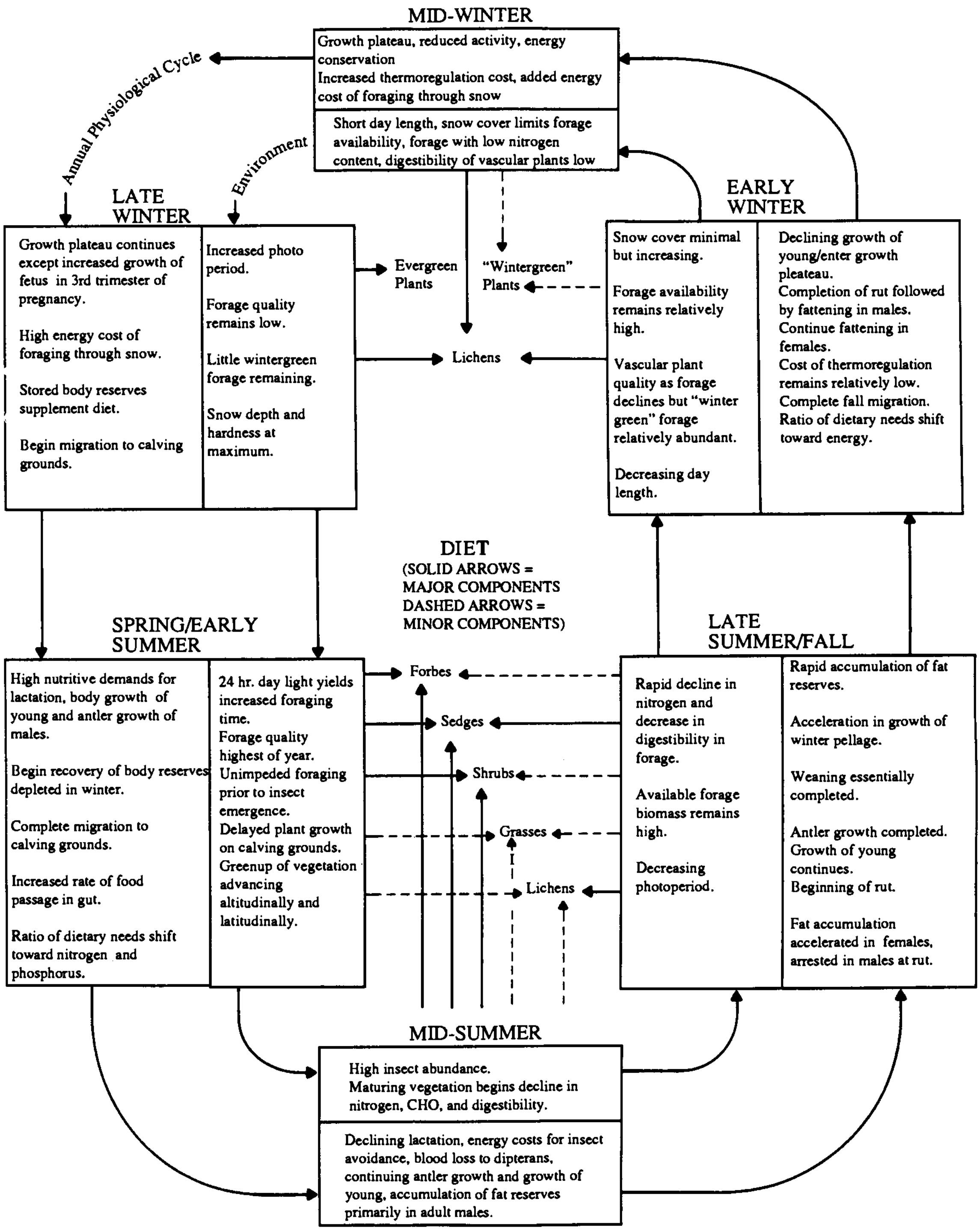

Fig. 2. Hypothetical model of the relationship of diet in caribou and reindeer to their annual physiological cycle and seasonal changes in the environment.

del of the annual foraging cycle ofi caribou and reindeer in relation to the annual physiological cycle and provides a basis for examination for variations from the model as well as verification of its components.

Conclusions

Although nitrogen levels of vascular plant forage are low in winter, some "winter green" forage has nitrogen levels in excess of 1.5% with exceptions to over 2 or even 3%. Among winter vascular plant forage, only carbohydrates showed a positive correlation with digestibility. In summer forage, nitrogen, phosphorus, and in some cases sodium, also are positively correlated with digestibility. New growth vegetation in early summer from shrubs and forbs has higher nitrogen and carbohydrate levels than later in the season, whereas graminoids show an increase in these levels during the first few weeks of growth. In shrubs, digestibility does not appear to be directly correlated with nitrogen and cabohydrate levels. Floral parts during anthesis, as a general rule, have higher nitrogen, phosphorus, and carbohydrate levels and higher digestibility than corresponding leaf material. The annual physiological cycle ofi caribou and reindeer has evolved to follow the annual cycle in forage quality and quantity, therefore the annual dietary cycle reflects this relationship.

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