

**Simulation of maintenance, growth
and reproduction of caribou and
reindeer as influenced by ecological
aspects of nutrition, climate change
and industrial development using
an energy-protein model**

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RANGIFER

**Research, Management and Husbandry of Reindeer
and other Northern Ungulates**

Volume 34, 2014 - Special Issue No. 22

Rangifer

Publisher: Swedish University of Agricultural Sciences
Department of Animal Nutrition and Management
Reindeer Husbandry Unit
P.O. Box 7024, 750 07 Uppsala
Sweden

Organisation number: SE 202100-2817

Editor in Chief: Birgitta Åhman

Editor: Eva Wiklund

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As from Volume 28 (2008), Rangifer is published as an open access online journal (ISSN 1890-6729 at www.rangiferjournal.com). A complete archive of all published issues of Rangifer including Rangifer Special Issues and Rangifer Report is also available at www.rangiferjournal.com.

The publication of Rangifer is supported by funds from the Swedish Ministry for Rural Affairs.

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*Manuscript recieved 15 February 2014
revision accepted 28 August 2014
manuscript published 30 December 2014*

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2014

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“An adequate study of any complex phenomenon ultimately requires an integrated analysis of major systems and not just fragments of them.”
(Holling, 1965)

Introduction

Northern caribou populations typically make seasonal migrations between lichen rich taiga forests in the winter and open tundra in the spring for calving (Kelsall, 1968; Bergerud *et al.*, 2008). Caribou and wild reindeer are adapted to characteristically high seasonal and annual variability that is typical of the higher latitudes. Variability includes accumulation and structure of winter snow, spring snow melt and linked plant phenological dynamics (Klein, 1990; Albon & Langvatn, 1992), quality and accessibility of summer forage and disruptive impacts of biting and parasitic insects in the summer (Klein, 1990; Russell *et al.*, 1993; Witter *et al.*, 2011; Cuyler *et al.*, 2012). Thus habitat characteristics and variability in risk (Kie, 1999) influence reproductive allocation patterns (Munns, 2006; Bårdsen *et al.*, 2008; 2009; Monteith *et al.*, 2013). Caribou have adapted to these ecological characteristics through evolutionary strategies that include trade-offs between survival and reproduction.

Biologists have made progress measuring seasonal responses to habitat drivers. In particular, measures of loss and gain of fat and protein (Reimers & Ringberg, 1983; Adamczewski *et al.*, 1987b; Huot, 1989; Chan-McLeod *et al.*, 1994; Cameron & White, 1996; Gerhart *et al.*, 1996b; Taillon *et al.*, 2011), allocation of resources to fetal growth (Robbins & Robbins, 1979; Skogland, 1984b; Reimers, 2002; Barboza & Parker, 2008) and milk production (Varo & Varo, 1971; Rognmo *et al.*, 1983; White & Luick, 1984; Parker *et al.*, 1990; Taillon *et al.*, 2013) combined with herd productivity (White, 1992; Russell *et al.*, 2000; Taillon *et al.*, 2013) allow for a rich discussion of caribou ecological and evolutionary processes. However, to take those results into understanding of how caribou adapt to environmental variation and change requires an integrative approach from the individual to the population scale and across timescales. The need for this approach, and to be able to project caribou responses is a key requirement for managers and users of northern caribou who are challenged by the requirement to assess incremental and cumulative impacts of climate change and industrial development (Cameron *et al.*, 2005; Gunn *et al.*, 2011).

In recent years meta-models are being developed to recognize and capture environmental complexity in assessing risks on biodiversity (Nyhus *et al.*, 2007; Lacy *et al.*, 2013; Munns, 2006). A meta-model has a central program that uses a suite of coupled sub-models. Importantly, those sub-models may represent different disciplines and may model processes at variable spatial and temporal scales that are linked and integrated through the central program. This means meta modeling is ideally suited to allow biologists to explore and project such complex and interacting threats as climate change and industrial development. In this report we provide the detailed description of a meta-model for caribou based on energy-protein interactions of individuals that can be done to typify cohorts of a caribou population in order to project on the cohorts the variable impacts of climate change and development.

The original version of our model was developed to integrate the substantial database on the Porcupine Caribou Herd (e.g. Russell *et al.*, 1993) to better understand how environmental factors combine to drive fat and protein dynamics in individual caribou and help guide further research priorities on the Porcupine Caribou Herd (Hovey *et al.*, 1989; Kremsater *et al.*, 1989). A brief historical account of the development of caribou models is given in White *et al.* (2013a). At the same time, because many of the relationships and parameter values utilized in the model relied heavily on data throughout the *Rangifer* literature, the model was the basis for a generalized *Rangifer* model that could be applied across other herds. Indeed as new research findings became available (e.g. Russell & White, 2000), those new relationships, particularly energy relationships, were incorporated into a new model structure (Russell *et al.*, 2005).

A shortcoming of Russell *et al.*'s (2005) model was that, although energy relations in the animal were detailed, protein dynamics, particularly the digestion and allocation of protein, were not explicitly represented in the model. Maternal protein reserves, in addition to fat reserves, are major determinants of *Rangifer* reproductive success (Gerhart *et al.*, 1997; Russell *et al.*, 1998) and birth weight (Allaye-Chan, 1991; Chan-McLeod *et al.*, 1999; Barboza & Parker, 2008; Bårdsen *et al.*, 2008). By modeling protein-nitrogen (protein-N) in concert with energy, a more realistic prediction of fetal growth and milk production is possible. This model uses general theory and experimental data to derive algorithms that drive energy (Blaxter, 1962; Kleiber, 1975; Hudson & White, 1986) and protein dynamics to determine the balance of dietary and maternal energy and protein during gestation and lactation (Robbins & Robbins, 1979; Parker *et al.*, 2005; Barboza & Parker, 2006; Barboza *et al.*, 2009; Parker *et al.*, 2009). Caribou as ruminants rely on microorganisms for digesting forage and so modeling of dietary energy intake is linked with nitrogen intake and metabolism to simulate microbial growth (ARC, 1980). Thus the current model estimates microbial protein synthesis and nitrogen recycling throughout the year, particularly in the winter when the ability to conserve nitrogen by recycling processes may be key to survival (Wales *et al.*, 1975; Swift *et al.*, 1980; Syrjälä & Salonen, 1983; Parker *et al.*, 2005; Barboza & Parker, 2006).

In its current version the model can project how individual members of a population respond to intra-specific competition for forage relative to environmental factors. Environmental factors may stress individuals at all population density levels differentially (Skogland, 1983; 1985), perhaps leading to selection for maternal reproductive strategies, as recently classified as “capital” and “income” breeders based on use of maternal reserves (capital) relative to forage intake (income), in meeting nutritional demands during terminal gestation and early lactation (Jönsson, 1997; Festa-Bianchet *et al.*, 1998; Barboza *et al.*, 2009). Although most large mammals have been considered capital breeders (Festa-Bianchet *et al.*, 1998), Barboza & Parker (2006) suggest that reindeer (*Rangifer tarandus tarandus*) display capital breeding phenomena relative to caribou (*R. t. grantii*, *R. t. greenlandicus*), which they classify as income breeders. As detailed by Bårdsen *et al.* (2009) and Barboza *et al.* (2009), capital and income breeding represent extremes in a continuum of breeding strategies. Thus by modeling the individual we account for ecological effects on reproduction and survival, the main drivers of population dynamics when individuals are summed to the population scale.

In addition to the forage and weather-derived factors that limit food quantity and quality, predators, including insects and parasites, as well as anthropogenic effects imposed by industrial development, differentially affect caribou growth, reproduction and survival (Cameron *et al.*, 2005). Integrating a suite of drivers (e.g. climate, development) that impact on forage, activ-

ity and diet, simulation modeling can be used in assessing impacts of variables individually or in combination (Murphy *et al.*, 2000; Russell, 2011) and thus contribute to our understanding of cumulative effects on populations (Gunn *et al.*, 2013). As populations approach or exceed peak abundance, intra-specific competition for forage may become more evident, especially through the female component of the population (Skogland, 1983; 1985; Festa-Bianchet & Jorgenson, 1998; Ballesteros *et al.*, 2013). Thus, female cohorts that show significant changes in nutritional condition in response to environmental factors will be impacted in respect to growth, reproduction and survival (Adams & Dale, 1998a; Festa-Bianchet, 1998; Parker, 2003; Bårdsen *et al.*, 2009). Skogland (1986) and Ballesteros *et al.* (2013) show that fluctuations due to density result in life history effects on individuals in the population. Conditions that could shape life history traits are those for which habitat availability is limited and where individuals can exhibit breeding pauses (Cameron, 1994), and die-offs of young-aged cohorts.

Wild reindeer and barren ground caribou exhibit reproductive plasticity (Russell & White, 2000; Bergerud *et al.*, 2008) and it is important to document the role played by individual nutritional condition, as a mediator of individual fitness, in life history response. What is not clear, and warrants wide scale analysis, is what regulatory processes occur in a species, such as wild reindeer and caribou, that appear to oscillate on a 30-90 year periodicity (White *et al.*, 1981; Gunn, 2003; Bergerud *et al.*, 2008; Gunn *et al.*, 2009). Capturing the way these many factors affect individuals and how individuals respond through their reproductive efforts can be simulated using known controlling relationships while inserting “best guesses” or expert opinions as surrogate variables or algorithms until unknown relations become established. Gaming with such simulation models then allows the user to analyze responses to a single variable or suites of variables. In this report we describe the logic, algorithms and equations we developed to model the energy-protein relations of an individual caribou. In subsequent manuscripts we will detail how scenarios are derived and provide practical applications of the model.

Overall Modeling Approach

Our model presented in this publication documents the effects of environmental drivers on an individual reindeer or caribou's forage intake, and projects how the animal allocates energy and protein from forage intake to survival and reproduction. The model projects the individual's nutritional status, as represented by its body weight, body composition (Hudson & White, 1985; Hobbs, 1989; Renecker & Samuel, 1991; Moen & Pastor, 1998) and energy and protein balance (Fancy, 1986) throughout the year on a daily time step. Although both body composition and skeletal size influence body mass or weight (Festa-Bianchet, 1998), this model assumes that the animal's body weight is simply the sum of body condition components.

The model consists of two sub-models:

- **Intake Submodel** which simulates hourly dry matter intake based on available forage biomass, diet and time spent eating, and then calculates the resulting daily metabolizable energy intake (MEI) and metabolizable protein-N intake (MNI) based on hourly rumen function, including nitrogen recycling and microbial protein-N synthesis.
- **Allocation Submodel** which simulates daily body weight and composition and calculates energy and nitrogen available for maintenance and productive processes (gestation, lactation), based on the animal's daily requirements for energy and protein-N, in relation to MEI and MNI.

Effects of biotic and abiotic variables on body condition are captured in the model through changes over time in model inputs such as forage quantity, forage quality, diet and activity budgets on a seasonal and annual timescale. For example different plant phenologies, as dictated by annual variability in growing degree-days, can be represented through seasonal changes in forage quality, quantity and diet; the main drivers of optimal foraging (Spalinger *et al.*, 1988; Spalinger, 1997; Kie, 1999). Likewise the effect of summer temperature and wind on insect harassment (Russell *et al.*, 1993; Bali *et al.*, 2013) can be represented through changes in activity budgets, while changes in winter weather, such as snow depth, rain-on-snow, freezing rain and spring freeze-thaw events (Griffith *et al.*, 2002; Chen *et al.*, 2012) can be represented through changes in activity budgets and forage availability.

The model can project effects of spatial displacements at the individual scale such as from industrial disturbance if habitats have been mapped. Using biomass estimates for major forage groups, forage intake can be estimated for caribou displaced to different habitats. Thus, the model can be used to explore the trade-offs and costs of predation, parasitism or industrial disturbance.

Intake Submodel

Throughout the simulated sub-models, input data such as forage intake are based on *Rangifer* studies wherever possible. In the absence of *Rangifer* data, data from wildlife and domestic ruminants are used. The latter is the case when algorithms are based on theory. For example, studies on foraging by wild and tractable deer (*Odocoileus hemionus hemionus/sikensis*), elk (*Cervus elaphus*, *C. nelsoni*) and moose (*Alces alces*) have been responsible for rich and detailed mechanistic analyses of the influence of forage biomass, structure and growth form on forage intake (Wickstrom *et al.*, 1984; Renecker & Hudson, 1985; 1986; Spalinger *et al.*, 1988; Shipley & Spalinger, 1992; Spalinger & Hobbs, 1992; Gross *et al.*, 1993a; 1993b; Shipley *et al.*, 1994; Spalinger, 1997; Pastor *et al.*, 1999; Hobbs *et al.*, 2003). Most theory for forage intake by wildlife species originated from that based on grazing by domestic sheep (Arnold & Dudzinski, 1967; Alden & Whittaker, 1970; Stobbs, 1973a; 1973b).

Generally bite size is the regulated process of eating, especially for animals specializing on shrubs. In our model intake (or eating) rate is the observed integral of bite size times bite rate and does not include time taken for searching and chewing a bite. Thus intake rate is the potential maximum for plant growth forms or species complex of the forage and is linearly related to biomass of the selected forage (see White *et al.*, 1975; White & Trudell, 1980a; 1980b; Trudell & White, 1981). Theory and data from other studies (Alden & Whittaker, 1970; Collins *et al.*, 1978; Wickstrom *et al.*, 1984; Renecker & Hudson, 1986) indicate that these relations should show a plateau intake, or saturation kinetics, *sensu* Holling (1965). However, some growth forms, such as shrubs are eaten as bites with little, or no, relation to biomass (Spalinger *et al.*, 1988; Shipley & Spalinger, 1992; 1995). This is not the case for coastal lowland tundra (White *et al.*, 1975), upland tundra inland from the coast (White & Trudell, 1980a; 1980b) and alpine tundra in Norway (Gaare & Skogland, 1975) for which all evidence supports a dependency of intake relative to the biomass with separate functional response curves representing each plant growth form.

Thus, forage biomass is used in this model as a driver of food intake as previously described (Kremsater *et al.*, 1989; Hovey *et al.*, 1989; Russell *et al.*, 2005). Observed diets are used to adjust potential intake attributed to all plant species or growth form (*e.g.* deciduous shrubs) to reflect

the proportions of those species or growth forms contained in the diet. However, where diet is not known, diet is predicted based on species preferences determined through experimentation with reindeer grazing lowland and upland tundra in Alaska (White *et al.*, 1975; White & Trudell, 1980a; 1980b; Trudell & White 1981) and alpine tundra in Norway (Skogland, 1980). In summary, forage intake, in grams per minute, is determined as a potential maximum based on biomass and is then corrected to reflect the diet composition. Intake is calculated hourly based on proportion of the day the animal spent foraging and proportion of the foraging time spent eating (eating intensity). The hourly time-step for determining forage intake allows more realistic simulation of rumen function.

Three constraints provide feedback on forage intake that alone and combined prevent overeating. The three constraints are a) a logistic constraint that prevents intake exceeding known maximum forage intake capacity, b) a rumen capacity constraint that prevents intake from exceeding the maximum rumen fill, and c) a metabolic constraint that prevents forage intake exceeding the maximum ability of the animal to utilize intakes of metabolizable energy and metabolizable protein.

Potential Forage Intake Rate

Based on theory and field measurements already detailed, a potential intake rate for each plant growth form (PFIP, $\text{gDM} \cdot \text{min}^{-1}$) is initially generated. In order to fit a maximum intake to extant data, mean intake rates of each plant species or growth form (Table 1, Trudell & White, 1981) were used to estimate a maximum intake rate (PCMAX, $\text{gDM} \cdot \text{min}^{-1}$) for each species or growth form. Equations approximating a Michaelis-Menton curve (used to describe rate of enzyme reactions) were used to relate PFIP to forage biomass (FB) of the selected growth form (FB, $\text{kg} \cdot \text{ha}^{-1}$) in order to generate PCMAX. Data for PFIP and FB (White *et al.*, 1975; Skogland, 1980; White & Trudell, 1980a; 1980b; Trudell & White, 1981) were fitted by sequentially adjusting the steepness of the curve (search efficiency; AR, $\text{gDM} \cdot \text{ha} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$, Figure 1) to give a least squares estimate of PCMAX (Simulation and Modeling Program, SAAM II 2002). Values for AR and PCMAX for each growth form are listed in Table 1. Also shown in Figure 1 are estimates of foraging effort (E), a measure of plant preference shown by reindeer foraging on lowland and upland tundra in Alaska and alpine tundra in Norway.

Potential rate at which forage can be ingested per minute for each plant group is calculated daily from available biomass as (see Table 1, Figure 1):

Table 1. Data used to generate foraging effort (E_i) based on relative plant biomass (A_i) and preference index, and estimates of search efficiency (AR_i) and maximum eating rate ($PCMAX_i$) in relation to forage growth form for *Rangifer*

Growth Form	Equation	AR_i	$PCMAX_i$
lichen	$E_i=1.1 A_i$	0.005	10
mushroom	$E_i=8,55 A_i$	0.09	20
horsetail	$E_i=1.131 A_i$	0.02	7.5
graminoid	$E_i=1.46\text{Ln}(A_i)+4.26$	0.015	7.5
deciduous	$E_i=0.81 A_i$	0.03	12
evergreen	$E_i=1.86\text{Ln}(A_i)+2.32$	0.02	5
forb	$E_i=30.0 A_i$	0.12	15
eriop vag bud	$E_i=15.0 A_i$	0.18	15
stand dead	$E_i=0.2 A_i$	0.005	7.5
moss	$E_i=0.2 A_i$	0.005	5

eriop vag bud: *Eriophorum vaginatum* flowering buds

$$PFIP_{p,d} = (AR_p \cdot FB_{p,d}) / (1 + ((AR_p \cdot FB_{p,d}) / PCMAX_{p,d})) \tag{1}$$

where:

- PFIP_{p,d}

= potential per minute forage intake rate of plant group *p* on day *d* (g · min⁻¹)

AR_p

= user-specified coefficient dictating the steepness of the curve relating eating rate to biomass for each forage class; in biological terms this coefficient is equivalent to a searching and handling efficiency for each forage class (g · ha · kg⁻¹ · min⁻¹)

FB_{p,d}

= user-specified available forage biomass for plant group *p* on day *d* (kg · ha⁻¹)

PCMAX_{p,d}

= user-specified maximum forage intake rate for plant group *p* on day *d* (g · min⁻¹)

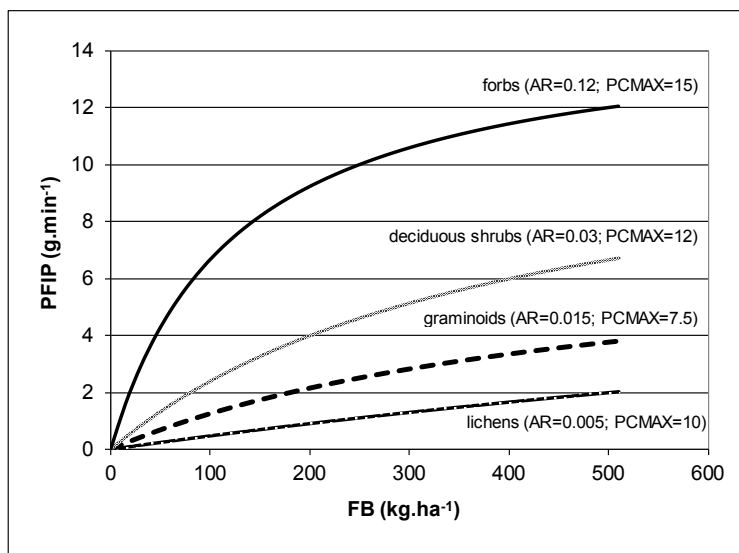


Figure 1. Relationship between potential forage intake (PFIP) and available forage biomass (FB) for different plant groups based on search efficiency (AR) and maximum eating rate (PCMAX) for *Rangifer*

Actual Forage Intake Rate

Based on the potential forage intake rate for each plant group, the actual forage intake of each plant group is then calculated by the model on an hourly basis. Because intake is related to biomass of the plant group, the diet is used to confine predictions to the plant groups composing the diet. Where diet is not known, then a prediction of likely diet is made based on forage preferences and relative availability. Forage use versus availability (expressed as relative biomass) was estimated for reindeer tethered on known vegetation types, of known species composition and species biomass (White & Trudell, 1980a; 1980b; Trudell & White, 1981). Thus, foraging effort (E , proportion of foraging time spent feeding on each plant group) = plant preference (P) · relative availability (A , proportion of total biomass) (Table 1). In these analyses graminoids and evergreen shrubs were preferred ($P > 1$) at low relative A , but were discriminated against ($P < 1$) at high A (Table 1). Mushrooms, forbs and buds (inflorescences) of *Eriophorum vaginatum* early growth were very highly preferred ($P \gg 1$), whereas dead plant material and moss were highly not preferred ($P = 0.2$) (Table 1). Thus, the foraging effort (E_i) estimated for each plant group can be substituted for diet if none is known.

Available Forage Intake

Because many functions within the rumen occur in a time frame less than a day, and several feeding periods occur each day (Skogland, 1984a; Collins & Smith, 1989; Russell *et al.*, 1993; Maier & White, 1998; Stimmelmayer & White, 2000; Colman *et al.*, 2001; 2003; 2004; van Oort *et al.*, 2005; 2007), the amount of forage dry matter entering the rumen is estimated on an hourly basis. The model begins by calculating “available” forage intake entering the rumen (AFI), referring to forage intake that would result if constrained only by the proportion of each plant group making up the daily diet (Table 2), the fraction of time spent eating in a foraging

bout and the fraction of the day spent foraging (Table 2). Available forage intake rate is given by:

$$AFI_{p,d} = PFIP_{p,d} \cdot 60 \cdot DIET_{p,d} \cdot PFOR_d \cdot PFOREAT_d \quad \text{for } h \text{ in } d \quad (2)$$

- where:
- $AFI_{p,d}$

= available dry-matter forage hourly intake rate for plant group p on day d ($g \cdot h^{-1}$)
- $PFIP_{p,d}$

= potential per minute forage intake rate of plant group p on day d ($g \cdot min^{-1}$)
- 60

= coefficient to convert units of potential forage intake rate from $g \cdot min^{-1}$ to $g \cdot h^{-1}$
- $DIET_{p,d}$

= user-specified proportion of time spent eating plant group p on day d
(proportion) – note that this generally approximates the diet
- $PFOR_d$

= user-specified proportion of day d spent foraging (proportion)
- $PFOREAT_d$

= user-specified proportion of foraging period spent eating on day d
(proportion)

Activity Budgets

Activity of the modeled animal is expressed as fraction of the day (24 h) spent in lying (ACTIVELIE), standing (ACTIVESTAND), walking (ACTIVEWALK), running (ACTIVERUN) and foraging (PFOR). Foraging includes proportion of time eating (PFOREAT) and in winter proportion spent pawing through the snow (PAWINT) (Table 2). The proportional time spent in searching behavior and walking while foraging makes up the balance of foraging time. Each datum is entered into an Excel spreadsheet commencing with Julian day 1 (January 1). Activity data supplied to the model can be as frequent as daily or may be changed seasonally based on known field observations. The model will then interpolate between input dates to calculate daily values. This same procedure applies to all input values such as biomass, forage chemistry or diet. Table 2 provides an example of possible input values for activity.

Table 2. Example of an activity budget typifying the first month of the year (Julian Day 1-31)

Activity Budget							
Activity Budget (Proportion)						Breakdown of Foraging	
Julian Day	Lying	Standing	Walking	Running	Foraging	Eating	Pawing
1	0.43	0.05	0.07	0.02	0.42	0.84	0.13
3	0.43	0.05	0.07	0.02	0.42	0.84	0.13
4	0.43	0.05	0.07	0.02	0.42	0.83	0.14
10	0.43	0.05	0.07	0.02	0.42	0.83	0.14
11	0.44	0.05	0.07	0.02	0.41	0.83	0.14
12	0.44	0.05	0.07	0.02	0.41	0.83	0.14
13	0.44	0.05	0.07	0.02	0.41	0.82	0.15
21	0.45	0.05	0.07	0.02	0.41	0.82	0.15
31	0.46	0.05	0.07	0.02	0.39	0.80	0.17
32	0.46	0.05	0.07	0.02	0.39	0.80	0.17

In this example activity budgets remained the same between Julian Days 1 and 3, 4 and 10, 11 and 13 but changed linearly for lying, foraging, eating and pawing between Julian Days 13 to 21 and 21 and 31.

Digestion, Rumen Metabolism & Assimilation

Measures of dry matter and protein entering the rumen-reticulum (hereafter the rumen) are maintained in the model at the dietary species level to determine contribution of dietary components to digestion, assimilation as metabolizable energy and metabolizable protein-N, and losses in urine and feces. The model incorporates fundamental relations with respect to food processing (ARC, 1980; Spalinger *et al.*, 1993; Aagnes *et al.*, 1996; Barboza *et al.*, 2009; Lechner *et al.*, 2009; Thompson & Barboza, 2013). Ruminal digestion of organic matter is used to determine microbial protein synthesis (ARC, 1980; NRC, 2007) and to estimate N recycling (NRC, 2007; Barboza *et al.*, 2009). Plant constituents that potentially bypass rumen fermentation are estimated before the remaining dry matter is fermented. Ruminal fermentation of plant cell contents and cell wall components, based on assay of Neutral Detergent Fiber (NDF) and Acid Detergent Fiber (ADF) (Goering & Van Soest, 1970; Van Soest *et al.*, 1991), is simulated using literature derived digestibilities that are corrected for inhibition by plant tannins (Robbins, 1993; McArt *et al.*, 2006), in the shrub component of the diet. Indigestible plant material is summed to give fecal DM and energy output.

The metabolizable energy system (ARC, 1980; NRC, 2007) is used to determine efficiency of use of metabolizable energy for allocation to maintenance metabolism (k_m) and use of metabolizable energy for retention as growth (k_g), hair/fiber (k_f), pregnancy/gestation (k_{preg}) and lactation (k_l) (Fig. 1). Separate estimates of the apparent metabolizable energy content of apparently digested energy for ruminants are taken from Robbins (1993 306). Apparent net energy available for maintenance and production (Robbins, 1993 312) depend on subtracting that heat produced during digestive and metabolic processes, which is termed the heat increment of feeding (HIF) in ruminants. In domestic animals, HIF of the meal is estimated as inefficiency in use of metabolizable energy ($1 - k_m$). However, in the free ranging animal these costs can be higher due to energy costs associated with foraging (Farrell *et al.*, 1972; Young & Corbett, 1972; Osuji, 1974; Webster, 1979). Forage type, quality and intake level and cold forage temperature are associated with feeding costs and therefore result in a wide range of apparent net energy coefficients (NEC) of metabolizable energy (NEC, 0.48-0.81) in ruminants (Robbins, 1993 308).

Urinary energy loss is based on the sum of energy associated with endogenous urinary nitrogen plus inefficiencies in use of metabolizable energy for retention. As a fraction of apparent digested energy, urine energy loss is low (0.028-0.19, Robbins, 1993 304). Gas loss as methane (CH_4) also lowers the available metabolizable energy and varies with diet; as a proportion of apparent digestible energy CH_4 loss is 0.025-0.12 (Robbins, 1993 305). Different efficiencies are used when body fat is mobilized to support metabolism, gestation and lactation (See Allocation Submodel and Table 4).

Use of digested protein-N for maintenance metabolism (k_{pm}) also reflects N losses to endogenous urinary N ($1 - k_{pm}$). To estimate net protein-N requirements for maintenance and production, efficiency of retention of metabolizable protein-N for gain (k_{pg} , body protein, antlers), fiber/hair growth (k_{pf}), pregnancy/gestation (k_{ppreg}) and lactation (k_{pl}) differ from those used when body

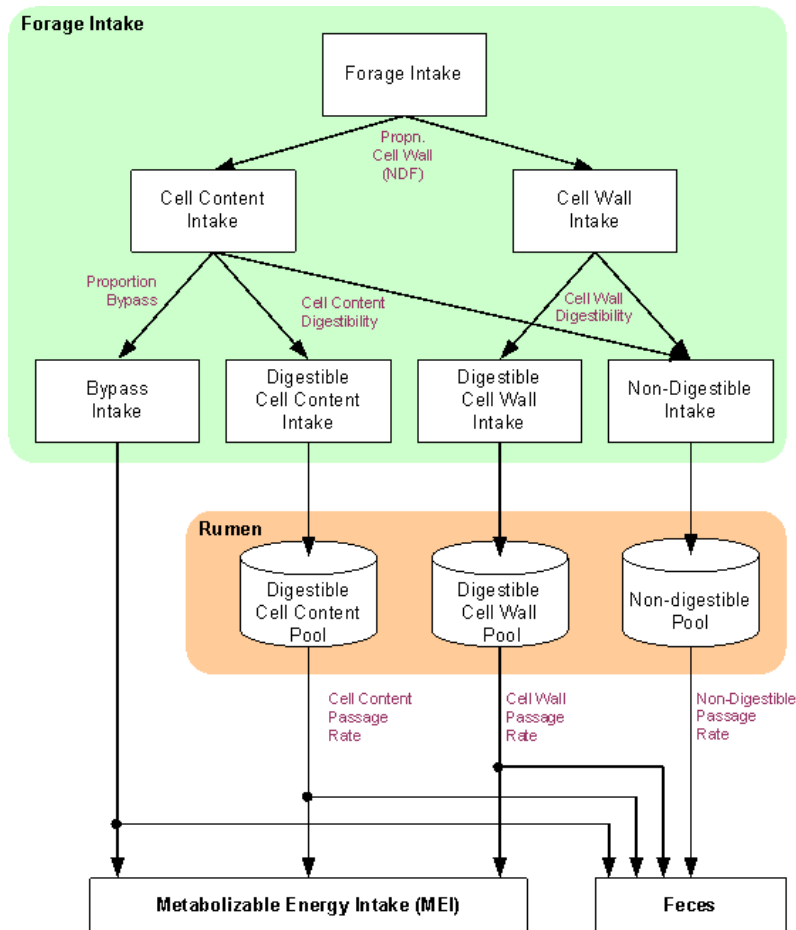


Figure 2. Intake, digestion, and passage dry matter flow to determine metabolizable energy intake and feces output

and reproduction (Stein *et al.*, 2002; Gunn & Irvine, 2003) through reduction in appetite (Steel *et al.*, 1980) and a loss in net N gain through leakage of plasma protein (Steel *et al.*, 1980). These metabolic costs are currently modeled through differences in efficiencies in use of ME and MN (Table 4) and as a component of maintenance requirements (NRC, 2007, Table 5). The user can modify values in Table 4 to reflect either the temporal or seasonal nature of the infection, effects of forage quality (Van Houtert *et al.*, 1995; Steel, 2003), vulnerability to infection of the individual modeled (Gunn & Irvine, 2003), and infection level (Kutz *et al.*, 2013; Steele *et al.*, 2013) as they are available in literature.

Calculating Metabolizable Energy Intake

The flow of information from food intake to determination of daily metabolizable energy intake is detailed in Fig. 3. Although ruminal digestion of dry matter and protein are inextricably linked (Van Soest, 1982; Leng & Nolan, 1984; Beever & Siddons, 1986; Preston & Leng, 1987; Leng, 1990; Poppi & McLennan, 1995), for ease of modeling dry matter/energy and protein

protein is mobilized to support metabolism, gestation and lactation. These values are taken from the literature (NRC, 2007) and other *Rangifer* models (Moen & Pastor, 1998).

Inefficiencies in absorption of amino acid-N from intestines contribute to fecal N output, while inefficiencies in use of metabolizable protein-N for gain contribute to urinary nitrogen loss. The sum of net energy and net protein-N intakes are then compared with energy and protein-N losses on a daily basis to compute whole body balances of energy and protein-N in the modeled animal.

Infections of gastrointestinal nematodes extract seasonal costs relative to weight gain

are simulated separately. Separate processing of dry matter and protein are then rationalized to provide balanced energy and N input to the rumen for allocation to meet the host's requirements and to calculate an energy and N balance. The main integrator of dry matter and protein digestion is the role that digestion and fermentation of dry matter makes in providing energy for microbial maintenance metabolism and for microbial growth (Richardson *et al.*, 2003). Outflow of microbial protein from the rumen can dominate the N economy of ruminants (NRC, 2007).

Rumen microbes ferment cell contents and cell wall material in the rumen (Hungate, 1966; Annison & Armstrong, 1970; Van Soest, 1982; Preston & Leng, 1987; Barboza *et al.*, 2009). However, digestions of cell wall and cell contents proceed at different rates and are controlled by different components of the rumination cycle (Baldwin *et al.*, 1977; Baker & Hobbs, 1987). Thus, to model digestibility within the rumen and passage of components out of the rumen, forage is first allocated to cell wall and cell contents components (Fig. 2, Eq. 3, 4) based on each plant's content of neutral detergent fiber (NDF, Van Soest, 1982). However, the NDF assay may underestimate the amount of cell wall and overestimate cell contents. In the Van Soest detergent system for determining plant constituents, pectin, a cell wall component, is soluble in neutral detergent and is removed from the cell wall (Robbins, 1993). Thus pectin becomes a component of the cell contents. Because pectin is very highly digestible (Van Soest *et al.*, 1991) it has the same attributes as cell contents. However, because pectin makes up a minor constituent of graminoid species and legumes ($1\text{--}6\text{ g} \cdot 100\text{gDM}^{-1}$), and somewhat more in shrub leaves and twigs ($6\text{--}12\text{ g} \cdot 100\text{gDM}^{-1}$, Van Soest, 1982; Robbins, 1993), the error imposed by not correcting for pectin solubility does not seriously affect estimates of digestible energy and metabolizable energy intakes, and Equations 3 and 4 give good approximations.

A variable component of some plants is not digested in the rumen (ARC, 1980) and is variably termed "bypass" or "undegradable" (ARC, 1980). The first step of simulating cell contents is to estimate the level of cell contents that may escape rumen fermentation (Eq. 5). Non-degradable cell contents then pass through the omasum to be digested post-ruminally. Speculation on whether non-degradable or bypass digesta is through chemical complexing by reversibly binding condensed tannins (Barry & Duncan, 1984; Barry & Manly, 1984; Barry & McNab, 1999; McArt *et al.*, 2009), or is through the operation of the esophageal groove mechanism that evolved to prevent milk from entering the rumen in suckled animals (Ørskov and MacDonald, 1969; Ørskov *et al.*, 1970) is not dealt with mechanistically by the model. It is assumed in the model that bypass constituents are confined to the cell contents, are mainly due to proteins, plus those carbohydrate components in dry matter such as starch, sugars etc. In the ARC (1980) and NRC (2007) systems, these rumen non-degradable constituents do not contribute energy or N to microbial synthesis. Values for the extent of protein degradation in the rumen (ARC, 1980 135) are used to estimate extent of non-degradability (1- degradability) of cell contents as a whole. These estimates are shown in Table 4. The remainder cell contents are then digested in the rumen (Eq. 9).

In the model, forage intake is composed of digestible and non-digestible material; the digestible portion can be further subdivided into cell content and cell wall (Fig. 2).

Cell wall intake

Total cell wall intake rate is calculated from the neutral detergent fiber (NDF) analysis as:

$$ACWFI_{p,d} = AFI_{p,d} \cdot NDF_{p,d} \quad \text{for } h \text{ in } d \quad (3)$$

where:

$ACWFI_{p,d}$ = available cell wall intake rate for plant group p on day d ($g \cdot h^{-1}$)
 $AFI_{p,d}$ = available forage intake rate for plant group p on day d ($g \cdot h^{-1}$)
 $NDF_{p,d}$ = user-specified proportion cell wall in plant group p on day d , as calculated from neutral detergent fiber analysis (proportion NDF in dry matter forage intake)

Cell content intake

Total cell content intake rate is calculated next as the remaining component of available forage intake:

$$ACCFI_{p,d} = AFI_{p,d} - ACWFI_{p,d} \quad (4)$$

where:

$ACCFI_{p,d}$ = available cell content intake rate for plant group p on day d ($g \cdot h^{-1}$)
 $AFI_{p,d}$ = available forage intake rate for plant group p on day d ($g \cdot h^{-1}$)
 $ACWFI_{p,d}$ = available cell wall intake rate for plant group p on day d ($g \cdot h^{-1}$)

Digestible bypass cell content

In the model it is assumed that only cell contents bypasses fermentation in the rumen. The portion of the digestible cell content intake that bypasses rumen digestion is calculated as:

$$ABYFI_{p,d} = ACCFI_{p,d} \cdot PCCIBY_{p,d} \quad (5)$$

where:

$ABYFI_{p,d}$ = available bypass intake rate for plant group p on day d ($g \cdot h^{-1}$)
 $ACCFI_{p,d}$ = available cell content intake rate for plant group p on day d ($g \cdot h^{-1}$)
 $PCCIBY_{p,d}$ = user-specified proportion of digestible cell content intake that is bypass for plant group p on day d (proportion)

The remaining digestible cell content intake can be calculated as:

$$ACCDFI_{p,d} = \text{Maximum} \{ ACCFI_{p,d} - ABYFI_{p,d} - (ACCFI_{p,d} \cdot (1 - PCCDIG_{p,d})), 0 \} \quad (6)$$

where:

$ACCDFI_{p,d}$ = available digestible cell content intake rate for plant group p on day d ($g \cdot h^{-1}$)
 $ACCFI_{p,d}$ = available cell content intake rate for plant group p on day d ($g \cdot h^{-1}$)
 $ABYFI_{p,d}$ = available bypass intake rate for plant group p on day d ($g \cdot h^{-1}$)
 $PCCDIG_{p,d}$ = dry matter digestibility of cell content for plant group p on day d (proportion)

Ruminal intake of digestible cell wall and cell contents

The level of plant ADF was used to estimate cell wall digestibility (Eq. 7 Fig. 3; Robbins *et al.*, 1987a). Again, Van Soest (1982) and Robbins (1993) show that errors can occur in application of the detergent analysis technique. In order to accurately estimate the ADF resistant material (e.g. lignin) estimations of NDF and ADF must be made sequentially, otherwise measured ADF levels can exceed those of NDF, which leads to a negative estimation of hemicellulose and an impossibly high estimation of lignin. Therefore, in compiling measures of ADF, literature values of ADF were rejected if ADF exceeded NDF.

Although true digestibility of cell contents is high (~0.98, Van Soest, 1982), apparent digestibility varies widely (0.51-0.66 for domestic forages, Van Soest, 1982) and for wildlife a set of analyses shows digestibility is associated with the cell contents level in the plant (Eq. 7, Fig. 4) and may range as low as 0.5 to a high of 0.76 (Robbins *et al.*, 1987a; Hagerman & Robbins, 1993). Plant secondary compounds such as tannins also can lower digestibility of cell contents (Eq. 10) probably through binding plant proteins (Robbins *et al.*, 1987b) and dry matter (Robbins *et al.*, 1987a; Hanley *et al.*, 1992; McArt *et al.*, 2009). However, studies with deer species indicate no reduction in digestibility of cell walls by tannins (Robbins *et al.*, 1987a). Irreversible binding by tannin can be estimated by the extent that bovine serum albumin (BSA) complexes with cell contents. The BSA complex gives a quantitative assay of tannin binding and reduction in potential digestibility of cell contents (Eq. 10 & 11, Fig. 5). BSA binding assays have not been made universally. Where no BSA analysis on shrubs is available in the literature, an estimate was made based on the strong correlation between BSA assay (mg/mg) and N content of leaves ($\text{gN} \cdot 100\text{gDM}^{-1}$) of deciduous shrubs ($\text{BSA} = 0.456 - 0.098 \cdot \text{N}$, $r^2 = 0.457$, $n = 26$, $P < 0.01$) and evergreen shrubs ($\text{BSA} = 0.295 - 0.06 \cdot \text{N}$, $r^2 = 0.949$, $n = 6$, $P < 0.01$) (based on analysis of data in McArt *et al.*, 2009).

Rationale for balancing rumen fermentation stoichiometry

Maceration of cell walls during eating releases most cell contents, and reduction in particle size during regurgitation, chewing and rumination is essential to cell wall digestibility as well as controlling passage of indigestible material from the rumen (Trudell-Moore & White, 1983; Spalinger *et al.*, 1986; Ulyatt *et al.*, 1986; Spalinger & Robbins, 1992). Continuous input of saliva is required to balance pH and add N and minerals to the fermentation medium. The rumen microbial system, mainly bacteria and protozoa (Hungate, 1966; Dehority, 1974; 1975; 1986; Orpin *et al.*, 1985; Orpin & Mathiesen, 1990; Dehority & Orpin, 1997), but also fungi in wild ruminants (Orpin & Joblin, 1988), break down forage carbohydrates and metabolize them to produce adenosine triphosphate (ATP) for use in microbial growth (Baldwin, 1970; Baldwin, 2010; Wolin, 1975; Van Soest, 1982), with a yield of about 13-20 g of microbial dry matter per mole of ATP (Walker & Nader, 1968; Hespell & Bryant, 1979; Van Soest, 1982). During synthesis of ATP, microbes produce volatile fatty acids (VFAs) as one set of end products of fermentation (Leng & Leonard, 1965; Hungate, 1966; Leng, 1970). Other end products are CO_2 and CH_4 . The same end products have been confirmed for wild ruminants (Gordon, 1968; Langer, 1974; Hoppe, 1977; Hoppe *et al.*, 1977; Kay *et al.*, 1980; Hume & Warner, 1980), including reindeer (White & Gau, 1975; White & Staalund, 1983; Sørmo *et al.*, 1997). VFA production directly reflects digestion of carbohydrates in the rumen (Baldwin, 1970; Leng, 1970; 1982)

and the relation between microbial protein synthesis in the rumen and VFA production is high (Walker & Nader, 1968; Walker *et al.*, 1975; Beever & Siddons, 1986). It is these relations that are used to link dry matter, energy and protein-N transactions in the rumen. Following absorption from the rumen, oxidation of VFAs to CO₂ and water yields about 60-80% of digestible energy intake in the ruminant (Annison *et al.*, 1967; Leng, 1970). In the reindeer about 60 % of the maintenance energy requirement is derived from oxidation of VFAs (White *et al.*, 1990).

VFAs absorbed from the rumen also support anabolic processes such as *de novo* synthesis of glucose from propionic acid and long-chained fatty acid from acetic acid (Leng, 1970). Generally, fermentative energy loss as CO₂ and CH₄ represent approximately 20% of the energy digested by microbes (Van Soest, 1982; Preston & Leng, 1987). In our model the many interacting factors that control pathways of VFA production and the efficiency of maintenance energy metabolism by microbes (i.e. microbial N formed/mole ATP) are not tracked as they are in rumen-centric models (Baldwin, 1970; Baldwin *et al.*, 1977; Black *et al.*, 1980-81). Instead, the model uses a mean yield of microbial N synthesized in relation to organic matter digested in the rumen (ARC, 1980; Van Soest, 1982 169). Thus for each 1 kg of organic matter degraded in the rumen, 32 g N (200g protein) is incorporated into the production of 320 g of new microbial cells (see protein-N digestion). The equations listed below reflect this basic stoichiometry of rumen digestion.

Cell wall digestibility

Digestibility of cell wall is calculated for each plant type as a function of the plant type's acid detergent fiber (ADF) content each day, using data from Robbins *et al.* (1987a) that was fitted to data between ADF values of 0.13 to 0.42 g · gDM⁻¹ (see Fig. 3):

$$\begin{aligned} \text{PCWDIG}_{p,d} &= 0.3 && \text{if } \text{ADF}_{p,d} \leq 0.129 \\ &= (93 \cdot \text{ADF}_{p,d}^3) - (91.88 \cdot \text{ADF}_{p,d}^2) + (27.103 \cdot \text{ADF}_{p,d}) - 1.8653 && \text{if } 0.129 < \text{ADF}_{p,d} < 0.421 \\ &= 0.2 && \text{if } \text{ADF}_{p,d} \geq 0.421 \end{aligned} \quad (7)$$

where:

PCWDIG_{p,d} = dry matter digestibility of cell wall for plant group *p* on day *d* (proportion)
 ADF_{p,d} = user-specified acid detergent fiber content for plant group *p* on day *d*
 (proportion ADF in dry matter forage)

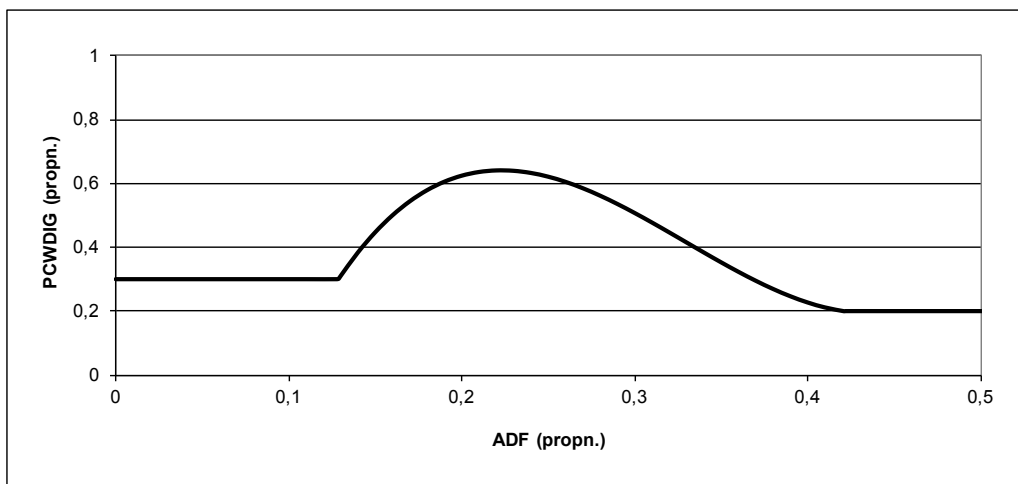


Figure 3. Relationship between cell wall digestibility (PCWDIG) and ADF content of the intake

Cell content digestibility

Digestibility of cell content is calculated in two steps. First, it is estimated for each plant type as a function of the proportion of cell content in the forage intake using data from Robbins *et al.* (1987a) for cell content level between 0.31 and 0.69 g.gDM⁻¹ (Fig. 4).

Proportion of cell content can be inferred from neutral detergent fiber (NDF) analysis as:

$$PCC_{p,d} = 1 - NDF_{p,d} \quad (8)$$

where:

$PCC_{p,d}$ = proportion of intake that is cell content for plant group p on day d (proportion)
 $NDF_{p,d}$ = user-specified proportion cell wall in plant group p on day d , as calculated from neutral detergent fiber content (proportion NDF in dry matter forage)

Digestibility of the cell content is determined from the relationship shown in Figure 4.

$$\begin{aligned} PCCDIGIN_{p,d} &= 0.5 && \text{if } PCC_{p,d} \leq 0.31 \\ &= (-1.83 \cdot PCC_{p,d}^2) + (2.53 \cdot PCC_{p,d}) - 0.1085 && \text{if } 0.31 < PCC_{p,d} < 0.691 \\ &= 0.766 && \text{if } PCC_{p,d} \geq 0.691 \end{aligned} \quad (9)$$

where:

$PCCDIGIN_{p,d}$ = initial estimate of the dry matter digestibility of cell content for plant group p on day d (proportion)
 $PCC_{p,d}$ = proportion cell content intake for plant group p on day d (proportion)

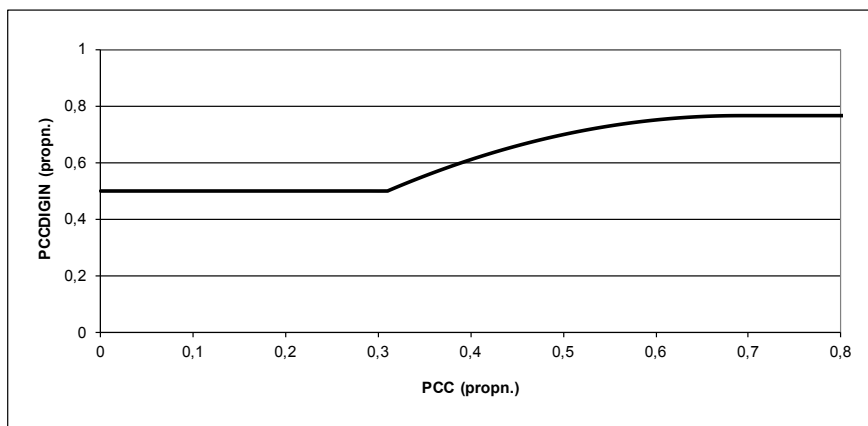


Figure 4. Relationship between cell content digestibility (PCCDIGIN) and the proportion of cell content intake (PCC)

The second step in estimation of digestibility of cell contents is to reduce the estimate made in Eq. 11, due to binding by plant tannins using the BSA assay (Robbins *et al.*, 1987b; McArt *et al.*, 2009). Reduction in cell content digestibility due to BSA was estimated from data of McArt *et al.* (2009) (Fig. 5).

$$\text{RCCTAN}_{p,d} = \begin{cases} (-0.64065 \cdot \text{BSA}_{p,d}^2) + (0.7031 \cdot \text{BSA}_{p,d}) & \text{if } \text{BSA}_{p,d} \leq 0.549 \\ 0.193 & \text{otherwise} \end{cases} \quad (10)$$

where:

$\text{RCCTAN}_{p,d}$ = reduction in the dry matter digestibility of cell content due to the presence of tannins for plant group p on day d (proportion reduction)
 $\text{BSA}_{p,d}$ = user-specified bovine serum albumin (BSA) content for plant group p on day d (proportion of BSA in dry matter forage)

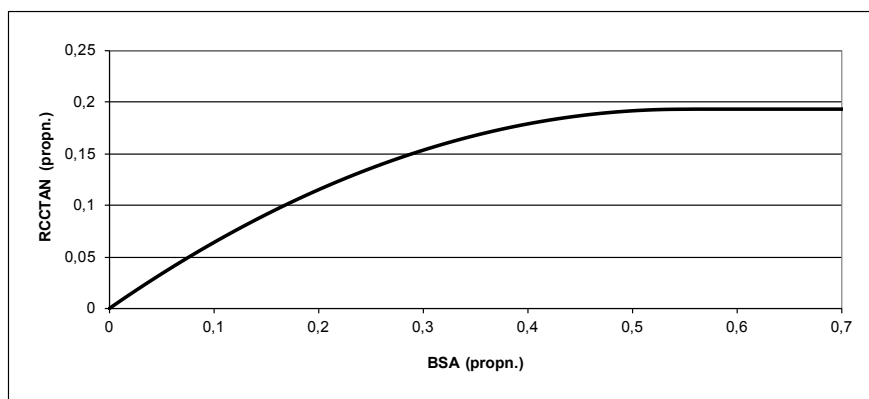


Figure 5. Relationship between the reduction in digestibility of cell content due to tannins (RCCTAN) and the BSA content of the shrub intake

This effect of tannins is then used to adjust the initial estimate of cell content digestibility:

$$\text{PCCDIG}_{p,d} = \text{PCCDIGIN}_{p,d} - \text{RCCTAN}_{p,d} \quad (11)$$

where:

- $\text{PCCDIG}_{p,d}$ = dry matter digestibility of cell content for plant group p on day d (proportion)
 $\text{PCCDIGIN}_{p,d}$ = initial estimate of the dry matter digestibility of cell content for plant group p on day d (proportion)
 $\text{RCCTAN}_{p,d}$ = reduction in the dry matter digestibility of cell content due to the presence of tannins (proportion)

Non-digestible intake and overall digestibility

Application of digestibility to the cell wall and cell contents entering the rumen allows estimation of the hourly intake of digestible cell wall (Eq. 12). Non-digestible cell contents and non-digestible cell walls are summed to determine intake of non-digestible dry matter (Eq. 13). Estimation of overall digestibility of forage is made by subtracting sum of non-digestible intake from the estimate of forage intake and dividing by forage intake of each plant group on a daily basis (Eq. 14).

Digestible cell wall intake can be calculated as:

$$\text{ACWDFI}_{p,d} = \text{ACWFI}_{p,d} \cdot \text{PCWDIG}_{p,d} \quad \text{for } h \text{ in } d \quad (12)$$

where:

- $\text{ACWDFI}_{p,d}$ = available digestible cell wall intake rate for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)
 $\text{ACWFI}_{p,d}$ = available cell wall intake rate for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)
 $\text{PCWDIG}_{p,d}$ = dry matter digestibility of cell wall for plant group p on day d (proportion)

The non-digestible portion of the available forage intake is calculated as the difference between the total forage intake and the digestible portion:

$$\text{ANDFI}_{p,d} = \text{AFI}_{p,d} - (\text{ACCDFI}_{p,d} + \text{ACWDFI}_{p,d} + \text{ABYFI}_{p,d}) \quad (13)$$

where:

- $\text{ANDFI}_{p,d}$ = available non-digestible forage intake rate for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)
 $\text{AFI}_{p,d}$ = available forage intake rate for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)
 $\text{ACCDFI}_{p,d}$ = available digestible cell content intake rate for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)
 $\text{ACWDFI}_{p,d}$ = available digestible cell wall intake rate for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)
 $\text{ABYFI}_{p,d}$ = available bypass intake rate for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)

The overall dry matter digestibility of the forage intake can be calculated as:

$$\text{PDIG}_{p,d} = (\text{AFI}_{p,d} - \text{ANDFI}_{p,d}) / \text{AFI}_{p,d} \quad (14)$$

where:

$\text{PDIG}_{p,d}$ = dry matter digestibility of forage intake for plant group p on day d (proportion)

$\text{AFI}_{p,d}$ = available forage intake rate for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)

$\text{ANDFI}_{p,d}$ = available non-digestible forage intake rate for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)

Residence of digesta in the rumen

Following allocation of forage to dry matter bypass, and estimation of hourly intakes of digestible cell contents, digestible cell wall and non-digestible cell wall, the intakes are added to these three rumen pools (Fig. 2). Loss from the non-digestible pool to the intestines (Eq. 15, Fig. 6) is based on rate-constants (KPND, proportion of non-digestible pool. h^{-1}). Because this pool is made up of indigestible material in the form of “solids” or “particles”, rate-constants from the literature were used based on a minimum rate-constant for solids (KPNDMIN, proportion. h^{-1}) that results in an exponential increase in KPND with an increase in dry matter digestibility (PDIG, Fig. 6). KPNDMIN can be adjusted to diet seasonally and Figure 6 shows relations for KPNDMIN of 0.005 during winter hypophagia and 0.02 for summer hyperphagia.

Timing of transition from winter to summer is assumed to occur with spring green-up and transition from summer to winter at first “hard frost”, snow accumulation, or 30th November, whichever occurs first. Validation of KPND in Figure 6 is based on literature values of rumen turnover rates (inverse of rate-constant) using non-digestible markers in captive animals. For reindeer/caribou, muskoxen and moose, the fractional outflow of fibrous (non-digestible) material is closely related to outflow of the liquid component (White *et al.*, 1984; Renecker & Schwartz, 1997; Schwartz & Renecker 1997) that has been measured more frequently than dry matter. Thus, fractional outflow rates for fiber (KPND) are projected at approximately 0.027 in winter, 0.073 in mid-summer and 0.10 at a peak intake of highly digestible forage. These values are based on rumen turnover times (Spalinger *et al.*, 1986; Holleman & White, 1989; Staaland & White, 1991; Spalinger & Robbins, 1992) and whole animal balance experiments (Schwartz *et al.*, 1988; Holleman & White, 1989). For reindeer and caribou rumen turnover times are more highly related to digestible dry matter intake than to dry matter digestibility (White *et al.*, 1984). However, predicted KPND from Eq. 15 approximates these experimentally based rate-constants using KPNDMIN of 0.008 in winter (KPND = 0.023, DMD 0.65) and 0.02 in summer (KPND = 0.07, DMD 0.7) with KPND = 0.1 at peak digestibility.

Non-digestible passage rate

The hourly passage rate of non-digestible material for each plant group from the rumen is calculated each day as a function of the plant group’s daily digestibility (see Fig. 6):

$$KPND_{p,d} = 1 / ((1/KPNDMIN) - (((1/KPNDMIN) \cdot PDIG_{p,d}))) \quad (15)$$

where:

$KPND_{p,d}$ = hourly passage rate of non-digestible material from the rumen for plant group p on day d (proportion $\cdot h^{-1}$)

$KPNDMIN$ = user-specified minimum hourly passage rate of non-digestible material from the rumen (proportion $\cdot h^{-1}$) – by default this value is set to 0.005 for winter and 0.02 for summer

$PDIG_{p,d}$ = dry matter digestibility for plant group p on day d (proportion)

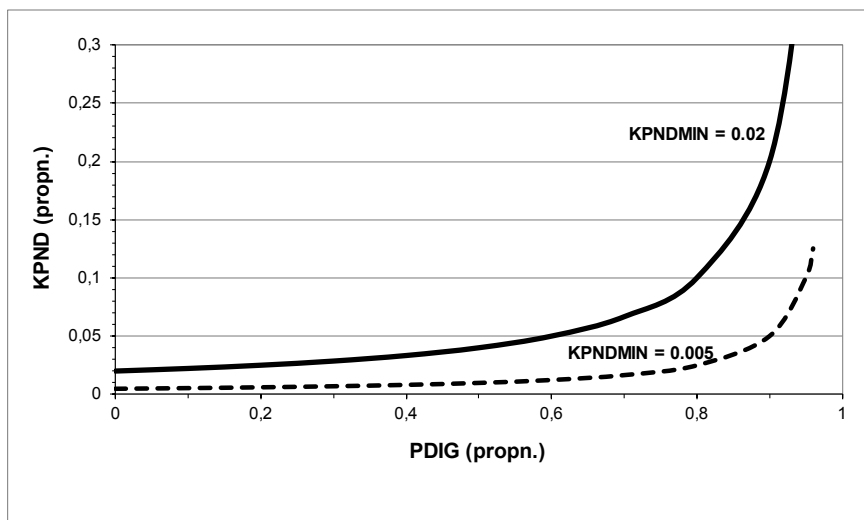


Figure 6. Relationship between hourly passage rate of non-digestible material (KPND) and dry matter digestibility (PDIG)

Rumen fill using available forage

Empirical estimates of rate-constants for digestion are usually based on the fractional disappearance of plant dry matter or protein-N from nylon bags suspended in the rumen (Ørskov & McDonald, 1979; Person *et al.*, 1980; White & Trudell, 1980a) and can be used to separate rates of digestion (proportion $\cdot h^{-1}$) of cell contents (KPCC, 0.09-0.27) and cell walls (KPCW, 0.004-0.015) (Table 3). These values agree with findings for sheep and cattle based on whole animal feeding studies (Beever & Siddons, 1986).

Values used for cell contents (KPCC ~ 0.2 , Eq. 16) and cell walls (KPCW ~ 0.01 , Eq. 17) are calculated means based on mean rate-constants for plant groups (Table 3) assuming a contribution of each plant group in proportion to the pool. Each hour dry matter loss from each pool ($g \cdot DM \cdot h^{-1}$) is the product of pool size and mean rate-constants for digestion plus passage. For cell contents digestion (0.1-0.2 proportion $\cdot h^{-1}$ Table 3) dominates over passage (0.02-0.07 proportion $\cdot h^{-1}$ Fig. 6), whereas for cell walls the relative contributions are more even (Table 3). These differences are used to estimate the proportion of cell contents (PMECC) and cell wall (PMECW)

that contribute energy to metabolizable energy (Eq. 43, 44), but not to feces production (Eq. 50, 51). In the model PMECC and PMECW can be set for each run with default values of 0.78 ± 0.03 and 0.2 ± 0.1 respectively. These year-round mean values are based on average rate-constants for cell contents and cell walls in Table 3 and seasonal KPND (Fig. 6).

Digestible cell content pool

Based on the previous hour's pool size, digestible cell content intake in the current hour is added to the pool then the pool is depleted by rate-constants for digestion plus outflow (KPCC).

Size of the rumen pool of cell contents at the end of the current hour is estimated as:

$$ACCPOOL_h = \sum_p ((CCPOOLHR_{p,h-1} + ACCDFI_{p,d})) \cdot (1 - KPCC_d) \quad \text{for } h \text{ in } d \quad (16)$$

where:

- $ACCPOOL_h$ = digestible cell content pool in hour h , based on available forage (g)
- $CCPOOLHR_{p,h-1}$ = actual digestible cell content pool for plant group p at the end of the previous hour $h-1$ (g)
- $ACCDFI_{p,d}$ = available digestible cell content intake rate for plant group p on day d , based on available forage ($g \cdot h^{-1}$)
- $KPCC_d$ = user-specified hourly digestion plus passage rate (Table 3) of cell content on day d (proportion $\cdot h^{-1}$)

Digestible cell wall pool

Similarly, loss of dry matter from the digestible cell wall pool is attributable to both digestion and outflow (KPCW).

Thus at the end of each hour digestible pool size is estimated as:

$$ACWPOOL_h = \sum_p ((CWPOOLHR_{p,h-1} + ACWDFI_{p,d})) \cdot (1 - KPCW_d) \quad \text{for } h \text{ in } d \quad (17)$$

where:

- $ACWPOOL_h$ = digestible cell wall pool in hour h , based on available forage (g)
- $CWPOOLHR_{p,h-1}$ = actual digestible cell wall pool for plant group p at the end of the previous hour $h-1$ (g)
- $ACWDFI_{p,d}$ = available digestible cell wall intake rate for plant group p on day d , based on available forage ($g \cdot h^{-1}$)
- $KPCW_d$ = user-specified hourly digestion plus passage rate (Table 3) of cell wall on day d (proportion $\cdot h^{-1}$)

Non-digestible pool

Size of the non-digestible pool (indigestible cell wall+ indigestible cell contents, Fig. 3) at the end of each hour is estimated as:

$$\text{ANDPOOL}_h = \sum_p ((\text{NDPOOLHR}_{p,h-1} + \text{ANDFI}_{p,d})) \cdot (1 - \text{KPND}_{p,d}) \quad \text{for } h \text{ in } d \quad (18)$$

where:

- ANDPOOL_h = non-digestible pool in hour h , based on available forage (g)
 $\text{NDPOOLHR}_{p,h-1}$ = actual non-digestible pool for plant group p at the end of the previous hour $h-1$ (g)
 $\text{ANDFI}_{p,d}$ = non-digestible forage intake rate of plant group p on day d , based on available forage ($\text{g} \cdot \text{h}^{-1}$)
 $\text{KPND}_{p,d}$ = hourly passage rate of non-digestible material from the rumen for plant group p on day d (proportion $\cdot \text{h}^{-1}$) (Eq. 15).

Table 3. Summary of rate-constants for digestion of cell contents that contributes to KPCC, and cell wall material that contributes to KPCW

Growth Form	Cell Content	Cell Wall
lichen	0.113	0.0127
mushroom	0.248	0.0064
horsetail	0.087	0.0150
graminoid	0.087	0.0150
deciduous shrub	0.243	0.0097
evergreen shrub	0.272	0.0045
forb	0.228	0.0050
<i>Eriophorum</i> heads	0.248	0.0064
standing dead vegetation	0.087	0.0150
moss	0.087	0.0050

Rate-constants (proportion $\cdot \text{h}^{-1}$) were estimated from disappearance curves deduced from nylon bags suspended in the rumen of reindeer grazing tundra ranges (White & Trudell, 1980a; 1980b). Values in bold were measured. Other values are based on rate constants and plant quality (NDF, cell contents and cell walls (Person *et al.*, 1980; White & Trudell, 1980a; 1980b).

Total rumen pools

At the end of each hour, the sum of all three pools (cell contents, cell wall, indigestible), based on available forage, is estimated as:

$$\text{ATPOOL}_h = \text{ACCPOOL}_h + \text{ACWPOOL}_h + \text{ANDPOOL}_h \quad (19)$$

where:

ATPOOL_h = total of all rumen forage pools at the end of hour h , based on available forage (g)

ACCPOOL_h = digestible cell content pool in hour h , based on available forage (g)

ACWPOOL_h = digestible cell wall pool in hour h , based on available forage (g)

ANDPOOL_h = non-digestible pool in hour h , based on available forage (g)

Rumen capacity constraint on food intake

Although the model emulates both digestion and rate of passage of dry material from the rumen, a mechanism is needed to prevent the rumen from overfilling. Movement of particles out of the rumen as they approach their potential for digestion is required to empty the rumen sufficiently to allow new forage to enter. In the model, an estimate of rumen capacity (RCAP, gDM) provides a constraint to overfilling, which also prevents overeating. RCAP is a variable that can be set for each run of the model because rumen fill varies between animals within the population (Reimers & Ringberg, 1983; Reimers *et al.*, 1983; Spalinger & Robbins, 1992; Gerhart *et al.*, 1996b), can be associated with diet (Staalnd *et al.*, 1979; 1984; Spalinger & Robbins, 1992; Munn & Barboza, 2008) and has been shown to be both larger in winter than summer on Coats Island (Adamczewski *et al.*, 1987b), but smaller in winter than summer in Norway and Svalbard (Staalnd & White, 1991). Although rumen fill is usually measured as wet mass, within the model the rumen fill (ATPOOL) and RCAP are expressed on a dry weight basis.

Given an estimate of the size of the rumen pools that would result if all available forage were ingested every hour, the model then compares this estimate to RCAP. If the total estimated size of the pools exceeds RCAP, then forage intake is adjusted downwards to reflect this constraint.

Excess forage intake

First, if estimated total rumen pool size exceeds the rumen capacity, then the model calculates excess forage intake is calculated as:

$$\text{EXCFI}_h = \text{Maximum} \{ (\text{ATPOOL}_h - \text{RCAP}_{d-1}), 0 \} \quad \text{for } h \text{ in } d \quad (20)$$

where:

EXCFI_h = available forage intake in excess of the rumen capacity for hour h (g)

RCAP_{d-1} = capacity of the rumen on the previous day $d-1$ (g)

ATPOOL_h = total of all rumen pools in hour h , based on available forage (g)

The proportion of total available forage intake that can be accepted into the rumen each hour, based upon the capacity of the rumen, is then calculated as:

$$\text{RPFI}_h = (\sum_p (\text{AFI}_{p,d}) - \text{EXCFI}_h) / \sum_p (\text{AFI}_{p,d}) \quad \text{if } (\text{EXCFI}_h < \sum_p (\text{AFI}_{p,d})) \text{ and } (\sum_p (\text{AFI}_{p,d}) > 0) \quad (21)$$

$$= 0 \quad \text{otherwise}$$

where:

- RPFI_h = proportion of the total available forage intake that can be accepted into the rumen in hour h , based on the rumen capacity (proportion)
- $\text{AFI}_{p,d}$ = available forage intake for plant group p on day d ($\text{g} \cdot \text{h}^{-1}$)
- EXCFI_h = available forage intake in excess of the rumen capacity for hour h ($\text{g} \cdot \text{h}^{-1}$)

This proportion is then used to lower the available forage intake to account for the rumen capacity:

$$\text{RBYFI}_{p,h} = \text{RPFI}_h \cdot \text{ABYFI}_{p,d} \quad \text{for } h \text{ in } d \quad (22)$$

where:

- $\text{RBYFI}_{p,h}$ = digestible bypass intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)
- RPFI_h = proportion of the total available forage intake that can be accepted into the rumen in hour h , based on the rumen capacity (proportion)
- $\text{ABYDFI}_{p,d}$ = digestible cell content intake rate for plant group p on day d , based on available forage ($\text{g} \cdot \text{h}^{-1}$)

$$\text{RCCDFI}_{p,h} = \text{RPFI}_h \cdot \text{ACCDFI}_{p,d} \quad \text{for } h \text{ in } d \quad (23)$$

where:

- $\text{RCCDFI}_{p,h}$ = digestible cell content intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)
- RPFI_h = proportion of the total available forage intake that can be accepted into the rumen in hour h , based on the rumen capacity (proportion)
- $\text{ACCDFI}_{p,d}$ = digestible cell content intake rate for plant group p on day d , based on available forage ($\text{g} \cdot \text{h}^{-1}$)

$$\text{RCWDFI}_{p,h} = \text{RPFI}_h \cdot \text{ACWDFI}_{p,d} \quad \text{for } h \text{ in } d \quad (24)$$

where:

- $\text{RCWDFI}_{p,h}$ = digestible cell wall intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)
- RPFI_h = proportion of the total available forage intake that can be accepted into the rumen in hour h , based on the rumen capacity (proportion)
- $\text{ACWDFI}_{p,d}$ = digestible cell wall intake rate for plant group p on day d , based on available forage ($\text{g} \cdot \text{h}^{-1}$)

$$\text{RNDFI}_{p,h} = \text{RPFI}_h \cdot \text{ANDFI}_{p,d} \quad \text{for } h \text{ in } d \quad (25)$$

where:

$\text{RNDFI}_{p,h}$ = non-digestible forage intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)

RPFI_h = proportion of the total available forage intake that can be accepted into the rumen in hour h , based on the rumen capacity (proportion)

$\text{ANDFI}_{p,d}$ = non-digestible forage intake rate for plant group p on day d , based on available forage ($\text{g} \cdot \text{h}^{-1}$)

Constrained pool sizes

Sizes of cell content and cell wall pools are recalculated based upon these revised estimates of forage intake:

$$\text{RCCPOOL}_h = \sum_p (\text{CCPOOLHR}_{p,h-1} + \text{RCCDFI}_{p,h}) \cdot (1 - \text{KPCC}_d) \quad (26)$$

where:

RCCPOOL_h = rumen digestible cell content pool in hour h , based on rumen capacity constrained forage intake (g)

$\text{CCPOOLHR}_{p,h-1}$ = actual rumen digestible cell content pool for plant group p at the end of the previous hour $h-1$ (g)

$\text{RCCDFI}_{p,h}$ = digestible cell content intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)

KPCC_d = user-specified hourly digestion plus passage rate of cell content on day d (proportion $\cdot \text{h}^{-1}$)

$$\text{RCWPOOL}_h = (\sum_p (\text{CWPOOLHR}_{p,h-1} + \text{RCWDFI}_{p,h})) \cdot (1 - \text{KPCW}_d) \quad (27)$$

where:

RCWPOOL_h = rumen digestible cell wall pool in hour h , based on rumen capacity constrained forage intake (g)

$\text{CWPOOLHR}_{p,h-1}$ = actual rumen digestible cell wall pool for plant group p at the end of the previous hour $h-1$ (g)

$\text{RCWDFI}_{p,h}$ = digestible cell wall intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)

KPCW_d = user-specified hourly digestion plus passage rate of cell wall on day d (proportion $\cdot \text{h}^{-1}$)

Metabolic constraint on forage intake

Because bypass, or ruminally non-degradable dry matter (ARC, 1980), is digested post-ruminally to yield metabolizable energy, this calculation is made prior to calculating metabolizable energy obtained from rumen pools. Metabolizable energy yield from the bypass intake (as constrained by rumen capacity) is calculated as:

$$\text{RENBY}_h = \sum_p (\text{RBYFI}_{p,d}) \cdot \text{DEBY} \cdot \text{PMEBY} \quad (28)$$

where:

- RENBY_h = metabolizable energy obtained in hour h from bypass, based on rumen capacity constrained forage intake ($\text{kJ} \cdot \text{h}^{-1}$)
- $\text{RBYFI}_{p,h}$ = digestible bypass intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)
- DEBY = user-specified energy content of bypass dry matter ($\text{kJ} \cdot \text{g}^{-1}$)
- PMEBY = user-specified proportion of bypass energy that can be absorbed and metabolized (proportion)

Metabolizable energy yield from the cell wall and cell content pools (as constrained by rumen capacity) are calculated as follows:

$$\text{RENCC}_h = \text{RCCPOOL}_h \cdot \text{KPCC}_d \cdot \text{DECC} \cdot \text{PMECC} \quad (29)$$

where:

- RENCC_h = metabolizable energy obtained in hour h from cell content, based on rumen capacity constrained forage intake ($\text{kJ} \cdot \text{h}^{-1}$)
- RCCPOOL_h = size of cell content pool in hour h , based on rumen capacity constrained forage intake (g)
- KPCC_d = user-specified hourly rate of digestion plus passage of cell content on day d (proportion $\cdot \text{h}^{-1}$)
- DECC = user-specified digestible energy concentration of cell content ($\text{kJ} \cdot \text{g}^{-1}$)
- PMECC = user-specified proportion of cell content that can be absorbed and metabolized (0.8)

$$\text{RENCW}_h = \text{RCWPOOL}_h \cdot \text{KPCW}_d \cdot \text{DECW} \cdot \text{PMECW} \quad (30)$$

where:

- RENCW_h = metabolizable energy obtained in hour h from cell wall, based on rumen capacity constrained forage intake ($\text{kJ} \cdot \text{h}^{-1}$)
- RCWPOOL_h = size of digestible cell wall pool in hour h , based on rumen capacity constrained forage intake (g)
- KPCW_d = user-specified hourly rate of digestion plus passage of cell wall on day d (proportion $\cdot \text{h}^{-1}$)
- DECW = user-specified digestible energy concentration in cell walls ($\text{kJ} \cdot \text{g}^{-1}$)
- PMECW = user-specified proportion of digestible energy of cell wall that can be absorbed and metabolized (0.3)

Total metabolizable energy produced, based on rumen capacity constrained forage intake, is calculated as:

$$REI_h = RENBY_h + RENCC_h + RENCW_h \quad (31)$$

where:

- REI_h = total metabolizable energy intake in hour h , based on rumen capacity constrained forage intake ($\text{kJ} \cdot \text{h}^{-1}$)
- $RENBY_h$ = metabolizable energy obtained in hour h from bypass, based on rumen capacity constrained forage intake ($\text{kJ} \cdot \text{h}^{-1}$)
- $RENCC_h$ = metabolizable energy obtained in hour h from cell content, based on rumen capacity constrained forage intake ($\text{kJ} \cdot \text{h}^{-1}$)
- $RENCW_h$ = metabolizable energy obtained in hour h from cell wall, based on rumen capacity constrained forage intake ($\text{kJ} \cdot \text{h}^{-1}$)

A target metabolic energy requirement is entered as an initial condition of the model (TER , $\text{kJ} \cdot \text{d}^{-1}$), but thereafter a new TER is estimated each day and is used as the target. Likewise, a target N requirement is entered and subsequently modified. The user can set initial target energy and N requirement for either winter or summer depending on the start date. Variables associated with energy and protein-N requirements are discussed in the Allocation Submodel section. Default target metabolic requirements for winter and summer depend on initial body weight and are estimated from literature maintenance requirements at respectively 560 and $660 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ and 326 and $484 \text{ mgN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ (see Allocation Submodel; Energy and Nitrogen Requirements, Base Requirements).

In order to calculate actual energy intake each hour, metabolizable energy is compared with the target metabolic energy requirement for the animal to ensure metabolizable energy intake, and thereby forage intake, does not exceed the animal's capacity to use metabolizable energy. If metabolizable energy intake is greater than the target, the model will limit forage intake accordingly.

Whenever the hourly estimated metabolizable energy available from forage exceeds target metabolic energy requirement, excess available energy is calculated:

$$\begin{aligned} EXCEI_h &= REI_h - (TER_{d-1} / 24) & \text{for } h \text{ in } d & & \text{if } REI_h > (TER_{d-1} / 24) \\ &= 0 & & & \text{otherwise} \end{aligned} \quad (32)$$

where:

- $EXCEI_h$ = available energy intake in excess of the target metabolic energy requirement for hour h ($\text{kJ} \cdot \text{h}^{-1}$)
- REI_h = total available energy intake in hour h , based on rumen capacity constrained forage intake ($\text{kJ} \cdot \text{h}^{-1}$)
- TER_{d-1} = target metabolic energy requirement on previous day $d-1$ ($\text{kJ} \cdot \text{d}^{-1}$)
- 24 = hours in a day ($\text{h} \cdot \text{d}^{-1}$)

The proportion of the total available forage intake that is actually taken in by the animal each hour, based upon the metabolic energy requirement constraint, is then calculated as:

$$\begin{aligned} \text{MPFI}_h &= (\text{REI}_h - \text{EXCEI}_h) / \text{REI}_h && \text{if } (\text{EXCEI}_h < \text{REI}_h) \text{ and } (\text{REI}_h > 0) \\ &= 0 && \text{otherwise} \end{aligned} \quad (33)$$

where:

MPFI_h = proportion of the total rumen capacity constrained forage intake that can be taken in by the animal, based on the metabolic constraint (proportion)

REI_h = total available energy intake in hour h , based on rumen capacity constrained forage intake ($\text{kJ} \cdot \text{h}^{-1}$)

EXCEI_h = available energy intake in excess of the rumen capacity ($\text{kJ} \cdot \text{h}^{-1}$)

Actual forage intake, energy intake and rumen pool sizes

Based upon available forage, rumen capacity, and metabolic requirements of the animal, the model calculates actual forage and energy intake.

Forage intake calculated based on the logistic constraint is adjusted downwards if available rumen capacity constrained energy intake is greater than the metabolic requirement:

$$\text{BYFIHR}_{p,h} = \text{MPFI}_h \cdot \text{RBYFI}_{p,h} \quad (34)$$

where:

$\text{BYFIHR}_{p,h}$ = actual bypass forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

MPFI_h = proportion of the total available energy intake that can be used by the animal in hour h , based on metabolic requirements (proportion)

$\text{RBYFI}_{p,h}$ = digestible bypass intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)

$$\text{CCDFIHR}_{p,h} = \text{MPFI}_h \cdot \text{RCCDFI}_{p,h} \quad (35)$$

where:

$\text{CCDFIHR}_{p,h}$ = actual digestible cell content forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

MPFI_h = proportion of the total available energy intake that can be used by the animal in hour h , based on metabolic requirements (proportion)

$\text{RCCDFI}_{p,h}$ = digestible cell content intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)

$$\text{CWDFIHR}_{p,h} = \text{MPFI}_h \cdot \text{RCWDFI}_{p,h} \quad (36)$$

where:

$\text{CWDFIHR}_{p,h}$ = actual digestible cell wall forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

MPFI_h = proportion of the total available energy intake that can be used by the animal in hour h , based on metabolic requirements (proportion)

$\text{RCWDFI}_{p,h}$ = digestible cell wall intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)

$$\text{NDFIHR}_{p,h} = \text{MPFI}_h \cdot \text{RNDFI}_{p,h} \quad (37)$$

where:

- $\text{NDFIHR}_{p,h}$ = actual non-digestible forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- MPFI_h = proportion of the total available energy intake that can be used by the animal in hour h , based on metabolic requirements (proportion)
- $\text{RNDFI}_{p,h}$ = non-digestible forage intake for plant group p in hour h , based on rumen capacity constrained forage intake ($\text{g} \cdot \text{h}^{-1}$)

$$\text{FIHR}_{p,h} = \text{BYFIHR}_{p,h} + \text{CCDFIHR}_{p,h} + \text{CWDFIHR}_{p,h} + \text{NDFIHR}_{p,h} \quad (38)$$

where:

- $\text{FIHR}_{p,h}$ = total forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{BYFIHR}_{p,h}$ = actual bypass forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{CCDFIHR}_{p,h}$ = actual digestible cell content forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{CWDFIHR}_{p,h}$ = actual digestible cell wall forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{NDFIHR}_{p,h}$ = actual non-digestible forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

Rumen pool sizes prior to passage

Actual rumen pool sizes, prior to digestion and passage each hour, are updated as follows:

$$\text{CCPRIOR}_{p,h} = \text{CCPOOLHR}_{p,h-1} + \text{CCDFIHR}_{p,h} \quad (39)$$

where:

- $\text{CCPRIOR}_{p,h}$ = actual rumen cell content pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- $\text{CCPOOLHR}_{p,h-1}$ = actual rumen cell content pool for plant group p at the end of the previous hour $h-1$ (g)
- $\text{CCDFIHR}_{p,h}$ = actual digestible cell content forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$$\text{CWPRIOR}_{p,h} = \text{CWPOOLHR}_{p,h-1} + \text{CWDFIHR}_{p,h} \quad (40)$$

where:

- $\text{CWPRIOR}_{p,h}$ = actual rumen cell wall pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- $\text{CWPOOLHR}_{p,h-1}$ = actual rumen cell wall pool for plant group p at the end of the previous hour $h-1$ (g)
- $\text{CWDFIHR}_{p,h}$ = actual digestible cell wall forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$$\text{NDPRIOR}_{p,h} = \text{NDPOOLHR}_{p,h-1} + \text{NDFIHR}_{p,h} \quad (41)$$

where:

- $\text{NDPRIOR}_{p,h}$ = actual rumen non-digestible pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- $\text{NDPOOLHR}_{p,h-1}$ = actual rumen non-digestible pool for plant group p at the end of the previous hour $h-1$ (g)
- $\text{NDFIHR}_{p,h}$ = actual non-digestible forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

Daily metabolizable energy intake

Actual metabolizable energy obtained through digestion each hour is re-calculated for bypass, cell content and cell wall as follows:

$$\text{BYMEIHR}_{p,h} = \text{BYFIHR}_{p,h} \cdot \text{DEBY} \cdot \text{PMEBY} \quad (42)$$

where:

- $\text{BYMEIHR}_{p,h}$ = actual metabolizable energy obtained from bypass for plant group p in hour h ($\text{kJ} \cdot \text{h}^{-1}$)
- $\text{BYFIHR}_{p,h}$ = actual bypass forage intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- DEBY = user-specified digestible energy associated with bypass ($\text{kJ} \cdot \text{g}^{-1}$)
- PMEBY = user-specified proportion of bypass dry matter that can be absorbed (proportion)

$$\text{CCMEIHR}_{p,h} = \text{CCPRIOR}_{p,h} \cdot \text{KPCC}_d \cdot \text{DECC} \cdot \text{PMECC} \quad (43)$$

where:

- $\text{CCMEIHR}_{p,h}$ = actual metabolizable energy obtained from cell content for plant group p in hour h ($\text{kJ} \cdot \text{h}^{-1}$)
- $\text{CCPRIOR}_{p,h}$ = actual digestible rumen cell content pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- KPCC_d = user-specified hourly rate of digestion plus passage of cell content on day d (proportion $\cdot \text{h}^{-1}$)
- DECC = user-specified digestible energy associated with cell content ($\text{kJ} \cdot \text{g}^{-1}$)
- PMECC = user-specified proportion of cell content dry matter that can be absorbed (proportion)

$$CWMEIHR_{p,b} = CWPRIOR_{p,b} \cdot KPCW_d \cdot DECW \cdot PMECW \quad (44)$$

where:

- $CWMEIHR_{p,b}$ = actual metabolizable energy obtained from cell wall for plant group p in hour b ($\text{kJ} \cdot \text{h}^{-1}$)
- $CWPRIOR_{p,b}$ = actual digestible rumen cell wall pool for plant group p in hour b , prior to the current hour's digestion and passage (g)
- $KPCW_d$ = user-specified hourly rate of digestion plus passage of cell wall on day d (proportion $\cdot \text{h}^{-1}$)
- $DECW$ = user-specified digestible energy associated with cell wall ($\text{kJ} \cdot \text{g}^{-1}$)
- $PMECW$ = user-specified proportion of cell wall dry matter that can be absorbed (proportion)

Energy intake from each digestible pool is summed to determine the hourly metabolizable energy intake (MEI):

$$MEIHR_{p,b} = BYMEIHR_{p,b} + CCMEIHR_{p,b} + CWMEIHR_{p,b} \quad (45)$$

where:

- $MEIHR_{p,b}$ = total hourly metabolizable energy intake in hour b ($\text{kJ} \cdot \text{h}^{-1}$)
- $BYMEIHR_{p,b}$ = actual metabolizable energy obtained from bypass for plant group p in hour b ($\text{kJ} \cdot \text{h}^{-1}$)
- $CCMEIHR_{p,b}$ = actual metabolizable energy obtained from cell content for plant group p in hour b ($\text{kJ} \cdot \text{h}^{-1}$)
- $CWMEIHR_{p,b}$ = actual metabolizable energy obtained from cell wall for plant group p in hour b ($\text{kJ} \cdot \text{h}^{-1}$)

Rumen pool sizes after passage

Rumen pool sizes are updated to reflect the current hour's digestion plus passage:

$$CCPOOLHR_{p,b} = CCPRIOR_{p,b} \cdot (1 - KPCC_d) \quad \text{for } b \text{ in } d \quad (46)$$

where:

- $CCPOOLHR_{p,b}$ = actual cell content pool for plant group p at the end of hour b (g)
- $CCPRIOR_{p,b}$ = actual rumen cell content pool for plant group p in hour b , prior to the current hour's digestion and passage (g)
- $KPCC_d$ = user-specified hourly rate of digestion plus passage of cell content on day d (proportion $\cdot \text{h}^{-1}$)

$$CWPOOLHR_{p,h} = CWPRIOR_{p,h} \cdot (1 - KPCW_d) \quad \text{for } h \text{ in } d \quad (47)$$

where:

- $CWPOOLHR_{p,h}$ = actual cell wall pool for plant group p at the end of hour h (g)
- $CWPRIOR_{p,h}$ = actual rumen cell wall pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- $KDCW_d$ = user-specified hourly rate of digestion plus passage of cell wall on day d (proportion)

$$NDPOOLHR_{p,h} = NDPRIOR_{p,h} \cdot (1 - KPND_{p,d}) \quad \text{for } h \text{ in } d \quad (48)$$

where:

- $NDPOOLHR_{p,h}$ = actual non-digestible pool for plant group p at the end of hour h (g)
- $NDPRIOR_{p,h}$ = actual rumen non-digestible pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- $KPND_{p,d}$ = hourly passage rate of non-digestible material for plant group p on day d (proportion · h⁻¹)

Fecal production

Total fecal production each hour is calculated as the portion of dry matter that passes into the intestine but is not converted to energy. This is calculated as:

$$BYFECHR_{p,h} = BYFIHR_{p,h} \cdot (1 - PMEBY) \quad (49)$$

where:

- $BYFECHR_{p,h}$ = fecal production from bypass dry matter for plant group p in hour h (g · h⁻¹)
- $BYFIHR_{p,h}$ = actual bypass forage intake for plant group p in hour h (g · h⁻¹)
- $PMEBY$ = user-specified proportion of bypass dry matter that can be absorbed (proportion)

$$CCFECHR_{p,h} = CCPRIOR_{p,h} \cdot KPCC_d \cdot (1 - PMECC) \quad (50)$$

where:

- $CCFECHR_{p,h}$ = fecal production from cell content dry matter for plant group p in hour h (g · h⁻¹)
- $CCPRIOR_{p,h}$ = actual digestible rumen cell content pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- $KPCC_d$ = user-specified hourly digestion plus passage rate of cell content on day d (proportion · h⁻¹)
- $PMECC$ = user-specified proportion of cell content dry matter that can be absorbed (proportion)

$$\text{CWFECHR}_{p,h} = \text{CWPRIOR}_{p,h} \cdot \text{KPCW}_d \cdot (1 - \text{PMECW}) \quad (51)$$

where:

- $\text{CWFECHR}_{p,h}$ = fecal production from cell wall dry matter for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{CWPRIOR}_{p,h}$ = actual digestible rumen cell wall pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- KPCW_d = user-specified hourly digestion plus passage rate of cell wall on day d (proportion $\cdot \text{h}^{-1}$)
- PMECW = user-specified proportion of cell wall dry matter that can be absorbed (proportion)

$$\text{NDFECHR}_{p,h} = \text{NDPRIOR}_{p,h} \cdot \text{KPND}_{p,d} \quad \text{for } h \text{ in } d \quad (52)$$

where:

- $\text{NDFECHR}_{p,h}$ = fecal production from non-digestible dry matter for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{NDPRIOR}_{p,h}$ = non-digestible dry matter for plant group p in hour h , prior to the current hour's passage (g)
- $\text{KPND}_{p,d}$ = hourly passage rate of non-digestible material for plant group p on day d (proportion $\cdot \text{h}^{-1}$)

Total fecal production each hour is calculated as:

$$\text{FECHR}_{p,h} = \text{BYFECHR}_{p,h} + \text{CCFECHR}_{p,h} + \text{CWFECHR}_{p,h} + \text{NDFECHR}_{p,h} \quad (53)$$

where:

- $\text{FECHR}_{p,h}$ = total dry matter fecal production for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{BYFECHR}_{p,h}$ = fecal production from bypass dry matter for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{CCFECHR}_{p,h}$ = fecal production from cell content dry matter for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{CWFECHR}_{p,h}$ = fecal production from cell wall dry matter for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{NDFECHR}_{p,h}$ = fecal production from non-digestible dry matter for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

Calculating Metabolizable Nitrogen Intake

The model simulates processing of N in dietary plant protein, including digestion in the rumen, by the complex microbial system and transfer of N from the rumen to the intestines for absorption as amino acids, termed the metabolizable N intake (MNI, Fig. 7). Although plant N is not all in the form of protein-N, the model considers all forms of organic- N, *e.g.* nucleic acids,

(DNA, RNA), etc., as equivalent to protein-N. Within the rumen a proportion of plant protein and organic-N is degraded to release NH_4^+ , and NH_4^+ also is added through saliva. NH_4^+ is subtracted from protein-N to yield “non-ammonia N (NAN)” (ARC, 1980; NRC, 1985). Flow of NAN from the abomasum is usually determined in studies that estimate amino acid absorption from the small intestines (Beever & Siddons, 1986). In the model NH_4^+ is treated separately as a dietary component, to estimate true N digestibility (Fig. 7). Dietary inorganic-N enters a common pool with endogenous N (urea plus NH_4^+) that enters the rumen through saliva and absorption from the blood stream to constitute the “protein regeneration cycle” (NRC, 2007 18), often termed the “urea cycle” (McDonald, 1952; Schmidt-Nielsen *et al.*, 1957; 1958; Houpt, 1970; Houpt & Houpt, 1968). Generation of microbial N by microbial reproduction during fermentation of forage cell contents and digestible cell walls uses recycled N (incorporation efficiency of 0.8 (ARC, 1980 128) plus ruminally-degradable plant proteins, assuming a 100% efficiency of conversion to microbial protein (ARC, 1980 128; NRC, 1985; 2007). Microbial protein plus “non-degradable plant protein” (ARC, 1980; NRC, 2007) are flushed from the rumen to be digested as amino acids, equivalent to NAN, in the intestines (Owens & Goetsch, 1986; Nolan & Leng, 1972). Literature values for the efficiency of absorption of protein-N between the abomasum and terminal small intestines (ileum), range from 0.63-0.73. For passage of ruminally non-degradable protein-N and microbial protein, an amino acid absorption efficiency of 0.73 is used (ARC, 1980 130). Once absorbed, N as amino acids is allocated to meet requirements of the animal in the joint energy-protein allocation sub-model. That N not absorbed, *i.e.* the fractional difference (0.27-0.34), is allocated to fecal N loss.

In parallel with treatment of dry matter, truly digestible plant protein-N is allocated to cell contents and cell wall (Fig. 7). N in cell contents is separated into ruminally un-degradable protein, including that portion that can bypass the rumen, and ruminally degradable protein that is available for microbial protein synthesis. Cell content that is complexed by tannins and thereby made non-digestible is allocated to non-digestible N intake. Non-digestible N intake also includes the indigestible component of cell wall N.

Component intakes are added to rumen pools of N on an hourly basis. These pools include undegradable N, degradable N, digestible cell wall N, microbial N, and non-digestible N (Fig. 7). Each hour microbial protein-N is increased from non-protein N, plus degradable-N intake as driven by the digestion of organic matter. Contents of rumen N pools are depleted on an hourly basis using rate-constants for cell contents and cell walls. Sum of net amino acid N absorbed from the intestines is the modeled estimate of metabolizable N intake (MNI) (Fig. 7).

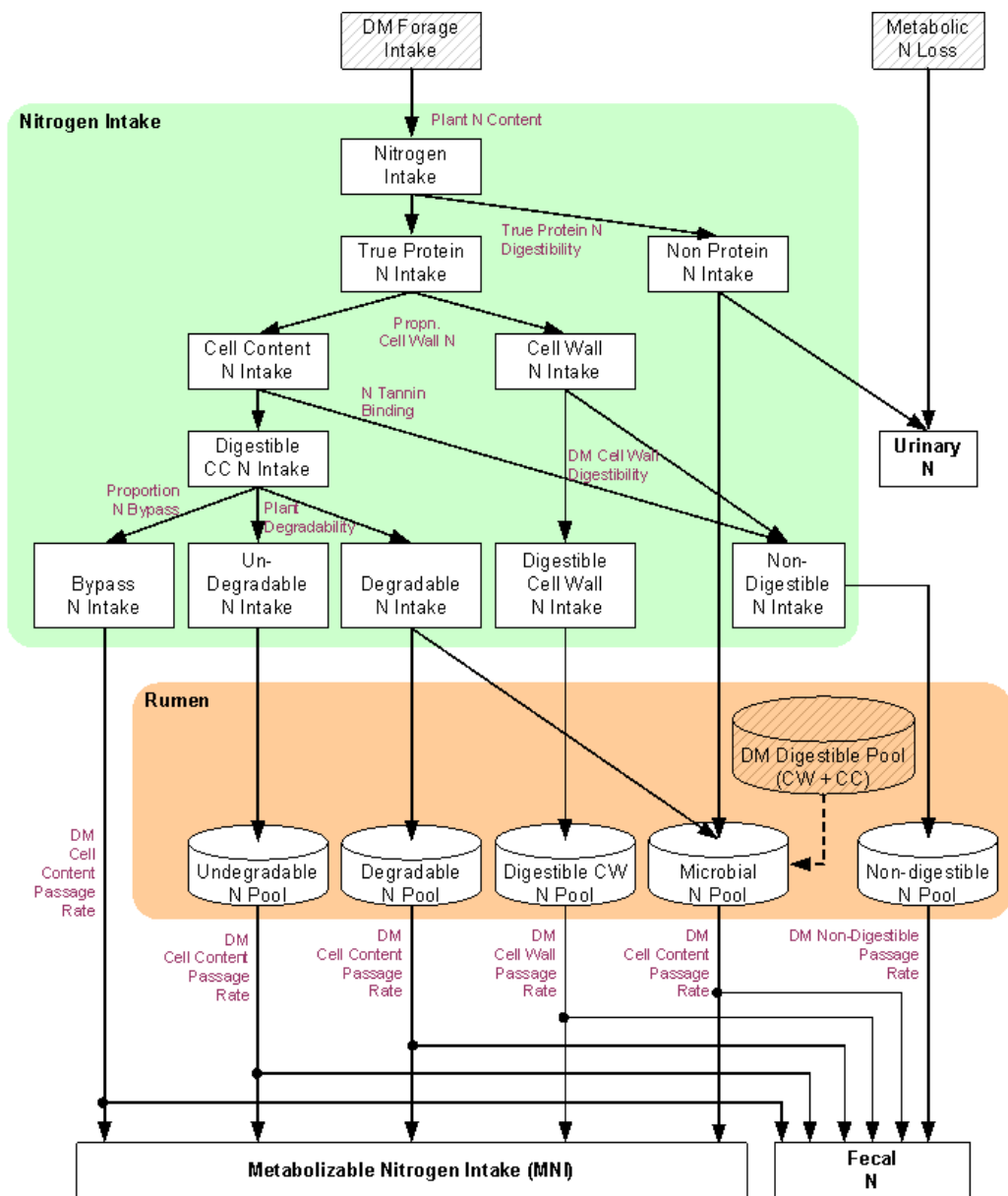


Figure 7. Calculation of metabolizable nitrogen intake and fecal N output

Protein-nitrogen intake

Nitrogen intake is calculated by plant type each hour based on hourly forage intake ($FIHR_{p,h}$ Eq. 38):

$$NIHR_{p,h} = PNIT_{p,d} \cdot FIHR_{p,h} \quad \text{for } h \text{ in } d \quad (54)$$

where:

$$\begin{aligned} NIHR_{p,h} &= \text{total nitrogen intake for plant group } p \text{ in hour } h \text{ (g} \cdot \text{h}^{-1}\text{)} \\ PNIT_{p,d} &= \text{user-specified nitrogen content for plant group } p \text{ on day } d \text{ (proportion)} \\ FIHR_{p,h} &= \text{total forage intake for plant group } p \text{ in hour } h \text{ (g} \cdot \text{h}^{-1}\text{)} \end{aligned}$$

Intake of true digestible protein-N is calculated assuming true digestibility is 0.92 (Robbins, 1993 294):

$$TPNIHR_{p,h} = PTPNDIG \cdot NIHR_{p,h} \quad (55)$$

where:

$$\begin{aligned} TPNIHR_{p,h} &= \text{true-protein nitrogen intake for plant group } p \text{ in hour } h \text{ (g} \cdot \text{h}^{-1}\text{)} \\ PTPNDIG &= \text{user-supplied true-protein nitrogen digestibility (proportion)} \\ &\quad - \text{by default this value is set to 0.92 (Robbins, 1993 p294)} \\ NIHR_{p,h} &= \text{total nitrogen intake for plant group } p \text{ in hour } h \text{ (g} \cdot \text{h}^{-1}\text{)} \end{aligned}$$

Non-protein N intake is calculated as:

$$NPNIHR_{p,h} = NIHR_{p,h} - TPNIHR_{p,h} \quad (56)$$

where:

$$\begin{aligned} NPNIHR_{p,h} &= \text{non-protein nitrogen intake for plant group } p \text{ in hour } h \text{ (g} \cdot \text{h}^{-1}\text{)} \\ NIHR_{p,h} &= \text{total nitrogen intake for plant group } p \text{ in hour } h \text{ (g} \cdot \text{h}^{-1}\text{)} \\ TPNIHR_{p,h} &= \text{true-protein nitrogen intake for plant group } p \text{ in hour } h \text{ (g} \cdot \text{h}^{-1}\text{)} \end{aligned}$$

Cell content and cell wall nitrogen intake

True-protein nitrogen intake is divided into two components in the model: cell content intake and cell wall intake with cell wall content based on NDF (Eq. 3). The proportion of the true protein-N intake that is cell wall is considered to be ADF-bound (Van Soest, 1982 235) for each plant group as a function of the nitrogen content of the plant group using the relationship shown in Figure 8 and calculated as:

$$\begin{aligned}
 \text{PTPCW}_{p,d} &= \text{YMAX} && \text{if } (\text{PNIT}_{p,d} \geq \text{XMAX}) \\
 &= \text{YMIN} && \text{if } (\text{PNIT}_{p,d} \leq \text{XMIN}) \\
 &= \text{YMIN} + ((\text{PNIT}_{p,d} - \text{XMIN}) \cdot (\text{YMAX} - \text{YMIN}) / (\text{XMAX} - \text{XMIN})) && \text{otherwise}
 \end{aligned} \tag{57}$$

where:

- PTPCW_{p,d} = proportion of the true-protein nitrogen intake that is cell wall for plant group *p* on day *d* (proportion)
- PNIT_{p,d} = user-specified nitrogen content for plant group *p* on day *d* (proportion)
- YMAX = maximum proportion of true-protein nitrogen intake that is cell wall (proportion) – by default set to 0.3 (Van Soest, 1982 p235)
- YMIN = minimum proportion of true-protein nitrogen intake that is cell wall (proportion) – by default set to 0.1 (Van Soest, 1982 p235)
- XMAX = nitrogen content at which the proportion of true-protein nitrogen intake that is cell wall reaches a maximum (proportion) – by default set to 0.055 (Van Soest, 1982 p235)
- XMIN = nitrogen content at which the proportion of true-protein nitrogen intake that is cell wall reaches a minimum (proportion) – by default set to 0.015 (Van Soest, 1980 p235)

Cell wall nitrogen intake is then calculated as a proportion of the total nitrogen intake:

$$\text{CWNIHR}_{p,h} = \text{PTPCW}_{p,d} \cdot \text{TPNIHR}_{p,h} \quad \text{for } h \text{ in } d \tag{58}$$

where:

- CWNIHR_{p,h} = cell wall nitrogen intake for plant group *p* in hour *h* (g · h⁻¹)
- PTPCW_{p,d} = proportion of the true protein nitrogen intake that is cell wall for plant group *p* on day *d* (proportion)
- TPNIHR_{p,h} = true protein-nitrogen intake for plant group *p* in hour *h* (g · h⁻¹)

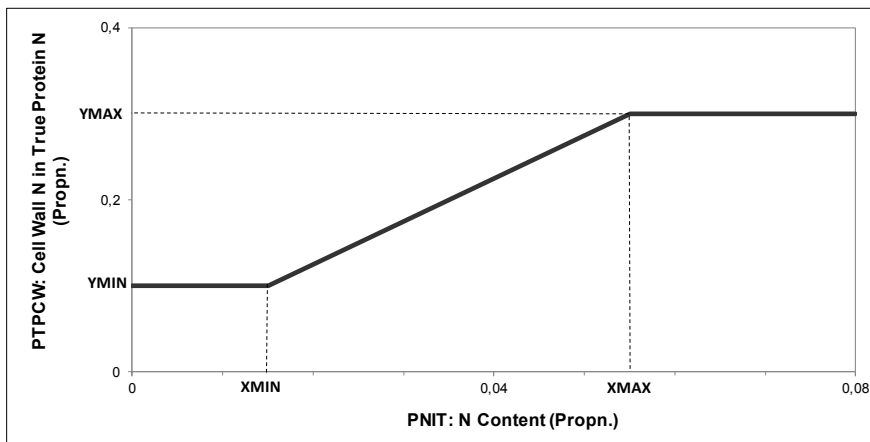


Figure 8. Relationship between the proportion of true-protein nitrogen intake that is cell wall (PTPCW) and the plant group's nitrogen content (PNIT)

Intake of N in cell content is calculated as total true nitrogen intake minus cell wall nitrogen intake, *viz*:

$$\text{CCNIHR}_{p,b} = \text{TPNIHR}_{p,b} - \text{CWNIHR}_{p,b} \quad (59)$$

where:

CCNIHR_{*p,b*} = cell content nitrogen intake for plant group *p* in hour *b* (g · h⁻¹)
 TPNIHR_{*p,b*} = true protein-nitrogen intake for plant group *p* in hour *b* (g · h⁻¹)
 CWNIHR_{*p,b*} = cell wall nitrogen intake for plant group *p* in hour *b* (g · h⁻¹)

Digestible and non-digestible nitrogen intake

Although true nitrogen intake is all potentially digestible, that in the cell wall is only released as the cell wall is digested. Digestibility of cell contents nitrogen is assumed to be 1.0, unless it is complexed by tannins when forage is in the mouth during prehension and chewing. Digestibility of cell content N is reduced due to the presence of tannins as assayed by BSA (Robbins *et al.*, 1987b; McArt *et al.*, 2006). This reduction is calculated according to the relationship shown in Figure 9:

$$\begin{aligned} \text{RNCCTAN}_{p,d} &= \text{YMAX} && \text{if } (\text{BSA}_{p,d} \geq \text{XMAX}) \\ &= \text{YMIN} && \text{if } (\text{BSA}_{p,d} \leq \text{XMIN}) \\ &= \text{YMIN} + ((\text{BSA}_{p,d} - \text{XMIN}) \cdot (\text{YMAX} - \text{YMIN}) / (\text{XMAX} - \text{XMIN})) && \text{otherwise} \end{aligned} \quad (60)$$

where:

RNCCTAN_{*p,d*} = reduction in nitrogen digestibility of cell content due to the presence of tannins for plant group *p* on day *d* (proportion reduction)
 BSA_{*p,d*} = user-specified bovine serum albumin (BSA) content for plant group *p* on day *d* (mg.mg⁻¹)
 YMAX = maximum reduction in nitrogen digestibility of cell content due to the presence of tannins (proportion) – by default set to 0.013 (Robbins *et al.*, 1987b)
 YMIN = minimum reduction in nitrogen digestibility of cell content due to the presence of tannins (proportion) – by default set to 0 (Robbins *et al.*, 1987b)
 XMAX = BSA level at which the reduction in nitrogen digestibility of cell content due to the presence of tannins reaches a maximum (proportion) – by default set to 0.07 (Robbins *et al.*, 1987b)
 XMIN = BSA level at which the reduction in nitrogen digestibility of cell content due to the presence of tannins reaches a minimum (proportion) – by default set to 0.006 (Robbins *et al.*, 1987b)

Intake of digestible N in cell content is calculated as:

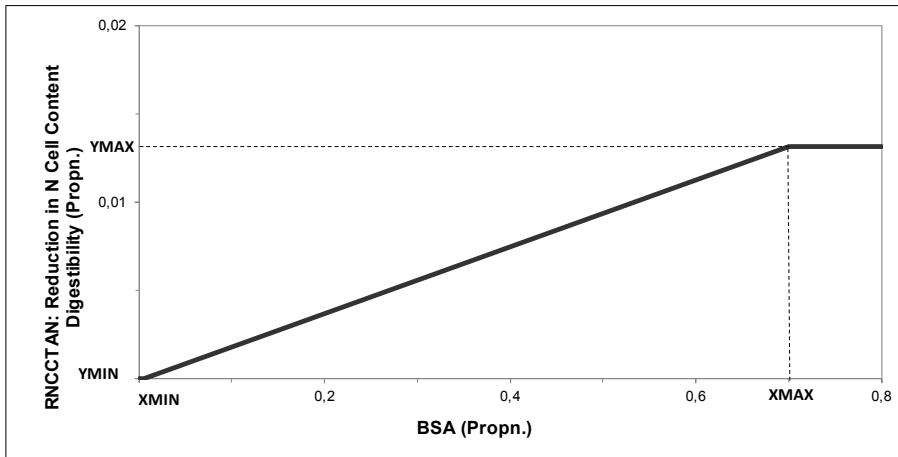


Figure 9. Relationship between the proportional reduction in nitrogen cell content digestibility (RNCCTAN) and the plant group BSA content

$$\text{CCDNIHR}_{p,h} = \text{CCNIHR}_{p,b} \cdot (1 - \text{RNCCTAN}_{p,d}) \quad \text{for } h \text{ in } d \quad (61)$$

where:

$\text{CCDNIHR}_{p,h}$ = digestible cell content nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{CCNIHR}_{p,b}$ = cell content nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{RNCCTAN}_{p,d}$ = reduction in nitrogen digestibility of cell content due to the presence of tannins for plant group p on day d (proportion reduction)

Digestible N in cell wall intake is released during digestion of the cell wall dry matter (see Eq. 7):

$$\text{CWDNIHR}_{p,h} = \text{CWNIHR}_{p,b} \cdot \text{PCWDIG}_{p,d} \quad \text{for } h \text{ in } d \quad (62)$$

where:

$\text{CWDNIHR}_{p,h}$ = digestible cell wall nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{CWNIHR}_{p,b}$ = cell wall nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{PCWDIG}_{p,d}$ = dry matter digestibility of cell wall for plant group p on day d (proportion)

Non-digestible N intake is calculated as:

$$\text{NDNIHR}_{p,h} = \text{CCNIHR}_{p,h} + \text{CWNIHR}_{p,h} - \text{CCDNIHR}_{p,h} - \text{CWDNIHR}_{p,h} \quad (63)$$

where:

$\text{NDNIHR}_{p,h}$ = non-digestible nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{CCNIHR}_{p,h}$ = cell content nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{CWNIHR}_{p,h}$ = cell wall nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{CCDNIHR}_{p,h}$ = digestible cell content nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{CWDNIHR}_{p,h}$ = digestible cell wall nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

Bypass, undegradable and degradable nitrogen intake

A portion of the cell content nitrogen intake can bypass the rumen (Table 4). This portion is calculated as:

$$\text{BYNIHR}_{p,h} = \text{CCDNIHR}_{p,h} \cdot \text{PCCIBY}_{p,d} \quad \text{for } h \text{ in } d \quad (64)$$

where:

$\text{BYNIHR}_{p,h}$ = bypass nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{CCDNIHR}_{p,h}$ = digestible cell content nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{PCCIBY}_{p,d}$ = user-specified proportion of cell content dry matter intake that is bypass for plant group p on day d (proportion)

Although most of the water-soluble leaf protein in spring forage is readily fermentable (Van Soest, 1982 p242), a variable proportion of cell content N is not degradable by the rumen microbiota (ARC, 1980; Van Soest, 1982). Thus, after accounting for bypass N, the remaining intake of digestible cell contents N is divided into degradable and undegradable protein-N intake. For each dietary type this split will vary seasonally.

Degradable cell content N is calculated as:

$$\text{DPNIHR}_{p,h} = \text{PDEG}_{p,d} \cdot (\text{CCDNIHR}_{p,h} - \text{BYNIHR}_{p,h}) \quad \text{for } h \text{ in } d \quad (65)$$

where:

$\text{DPNIHR}_{p,h}$ = degradable protein-nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{PDEG}_{p,d}$ = user-specified nitrogen degradability of plant group p in day d (proportion)

$\text{CCDNIHR}_{p,h}$ = digestible cell content nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{BYNIHR}_{p,h}$ = bypass nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

Undegradable cell contents N is calculated as:

$$\text{UPNIHR}_{p,h} = \text{CCDNIHR}_{p,h} - \text{BYNIHR}_{p,h} - \text{DPNIHR}_{p,h} \quad (66)$$

where:

- $\text{UPNIHR}_{p,h}$ = undegradable protein-nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
 $\text{CCDNIHR}_{p,h}$ = digestible cell content nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
 $\text{BYNIHR}_{p,h}$ = bypass nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
 $\text{DPNIHR}_{p,h}$ = degradable protein-nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

Microbial nitrogen intake

The size of the microbial N pool is constrained according to the amount of digestible organic matter in the rumen and the ruminal intakes of degradable protein-N plus inorganic N. The generally accepted generation of microbial protein and biomass from organic matter is used in the model (Walker *et al.*, 1975; ARC, 1980; Preston & Leng, 1987; NRC, 2007), namely 1 kg organic matter fermented produces 32 g microbial nitrogen and 325 g microbial biomass. To allow estimation of volatile fatty acid and CH_4 production the following stoichiometry is assumed (Preston and Leng, 1987): 1 kg organic matter containing 6.25 mole glucose (MW = 160) is fermented to give rise to 5.25 mole acetic acid, 1.5 mole propionic acid, 0.75 mole butyric acid, 2.375 mole CH_4 and 325 g microbial cells (32 g N).

The limit on size of the microbial N pool each hour due to the availability of digestible organic matter is calculated as:

$$\text{MCDOMMX}_h = \sum_p (\text{CCPOOLHR}_{p,h} + \text{CWPOOLHR}_{p,h}) \cdot \text{PDOM} \cdot \text{PMCDOM} \quad (67)$$

where:

- MCDOMMX_h = maximum size of microbial nitrogen pool based on the availability of dry organic matter in the rumen in hour h (g)
 $\text{CCPOOLHR}_{p,h}$ = actual digestible cell content pool for plant group p at the end of hour h (g)
 $\text{CWPOOLHR}_{p,h}$ = actual digestible cell wall pool for plant group p at the end of hour h (g)
 PDOM = proportion of the digestible material that is dry organic matter (proportion) – by default this value is set to 0.88 (Van Soest, 1982)
 PMCDOM = ratio of microbial nitrogen to dry organic matter in the rumen (proportion $\cdot \text{h}^{-1}$) – by default this value is set to 0.032 (ARC, 1980 p127)

Limit on size of the microbial nitrogen pool due to the availability of nitrogen intake is calculated as:

$$MCNIMX_h = \sum_p (MCNPLHR_{p,h-1} + DPNIHR_{p,h} + NPNIHR_{p,h}) \quad (68)$$

where:

- MCNIMX_h = maximum size of microbial nitrogen pool based on the availability of nitrogen intake in hour *h* (g)
- MCNPLHR_{p,h-1} = microbial nitrogen pool for plant group *p* at the end of the previous hour *h*-1 (g)
- DPNIHR_{p,h} = degradable protein-nitrogen intake for plant group *p* in hour *h* (g · h⁻¹)
- NPNIHR_{p,h} = non-protein nitrogen intake for plant group *p* in hour *h* (g · h⁻¹)

Proportion of the available N intake that enters the microbial N pool is calculated as:

$$PMCNI_h = \text{Minimum} \{ MCDOMMX_h, MCNIMX_h \} / MCNIMX_h \quad (69)$$

where:

- PMCNI_h = proportion of available nitrogen intake that enters the microbial nitrogen pool in hour *h* (proportion)
- MCDOMMX_h = maximum size of the microbial nitrogen pool based on the availability of dry organic matter in the rumen in hour *h* (g)
- MCNIMX_h = maximum size of the microbial nitrogen pool based on the availability of nitrogen intake in hour *h* (g)

Nitrogen rumen pool sizes prior to passage

Actual nitrogen rumen pool sizes, prior to digestion and passage each hour, are updated as follows:

$$UPNPRIOR_{p,h} = UPNPLHR_{p,h-1} + UPNIHR_{p,h} \quad (70)$$

where:

- UPNPRIOR_{p,h} = rumen undegradable protein nitrogen pool for plant group *p* in hour *h*, prior to the current hour's absorption and passage (g)
- UPNPLHR_{p,h-1} = rumen undegradable protein nitrogen pool for plant group *p* at the end of the previous hour *h*-1 (g)
- UPNIHR_{p,h} = undegradable protein-nitrogen intake for plant group *p* in hour *h* (g · h⁻¹)

$$\text{DPNPRIOR}_{p,h} = \text{DPNPLHR}_{p,h-1} + (\text{DPNIHR}_{p,h} \cdot (1 - \text{PMCNI}_h)) \quad (71)$$

where:

- $\text{DPNPRIOR}_{p,h}$ = rumen degradable protein nitrogen pool for plant group p in hour h , prior to the current hour's absorption and passage (g)
 $\text{DPNPLHR}_{p,h-1}$ = rumen degradable protein nitrogen pool for plant group p at the end of the previous hour $h-1$ (g)
 $\text{DPNIHR}_{p,h}$ = degradable protein-nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
 PMCNI_h = proportion of available nitrogen intake that enters the microbial nitrogen pool in hour h (proportion)

$$\text{CWNPRIOR}_{p,h} = \text{CWNPLHR}_{p,h-1} + \text{CWDNIHR}_{p,h} \quad (72)$$

where:

- $\text{CWNPRIOR}_{p,h}$ = rumen digestible cell wall nitrogen pool for plant group p in hour h , prior to the current hour's absorption and passage (g)
 $\text{CWNPLHR}_{p,h-1}$ = rumen digestible cell wall nitrogen pool for plant group p at the end of the previous hour $h-1$ (g)
 $\text{CWDNIHR}_{p,h}$ = digestible cell wall nitrogen intake rate for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$$\text{MCNPRIOR}_{p,h} = \text{MCNPLHR}_{p,h-1} + (\text{PMCNI}_p \cdot (\text{DPNIHR}_{p,h} + \text{NPNIHR}_{p,h})) \quad (73)$$

where:

- $\text{MCNPRIOR}_{p,h}$ = rumen microbial nitrogen pool for plant group p in hour h , prior to the current hour's absorption and passage (g)
 $\text{MCNPLHR}_{p,h-1}$ = rumen microbial nitrogen pool for plant group p at the end of the previous hour $h-1$ (g)
 PMCNI_p = proportion of available nitrogen intake that enters the microbial nitrogen pool in hour h (proportion)
 $\text{DPNIHR}_{p,h}$ = degradable protein-nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
 $\text{NPNIHR}_{p,h}$ = non-protein nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$$\text{NDNPRIOR}_{p,h} = \text{NDNPLHR}_{p,h-1} + \text{NDNIHR}_{p,h} \quad (74)$$

where:

- $\text{NDNPRIOR}_{p,h}$ = rumen non-digestible nitrogen pool for plant group p in hour h , prior to the current hour's absorption and passage (g)
 $\text{NDNPLHR}_{p,h-1}$ = rumen non-digestible nitrogen pool for plant group p at the end of the previous hour $h-1$ (g)
 $\text{NDNIHR}_{p,h}$ = non-digestible nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

Metabolizable nitrogen

Metabolizable nitrogen obtained each hour through passage to and absorption from the small intestine is calculated for bypass and each of the digestible rumen N pools based on average absorption values for amino acids in proteins (ARC, 1980 130) as follows:

$$\text{BYMNIHR}_{p,h} = \text{BYNIHR}_{p,h} \cdot \text{PBYN} \quad (75)$$

where:

- $\text{BYMNIHR}_{p,h}$ = metabolizable nitrogen intake obtained from bypass for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{BYNIHR}_{p,h}$ = bypass nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- PBYN = user-specified proportion of bypass nitrogen that can be absorbed (proportion) – by default set to 0.73 (ARC, 1980 p130)

$$\text{UPMNIHR}_{p,h} = \text{UPNPRIOR}_{p,h} \cdot \text{KPCC}_d \cdot \text{PUPN} \quad (76)$$

where:

- $\text{UPMNIHR}_{p,h}$ = metabolizable nitrogen intake obtained from undegradable protein nitrogen for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{UPNPRIOR}_{p,h}$ = undegradable protein nitrogen pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- KPCC_d = user-specified hourly passage rate of cell content on day d (proportion $\cdot \text{h}^{-1}$)
- PUPN = user-specified proportion of undegradable protein nitrogen that can be absorbed (proportion) – by default set to 0.73 (ARC, 1980 p130)

$$\text{DPMNIHR}_{p,h} = \text{DPNPRIOR}_{p,h} \cdot \text{KPCC}_d \cdot \text{PDPN} \quad (77)$$

where:

- $\text{DPMNIHR}_{p,h}$ = metabolizable nitrogen intake obtained from degradable protein nitrogen for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{DPNPRIOR}_{p,h}$ = degradable protein nitrogen pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- KPCC_d = user-specified hourly passage rate of cell content on day d (proportion $\cdot \text{h}^{-1}$)
- PDPN = user-specified proportion of degradable protein nitrogen that can be absorbed (proportion) – by default set to 0.73 (ARC, 1980 p130)

$$CWMNIHR_{p,h} = CWNPRIOR_{p,h} \cdot KPCW_d \cdot PCWN \quad (78)$$

where:

- $CWMNIHR_{p,h}$ = metabolizable nitrogen intake obtained from digestible cell wall for plant group p in hour h ($g \cdot h^{-1}$)
- $CWNPRIOR_{p,h}$ = digestible cell wall nitrogen pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- $KPCW_d$ = user-specified hourly passage rate of cell wall on day d (proportion $\cdot h^{-1}$)
- $PCWN$ = user-specified proportion of cell wall nitrogen that can be converted to microbial protein nitrogen (proportion) – by default set to 1.0 (ARC, 1980 p128)

$$MCMNIHR_{p,h} = MCNPRIOR_{p,h} \cdot KPCC_d \cdot PMCN \quad (79)$$

where:

- $MCMNIHR_{p,h}$ = metabolizable nitrogen intake obtained from microbial nitrogen for plant group p in hour h ($g \cdot h^{-1}$)
- $MCNPRIOR_{p,h}$ = microbial nitrogen pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- $KPCC_d$ = user-specified hourly passage rate of cell content on day d (proportion $\cdot h^{-1}$)
- $PMCN$ = user-specified proportion of microbial nitrogen that can be absorbed (proportion) – by default set to 0.70 (ARC, 1980 p129)

Total metabolizable N intake is then calculated each hour as:

$$\frac{MNIHR_{p,h}}{MCMNIHR_{p,h}} = \frac{BYMNIHR_{p,h} + UPMNIHR_{p,h} + DPMNIHR_{p,h} + CWMNIHR_{p,h} + MCMNIHR_{p,h}}{MCMNIHR_{p,h}} \quad (80)$$

where:

- $MNIHR_{p,h}$ = total hourly metabolizable nitrogen intake for plant group p in hour h ($g \cdot h^{-1}$)
- $BYMNIHR_{p,h}$ = metabolizable nitrogen intake obtained from bypass for plant group p in hour h ($g \cdot h^{-1}$)
- $UPMNIHR_{p,h}$ = metabolizable nitrogen intake obtained from undegradable protein nitrogen for plant group p in hour h ($g \cdot h^{-1}$)
- $DPMNIHR_{p,h}$ = metabolizable nitrogen intake obtained from degradable protein nitrogen for plant group p in hour h ($g \cdot h^{-1}$)
- $CWMNIHR_{p,h}$ = metabolizable nitrogen intake obtained from digestible cell wall for plant group p in hour h ($g \cdot h^{-1}$)
- $MCMNIHR_{p,h}$ = metabolizable nitrogen intake obtained from microbial nitrogen for plant group p in hour h ($g \cdot h^{-1}$)

Nitrogen rumen pool sizes after passage

Sizes of rumen pools of N are all updated to reflect the current hour's passage:

$$\text{UPNPLHR}_{p,h} = \text{UPNPRIOR}_{p,h} \cdot (1 - \text{KPCC}_d) \quad \text{for } h \text{ in } d \quad (81)$$

where:

- $\text{UPNPLHR}_{p,h}$ = undegradable nitrogen pool for plant group p at the end of hour h (g)
- $\text{UPNPRIOR}_{p,h}$ = undegradable protein nitrogen pool for plant group p in hour h , prior to the current hour's absorption and passage (g)
- KPCC_d = user-specified hourly passage rate of cell content on day d (proportion $\cdot \text{h}^{-1}$)

$$\text{DPNPLHR}_{p,h} = \text{DPNPRIOR}_{p,h} \cdot (1 - \text{KPCC}_d) \quad \text{for } h \text{ in } d \quad (82)$$

where:

- $\text{DPNPLHR}_{p,h}$ = degradable nitrogen pool for plant group p at the end of hour h (g)
- $\text{DPNPRIOR}_{p,h}$ = degradable protein nitrogen pool for plant group p in hour h , prior to the current hour's absorption and passage (g)
- KPCC_d = user-specified hourly passage rate of cell content on day d (proportion $\cdot \text{h}^{-1}$)

$$\text{CWNPLHR}_{p,h} = \text{CWNPRIOR}_{p,h} \cdot (1 - \text{KPCW}_d) \quad \text{for } h \text{ in } d \quad (83)$$

where:

- $\text{CWNPLHR}_{p,h}$ = degradable nitrogen pool for plant group p at the end of hour h (g)
- $\text{CWNPRIOR}_{p,h}$ = degradable protein nitrogen pool for plant group p in hour h , prior to the current hour's absorption and passage (g)
- KPCW_d = user-specified hourly passage rate of cell wall on day d (proportion $\cdot \text{h}^{-1}$)

$$\text{MCNPLHR}_{p,h} = \text{MCNPRIOR}_{p,h} \cdot (1 - \text{KPCC}_d) \quad \text{for } h \text{ in } d \quad (84)$$

where:

- $\text{MCNPLHR}_{p,h}$ = rumen microbial nitrogen pool for plant group p at the end of hour h (g)
- $\text{MCNPRIOR}_{p,h}$ = rumen microbial nitrogen pool for plant group p in hour h , prior to the current hour's absorption and passage (g)
- KPCC_d = user-specified hourly passage rate of cell content on day d (proportion $\cdot \text{h}^{-1}$)

$$\text{NDNPLHR}_{p,h} = \text{NDNPRIOR}_{p,h} \cdot (1 - \text{KPND}_{p,d}) \quad \text{for } h \text{ in } d \quad (85)$$

where:

$\text{NDNPLHR}_{p,h}$ = rumen non-digestible nitrogen pool for plant group p at the end of hour h (g)

$\text{NDNPRIOR}_{p,h}$ = non-digestible nitrogen pool for plant group p in hour h , prior to the current hour's passage (g)

$\text{KPND}_{p,d}$ = hourly passage rate of non-digestible material for plant group p on day d (proportion $\cdot h^{-1}$)

Fecal nitrogen loss

Fecal N loss each hour contributed by each rumen pool is calculated as the portion of the N that passes into the intestine but is not absorbed by the animal, *viz*:

$$\text{BYNFECHR}_{p,h} = \text{BYNIHR}_{p,h} \cdot (1 - \text{PBYN}) \quad (86)$$

where:

$\text{BYNFECHR}_{p,h}$ = fecal nitrogen loss from bypass for plant group p in hour h ($g \cdot h^{-1}$)

$\text{BYNIHR}_{p,h}$ = bypass nitrogen intake for plant group p in hour h ($g \cdot h^{-1}$)

PBYN = user-specified proportion of bypass nitrogen that can be absorbed (proportion) – by default set to 0.73 (ARC, 1980 p130)

$$\text{UPNFECHR}_{p,h} = \text{UPNPRIOR}_{p,h} \cdot \text{KPCC}_d \cdot (1 - \text{PUPN}) \quad (87)$$

where:

$\text{UPNFECHR}_{p,h}$ = fecal nitrogen loss from undegradable protein nitrogen for plant group in hour h ($g \cdot h^{-1}$)

$\text{UPNPRIOR}_{p,h}$ = undegradable protein nitrogen pool for plant group p in hour h , prior to the current hour's digestion and passage (g)

KPCC_d = user-specified hourly passage rate of cell content on day d (proportion $\cdot h^{-1}$)

PUPN = user-specified proportion of undegradable protein nitrogen that can be absorbed (proportion) – by default set to 0.73 (ARC, 1980 p130)

$$\text{DPNFECHR}_{p,h} = \text{DPNPRIOR}_{p,h} \cdot \text{KPCC}_d \cdot (1 - \text{PDPN}) \quad (88)$$

where:

- $\text{DPNFECHR}_{p,h}$ = fecal nitrogen loss from degradable protein nitrogen for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{DPNPRIOR}_{p,h}$ = degradable protein nitrogen pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- KPCC_d = user-specified hourly passage rate of cell content on day d (proportion $\cdot \text{h}^{-1}$)
- PDPN = user-specified proportion of degradable protein nitrogen that can be absorbed (proportion) – by default set to 0.73 (ARC, 1980 p130)

$$\text{CWNFECHR}_{p,h} = \text{CWNPRIOR}_{p,h} \cdot \text{KPCW}_d \cdot (1 - \text{PCWN}) \quad (89)$$

where:

- $\text{CWNFECHR}_{p,h}$ = fecal nitrogen loss from digestible cell wall nitrogen for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{CWNPRIOR}_{p,h}$ = digestible cell wall nitrogen pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- KPCW_d = user-specified hourly passage rate of cell wall on day d (proportion $\cdot \text{h}^{-1}$)
- PCWN = user-specified proportion of cell wall nitrogen that can be absorbed (proportion) – by default set to 0.73 (ARC, 1980 p130)

$$\text{MCNFECHR}_{p,h} = \text{MCNPRIOR}_{p,h} \cdot \text{KPCC}_d \cdot (1 - \text{PMCN}) \quad (90)$$

where:

- $\text{MCNFECHR}_{p,h}$ = fecal nitrogen loss from microbial nitrogen for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)
- $\text{MCNPRIOR}_{p,h}$ = microbial nitrogen pool for plant group p in hour h , prior to the current hour's digestion and passage (g)
- KPCC_d = user-specified hourly passage rate of cell content on day d (proportion $\cdot \text{h}^{-1}$)
- PMCN = user-specified proportion of microbial nitrogen that can be absorbed (proportion) – by default set to 0.70 (ARC, 1980 p130)

$$\text{NDNFECHR}_{p,h} = \text{NDNPRIOR}_{p,h} \cdot \text{KPND}_{p,d} \quad \text{for } h \text{ in } d \quad (91)$$

where:

$\text{NDNFECHR}_{p,h}$ = fecal nitrogen loss from non-digestible material for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{NDNPRIOR}_{p,h}$ = non-digestible nitrogen pool for plant group p in hour h , prior to the current hour's passage (g)

$\text{KPND}_{p,d}$ = hourly passage rate of non-digestible material for plant group p on day d (proportion $\cdot \text{h}^{-1}$)

Total fecal nitrogen loss each hour attributable to forage digestion is calculated as:

$$\text{NFECHR}_{p,h} = \text{BYNFECHR}_{p,h} + \text{UPNFECHR}_{p,h} + \text{DPNFECHR}_{p,h} + \text{CWNFECHR}_{p,h} + \text{MCNFECHR}_{p,h} + \text{NDNFECHR}_{p,h} \quad (92)$$

where:

$\text{NFECHR}_{p,h}$ = total fecal nitrogen loss for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{BYNFECHR}_{p,h}$ = fecal nitrogen loss from bypass for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{UPNFECHR}_{p,h}$ = fecal nitrogen loss from undegradable protein nitrogen for plant group in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{DPNFECHR}_{p,h}$ = fecal nitrogen loss from degradable protein nitrogen for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{CWNFECHR}_{p,h}$ = fecal nitrogen loss from digestible cell wall nitrogen for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{MCNFECHR}_{p,h}$ = fecal nitrogen loss from microbial nitrogen for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{NDNFECHR}_{p,h}$ = fecal nitrogen loss from non-digestible material for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$) $\cdot \text{NFECHR}_{p,h}$ does not include the contribution made by endogenous fecal loss.

Urinary nitrogen loss from non-protein nitrogen

One component of the hourly urinary N loss for the animal is the portion of the non-protein N intake that does not contribute to the rumen microbial nitrogen pool. This loss is calculated as:

$$\text{NPURNHR}_{p,h} = \text{NPNIHR}_{p,h} \cdot (1 - \text{PMCNI}_h) \quad (93)$$

where:

$\text{NPURNHR}_{p,h}$ = urinary nitrogen loss from non-protein nitrogen intake for plant group in hour h ($\text{g} \cdot \text{h}^{-1}$)

$\text{NPNIHR}_{p,h}$ = non-protein nitrogen intake for plant group p in hour h ($\text{g} \cdot \text{h}^{-1}$)

PMCNI_h = proportion of available nitrogen intake that enters the microbial nitrogen pool in hour h (proportion)

Additional Indicators

A number of additional indicators are calculated by the model:

Daily forage intake

$$FI_{p,d} = \sum_b (DFIHR_{p,b} + NDFIHR_{p,b}) \quad \text{for } b \text{ in } d \quad (94)$$

where:

- $FI_{p,d}$ = daily forage intake for plant group p ($\text{g} \cdot \text{day}^{-1}$)
- $DFIHR_{p,b}$ = digestible forage intake for plant group p in hour b ($\text{g} \cdot \text{h}^{-1}$)
- $NDFIHR_{p,b}$ = non-digestible forage intake for plant group p in hour b ($\text{g} \cdot \text{h}^{-1}$)

Daily metabolizable energy intake

$$MEI_{p,d} = \sum_b (MEIHR_{p,b}) \quad \text{for } b \text{ in } d \quad (95)$$

where:

- $MEI_{p,d}$ = daily metabolizable energy intake for plant group p ($\text{kJ} \cdot \text{day}^{-1}$)
- $MEIHR_{p,b}$ = metabolizable energy intake for plant group p in hour b ($\text{kJ} \cdot \text{h}^{-1}$)

Daily metabolizable nitrogen intake

$$MNI_{p,d} = \sum_b (MNIHR_{p,b}) \quad \text{for } b \text{ in } d \quad (96)$$

where:

- $MNI_{p,d}$ = daily metabolizable nitrogen intake for plant group p ($\text{g} \cdot \text{day}^{-1}$)
- $MNIHR_{p,b}$ = metabolizable nitrogen intake for plant group p in hour b ($\text{g} \cdot \text{h}^{-1}$)

Daily forage rumen pools

End-of-day values for the forage rumen pools:

$$CCPOOL_{p,b} = CCPOOLHR_{p,h=24} \quad \text{for } b \text{ in } d \quad (97)$$

where:

- $CCPOOL_{p,b}$ = digestible cell content pool for plant group p at the end of day d (g)
- $CCPOOLHR_{p,b}$ = digestible cell content pool for plant group p at the end of hour $h=24$ (g)

$$CWPOOL_{p,d} = CWPOOLHR_{p,h=24} \quad \text{for } h \text{ in } d \quad (98)$$

where:

$CWPOOL_{p,d}$ = digestible cell wall pool for plant group p at the end of day d (g)

$CWPOOLHR_{p,h}$ = digestible cell wall pool for plant group p at the end of hour $h=24$ (g)

$$NDPOOL_{p,d} = NDPOOLHR_{p,h=24} \quad \text{for } h \text{ in } d \quad (99)$$

where:

$NDPOOL_{p,d}$ = non-digestible pool for plant group p at the end of day d (g)

$NDPOOLHR_{p,h}$ = non-digestible pool for plant group p at the end of hour $h=24$ (g)

Total end-of-day rumen content

$$WTRUM_d = \sum_p (CCPOOL_{p,d} + CWPOOL_{p,d} + NDPOOL_{p,d}) \quad \text{for } h \text{ in } d \quad (100)$$

where:

$WTRUM_d$ = total dry weight of rumen contents at the end of day d (g)

$CCPOOL_{p,d}$ = digestible cell content pool for plant group p at the end of day d (g)

$CWPOOL_{p,d}$ = digestible cell wall pool for plant group p at the end of day d (g)

$NDPOOL_{p,d}$ = non-digestible pool for plant group p at the end of day d (g)

Allocation Submodel

Retention and use of body components depend not only on supply and demand, but also on evolved seasonal changes in the propensity to fatten (Larsen *et al.*, 1985), to replace and retain body protein, to regulate fat draw-down in winter (Larsen *et al.*, 1985), to retain reserves for spring migration (Bergerud *et al.*, 2008), and to conserve fat and protein reserves for gestation (Tyler, 1987) and lactation (White & Luick, 1984; Tyler & Blix, 1990; Gerhart *et al.*, 1996a; 1996b). Thus, allocation of metabolizable energy and metabolizable N to maintenance, activity and retention as fat and protein, and the mobilization of reserves to meet demand, are achieved through a hierarchal process depending on the physiological condition of the modeled animal and evolved intrinsic drivers.

What constitutes maintenance requirements for the free-ranging wildlife species is not easily defined (Osuji, 1974; Webster, 1979). Therefore, we have chosen to use an Allocation submodel that is based on a hierarchical allocation of metabolizable energy and metabolizable N. The user can determine which functions are considered maintenance and which are production. For example, is summer coat growth requirement a maintenance or production function? If coat growth must be at a determined rate, then it could be considered a summer maintenance requirement

and must be placed high in the allocation hierarchy. However, if it can be shown that coat growth rate is related to protein availability, then it would be placed lower in the allocation hierarchy. The model default is a high allocation priority.

Many regulated processes in nutritional physiology are timed by photoperiod and season (e.g. appetite (McEwan & Whitehead, 1970; Peltier *et al.*, 2003)), coat shedding, antler regrowth (Suttie & Simpson, 1985), rutting activity (Suttie & Simpson, 1985); thus Julian date can be a decision point to express a change in mechanisms. For instance, production/growth of hair and underwool of the animal is a summer function that is so high in priority it is timed by photoperiod. Simulating energy and protein costs of hosting internal parasites, timing of infestation etc., is based on Julian date.

Because the animal must move to forage, and avoid predators and parasites, activity costs are given a high hierarchical position. An implication of high hierarchy is that energy might be withdrawn from fat reserves to meet activity costs. In summer, replenishing protein lost during winter is high in hierarchy (Russell *et al.*, 1996; Barboza *et al.*, 2009). For modeling purposes the amount of protein mobilized and restored annually is termed the “labile (mobilizable) protein reserve”. Allocation of metabolizable and net protein to the mobilizable reserve could result in a decrease in milk synthesis if protein intake cannot meet requirements for deposition and lactation (White, 1983). Projecting target daily requirements for energy and protein, and then estimating whether or not daily intakes of net energy and net protein-N can meet the targets, is used to determine actual daily energy and protein costs of gestation and lactation. Where necessary a drawdown from reserves can occur to meet targets. When drawdown cannot meet targets of fetal growth rate, or level of milk production, then fetal growth rates and milk production are reduced accordingly from the target rates. Thus, birth weight is variable and is a product of maternal body condition entering winter as well as metabolizable energy and protein intake throughout winter. Milk production can be highly variable and have direct effects on calf growth due to pre-calving maternal reserves, followed by plane of nutrition and activity costs during the calving and post calving period. In addition, milk production can cease if requirements cannot be met. Five weaning strategies have been documented (Russell *et al.*, 1996; 2000; Russell & White 2000) for caribou and have been supported in a previous version of the model (Russell *et al.*, 2005). In the model weaning is related to the interaction of intake with body protein and fat reserves at key points during the summer, autumn and early winter (Russell *et al.*, 1996; 1998), and probabilities of terminating lactation are determined at these dates (Figs. 10 and 12).

Updating pregnancy and lactation status of a cow, as the cow moves from day to day in the model, can be modeled in two ways: “user-controlled”, where the user explicitly specifies when changes in pregnancy and lactation occur; and “modeled”, where the model calculates these changes. When “user-controlled” is selected, the user specifies whether or not the cow will become pregnant each year of the model run; similarly, the user also specifies the subsequent wean date of the calf each year. When “modeled” is selected, the model predicts changes in pregnancy and lactation status of the cow each year based upon the weight and composition (fat and protein reserves) of the cow and calf at various times of the summer and fall. Reproductive strategies represented in the model, when the changes in reproductive status are “modeled”, are shown in Figure 10 (Russell *et al.*, 1996; 2000; Reimers 1983b; Gerhart *et al.*, 1997; Pritchard *et al.*, 1999;

Russell & White, 2000). The model determines whether or not the cow becomes pregnant each year based upon whether or not she has reached a threshold minimum body weight or fat weight in the fall (Cameron *et al.*, 1993; Cameron & Ver Hoef 1994; Gerhart *et al.*, 1997). Similarly, the model determines the weaning strategy, based upon whether or not the calf and/or cow reach a series of weight- related thresholds through the spring, summer and fall (Russell *et al.*, 2005). Thus the model is a rational framework to project the relation of summer weight gain on reproduction (Cameron & White, 1996; Cameron *et al.*, 1993) and calf survival and to simulate breeding pauses (Cameron, 1994; Cameron & Ver Hoef, 1994).

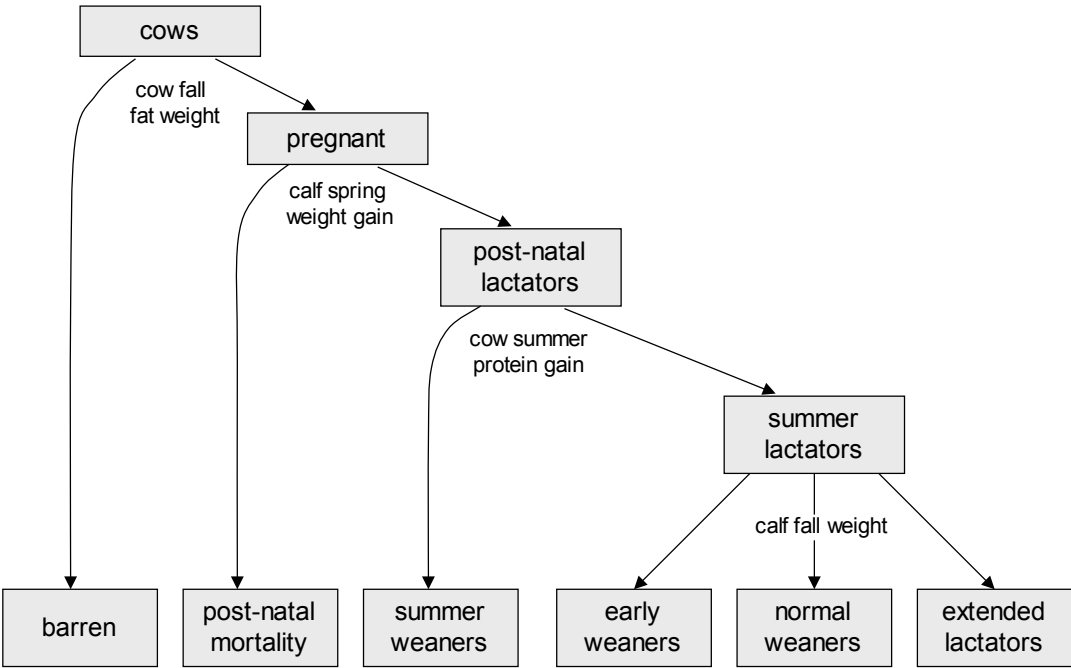


Figure 10. Weaning strategies of caribou simulated in the ALLOCATION SUB-MODEL

In late summer, the propensity to divert energy to fattening rather than protein deposition is well established (Larsen *et al.*, 1985) and is captured in the hierarchical decision process. At the lower level of hierarchy are requirements for antler growth, protein deposition in excess of summer deposition and general levels of fat deposition. As fat and protein are added and removed the body weight and composition are updated to provide indices to compare with field data (e.g. Parker, 1981; Adamczewski *et al.*, 1987b; Gerhart *et al.*, 1996b; Kofinas *et al.*, 2002; 2003; Lyver & Gunn, 2004) and to verify that the modeling process remains credible.

The purpose of the ALLOCATION SUB-MODEL is to estimate body weights and compositions of caribou and reindeer on a daily time-step. The model first calculates energy and N requirements of the animal each day; these requirements are determined for each of several “allocation

stages” as illustrated in Figure 11. The model then calculates the energy and N available for use by the animal each day from several sources. Sources of available N include daily MNI (Eq. 96) and body protein reserves, while energy sources include MEI (Eq. 95), body protein reserves and body fat reserves. Finally the model allocates the available energy and N each day according to the requirements of each stage. A user-specified order of priority defines how the available energy and N is allocated to each stage – if

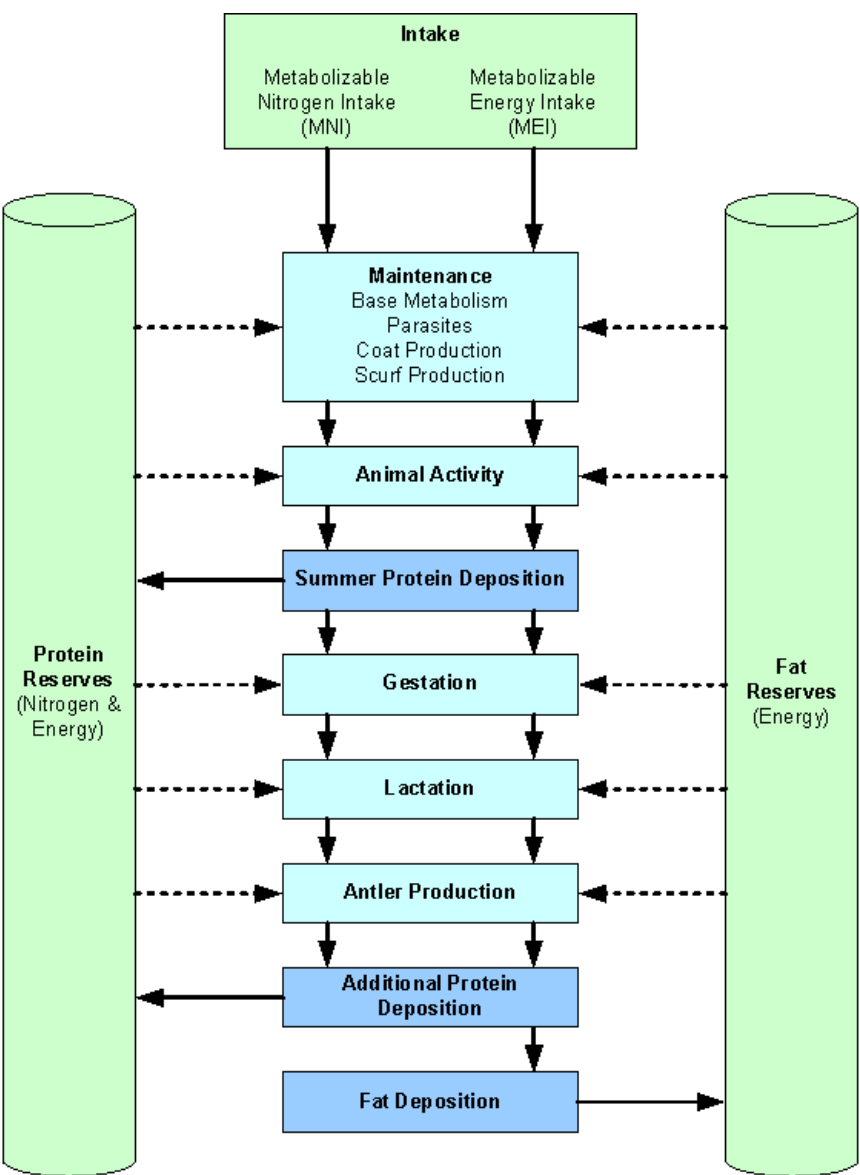


Figure 11. Daily allocation of nitrogen and energy in the model, showing the default order of priority for each allocation stage

insufficient energy and/or N is available on a particular day to meet the requirements of all the allocation stages, then the requirements of each stage are met in order of priority (Fig. 11). Energy and N available from intake (i.e. MEI and MNI) are the first priority source each day. If the N and/or energy available from intake is insufficient to meet the requirements of all stages, additional N and/or energy is catabolized from body protein and/or fat reserves. If excess N and/or energy is available from intake, then protein and/or fat is deposited. The model allows users to specify efficiencies in use of energy and N for each allocation stage, depending on the source of the energy (i.e. forage intake or body reserves) – these efficiencies, in turn, are used to calcu-

late the heat production and metabolic N losses each day.

Because the first step of the ALLOCATION sub-model is to estimate energy and protein requirements of the modeled animal, the use of values from NRC (2007) could be used because these were estimated based on published data on wild ruminants including *Rangifer*. However, because the model deals with individuals, not all values in the NRC publication are directly applicable and we have used values from the literature in addition to those in NRC (2007) to formulate some default estimates. For most model variables the user can substitute a value into the model. A function of published recommended requirements, whether from Robbins (1993), the NRC (NRC, 2007 300-307), Barboza *et al.* (2009) or the literature, is that they can be used to check model output when simulating unusual and unique scenarios.

Within the ALLOCATION sub-model we assumed that dietary MNI, i.e. that N absorbed as amino acids, is used with differential efficiencies depending on allocation to maintenance and growth in the hierarchy outline above and Fig. 11 (NRC, 2007: Table 4). The efficiency of use of metabolic N (MN) from mobilized body protein is assumed to be 1.0. Inefficiencies of MN use are combined to give the estimate of urinary N loss (NRC, 2007). Likewise, we assumed that dietary MEI is used to meet maintenance and production requirements with efficiencies (Table 4) less than 1.0 (ARC, 1980; Robbins, 1993; NRC, 2007), and an efficiency approaching or at 1.0 for ME resulting from mobilized reserves. Combined inefficiencies of use of ME represent energy lost in the heat increment of feeding (HIF).

Maintenance requirements for energy and N include those that maintain life process plus those that meet activity, parasite burden, coat growth in summer and skin sloughing (scurf) in winter. Over and above these requirements, intake is then allocated to production requirements such as summer protein deposition, gestation, lactation, antler production, additional deposition of protein and fat as a part of growth and seasonal cyclical body condition regain. Figure 11 shows the general flow of N and energy within the ALLOCATION sub-model. Given that energetically costly events such as seasonal migration are essential for survival it is argued that the activity budget should be allocated to the maintenance cost (Robbins, 1993 312). However, some components of the activity budget, such as that attributable to insect harassment, are ephemeral and highly dynamic, and these costs therefore could be considered above normal maintenance. Even when not included as a maintenance cost, activity costs are at the top of the allocation hierarchy (Fig. 11). Thus, under some circumstances activity patterns can exact a cost to fattening and protein deposition as proposed by Reimers (1980; 1983a). The model does not simulate a feedback loop to lower activity in response to depletion of reserves; rather an estimate is made of probability of survival as reserves are depleted. The user can game with this aspect of the activity budget to test hypotheses about such a feedback.

Of special concerns are pregnancy and lactation. Balancing intakes with requirements throughout the year is used to simulate fetal growth including uterine tissues (the conceptus, or gravid uterus, Robbins & Moen, 1975) and birth weight followed by milk production and calf growth to weaning. The animal's body weight and condition are updated daily based on an energy and N balance. To meet fluctuating daily MEI and MNI in relation to gestation and lactational requirements, reserves of energy as fat and N as body protein are available for mobilization (Taillon *et al.*, 2013). Where target requirements for fetal growth and lactation cannot be met by dietary MEI and/or dietary MNI plus those from mobilization from reserves, the actual growth rate of the fetus or the daily amount of milk produced is reduced.

Mobilization of energy and N from body reserves depends on the absolute amount of fat and body protein minus a minimal fat and protein reserve. The user can set both reserves. Default value for the minimal fat reserve (3% bodyweight, Eq. 147) is based on measured and predicted fat remaining in carcasses of adults presumed to have died from starvation (Gerhart *et al.*, 1996b). An absolute default value for body protein of 13.5 kg dry protein (2.2 kg N, Eq. 142) is proposed based on the minimal body protein of a caribou/reindeer female that is required to maintain a 50% probability of being pregnant (April body weight 68 kg, Thomas, 1982; Bergerud *et al.*, 2008 p258). However, a further 1 kg protein (0.16 kg N) is used to initiate lactation resulting in a minimum body protein reserve of 12.5 kg. In addition, the user can set the maximum daily rate of drawdown of fat and protein. Default values of 250 g · day⁻¹ for fat and 40 g · day⁻¹ protein (6.5 gN · day⁻¹) are based on maximum loss of fat reserve of Svalbard reindeer (Reimers *et al.*, 1982) and Coats Island caribou (Adamczewski *et al.*, 1987b). Drawdown of protein reserves by caribou is calculated from the George River (Huot, 1989) and Porcupine (Gerhart *et al.*, 1996b) herds. If energy and N balances require mobilization from the minimal reserves, then drawdown rates are minimized and gestation or lactation is terminated to prevent unrealistic reduction of reserves. The likelihood that fetal growth will be limited or that gestation might be terminated is dependent on the level of reserves entering winter. In some Rangifer studies the labile protein reserve can be 5-6 kg (26-32% of November protein reserve; calculated from Gerhart *et al.*, 1996b; Chan-McLeod *et al.*, 1999) and a combined body weight reserve of 10-14 kg representing 17-21% of the reserve at weaning (calculated from Taillon *et al.*, 2011 for the George and Leaf River herds). Based on the amount of protein lost overwinter, approximately 16-21% is captured by the fetus and 27-36% by concepta (White *et al.*, 2013b). Birth weights represent 42-53% of body weight loss during gestation (calculated from Gerhart *et al.*, 1996b; Taillon *et al.*, 2011; White *et al.*, 2013b). Fetal protein is mainly gained from maternal protein (91-96%, Barboza & Parker, 2008) as opposed to dietary protein even on rations sufficiently high in protein to allow protein deposition over winter (Barboza & Parker, 2006).

Fetus and concepta target growth curves were taken from Roine *et al.* (1982), but modified by input from larger data sets from Skogland (1984b), Reimers (2002) and Bergerud *et al.* (2008 188). Although in white-tailed deer mean fetal weight as a fraction of gravid uterus weight increases from 0.21 at gestation age 100 day to 0.58 at day 190 (Robbins and Moen, 1975 686), a default value of 0.55 is used in the model for Rangifer. A tight linearity exists in fetal weight gain over conception age between 120 and 190 days (fetus weight range 2.6-3.8 kg at day 190). Major differences in gain occur from day 190 to birth (weight range 4-8 kg) where birth was between 227 to 233 days (Bergerud *et al.*, 2008). Although gestation duration may vary in relation to female age and condition it also could vary to enhance synchrony of calving (Adams & Dale, 1988b). Because genetic and other factors also affect duration, gestation length can vary between 211 and 235 days (Ropstad, 2000; Mysterud *et al.*, 2009; Muuttoranta *et al.*, 2013) in Scandinavia and between 203 and 240 days (Rowell & Shipka, 2009) in Alaska, the user can simulate this variation by adjusting gestation length or dates of conception and birth date.

Fetal growth rates in the final trimester vary from a high of 113 g · d⁻¹ for birth weights of approximately 7.5 kg, a median of 83 g · d⁻¹ for birth weights about 6.5 kg (Bergerud *et al.*, 2008) and a low of 15-30 g · d⁻¹ when many calves die at birth and birth weight of surviving calves is approximately 4.1 kg (Couturier *et al.*, 1996). High to median fetal growth rates are associated with a negative maternal protein balance of ~25 g · d⁻¹ (Barboza & Parker, 2006). Because most fetal

protein is derived from maternal protein, the rate of protein mobilization is set at $26 \text{ g} \cdot \text{d}^{-1}$. Actual birth weights thus reflect maternal reserves entering winter and overwinter nutrition. However, the user also can set a target birth weight. The default birth weight is 6.5 kg, which represents that for females of the Porcupine Caribou Herd during a period of population growth (Whitten *et al.*, 1992; Whitten, 1996; Griffith *et al.*, 2002). In simulating energy costs of gestation the efficiency of use of ME (KEINT in Table 4; kg in NRC, 2007) is only 0.13 because it takes into account the maintenance energy requirements of the conceptus (ARC, 1980; NRC, 2007). As gestation progresses a check on energy and N contents of the gravid uterus expressed as a fraction of fetus weight at parturition can be made using relations for caribou established by Robbins & Moen (1975 689). Likewise, at any gestation date energy and N gain by the uterus and contents as a fraction of fetal weight at parturition can be compared with model predictions of daily energy and N deposition using estimates made for caribou by Robbins & Moen (1975 689).

Milk production in reindeer and caribou is highly variable based on experimental measurements (Varo & Varo, 1971; White & Luick, 1984) and inference from calf growth rates (Rognmo *et al.*, 1983; Griffith *et al.*, 2002). In order to simulate energy and N requirements, a target milk production curve is described based on female caribou given optimal grazing and supplemental feeding (Parker *et al.*, 1990). A near maximum milk production is associated with a negative maternal protein balance of $25 \text{ g} \cdot \text{d}^{-1}$ based on data calculated from Barboza & Parker (2006) (see White *et al.*, 2013b). This protein mobilization rate is equivalent to that in the last trimester of gestation. In early lactation 88-91% of milk protein-N is derived from maternal protein-N (Tailon *et al.*, 2013). Nutrient content of milk is based on trends related to days post-calving (Luick *et al.*, 1974; Rognmo *et al.*, 1983; White *et al.*, 2000), but also is adjusted for level of milk production (White & Luick, 1984). Over summer, calf growth rates are simulated assuming growth rate is related to milk intake (White & Luick, 1984; White, 1992). These algorithms are based on milk intake of calves reared with their dams on a wide range of nutritional treatments imposed by grazing intensity and supplemental feeding. These studies show that the slope and elevation of regression lines between calf growth rate and milk intake differ with calf age between birth-3 week, 3-6 week and > 6 week. The changes reflect the increase in importance of the calf's developing rumen in meeting maintenance energy and N requirements (White & Luick, 1984; White, 1992; Chan-McLeod *et al.*, 1994).

Weaning date also is variable in caribou and Russell *et al.* (1996; 2000) and Russell & White (2000) report five time periods for calf loss or weaning (Fig. 10 and 12). These calf losses include non-predator induced loss on the calving ground, summer weaning, early weaning, normal weaning and extended lactation to the end of winter (Cuyler *et al.*, 2012). Weaning date can be set by the user for dates other than the default date of mid- October or can be decided by the model based on the decision tree in Figure 12 as summarized from Russell & White (2000) and Russell *et al.* (2000). When lactation is extended beyond normal weaning, a daily milk production of $6.9 \text{ ml} \cdot \text{kg}^{-0.75}$ (~190 ml for 85 kg female) is assumed based on data from muskoxen undergoing extended lactation (R. G. White, unpub. observations).

Table 4. Summary of proportional use of metabolizable protein-N (MN) and metabolizable energy (ME) for use and deposition by Allocation Stage in the ALLOCATION SUB-MODEL. Efficiencies are variable because of diet type and quality and/or the body reserve (protein, fat) in the simulation

Allocation Stage	KNIT: N from intake (propn)	KNPRO: N from protein (propn)	KEINT: Ene from intake (propn)	KEPRO: Ene from protein (propn)	KEFAT: Ene from fat (propn)
Activity	0.75	1	0.7	0.84	0.65
Add. Protein Dep.	0.75	1	0.47	1	0.84
Antlers	0.25	0.6	0.25	0.84	0.65
Base	0.75	0.67	0.7	0.84	0.65
Fat Deposition	1	1	0.47	1	1
Gestation	0.7	0.95	0.16	0.84	0.84
Lactation	0.68	0.95	0.63	0.84	0.84
Parasites	0.7	0.7	0.8	0.84	0.8
Summer Coat	0.6	0.5	0.18	0.84	0.8
Summer Protein Dep.	0.75	1	0.45	1	0.84
Winter Scurf	0.6	0.95	0.47	0.84	0.8

KNIT: Efficiency in use of dietary MN for maintenance (k_{pm}), hair/fiber (k_{pf}), pregnancy/gestation (k_{ppreg}) and lactation (k_{pl}) (see NRC, 2007)

KNPRO: Efficiency in use of N derived from mobilized body protein tissue (t) for maintenance (k_{pm-t}), hair/fiber (k_{pf-t}), pregnancy/gestation ($k_{ppreg-t}$) and lactation (k_{pl-t}) (see NRC, 2007)

KEINT: Efficiency in use of dietary ME (ene) for maintenance (k_m), hair/fiber (k_f), pregnancy/gestation (k_{preg}) and lactation (k_l) (see NRC, 2007)

KEPRO: Efficiency in use of energy (ene) from mobilized protein tissue (t) for maintenance (k_{m-t}), hair/fiber (k_{f-t}), pregnancy/gestation (k_{preg-t}) and lactation (k_{l-t}) (see NRC, 2007)

KEFAT: Efficiency in use of energy (ene) derived from mobilized body fat tissue (t) for maintenance (k_{m-t}), hair/fiber (k_{f-t}), lactation/gestation (k_{preg-t}) and lactation (k_{l-t}) (see NRC, 2007)

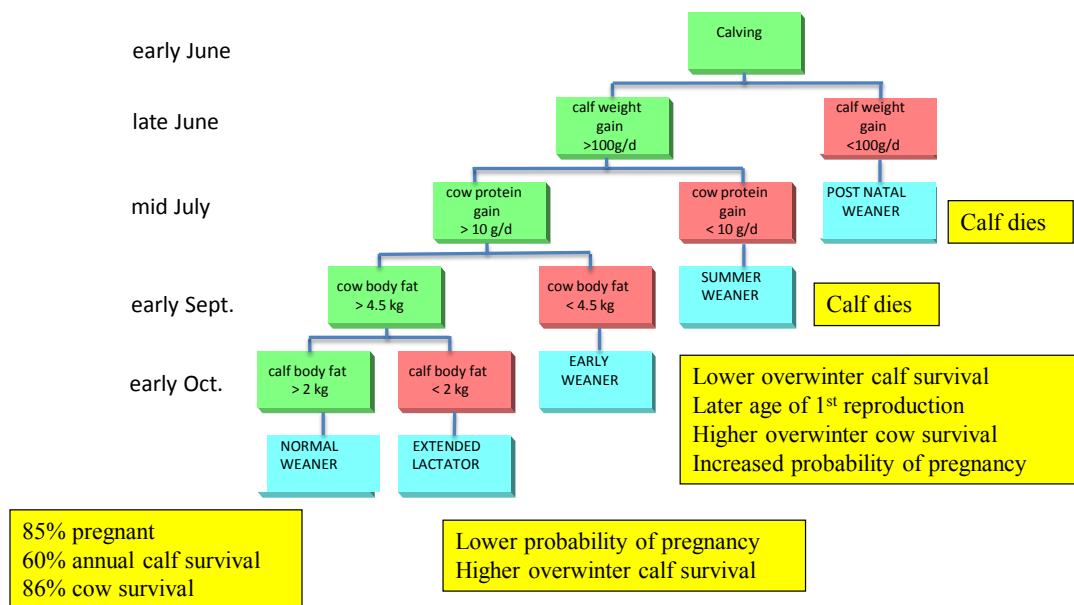


Figure 12. Summary of calf losses and associated correlates of calf or condition related performance of the dam. Data from the Porcupine Caribou Herd (Gerhart, 1995; Gerhart *et al.*, 1996b) and summarized by Russell *et al.* (1991; 2000) and Russell & White (2000)

Although antlers appear to have a high priority for growth, especially in males where they contribute to reproductive success (Bergerud *et al.*, 2008), priority in females is balanced against requirements for lactation and replenishment of body condition in early summer. Even though energy and protein requirements for antler growth are small compared with other costs (Moen & Pastor, 1998), in variable and extreme environments, such as reindeer ranges in Norway and Svalbard (Reimers, 1993; Jacobson *et al.*, 1998) and North American caribou of Newfoundland and the George River herd (Bergerud *et al.*, 2008), antler size in females can be highly variable. Incidence of antlerless is variable, due to a genetic component to antlerlessness in females but also due to nutrition. The relative balance in cause is not known (Cronin *et al.*, 2003). Thus, female reindeer and caribou may not grow antlers in some years and may delay antler growth perhaps in pace with delayed age of first breeding. Because of the minimal energy and protein costs of antler growth, we hypothesize that mineral limitation, particularly calcium and phosphorus, may be regulating antler growth. This is particularly the case for females attempting to maintain lactation under conditions of mineral limitation combined with insufficient body reserves to meet both lactation and antler growth. Setting priority for nutrients to grow antlers when mineral intake is not represented in the model presents a challenge to realistic simulation of antler growth. The user can set antler characteristics when the default is not used. Because it is highly unlikely that nutrient allocation is an all or none process, we prioritize energy and nitrogen requirements for lactation over antler growth (Fig. 11), with a propensity of 80:1 lactation: antlers in early lactation and closer to 60:1 as requirements for lactation declining following three weeks postpartum.

Energy and Nitrogen Requirements

Base requirements

Base requirements for energy and protein-N are assumed to reflect basal metabolism (Sibly *et al.*, 2012), plus added costs attributable to field existence and food processing because we are modeling animals in free existence (Osuji, 1974; Hudson & Christopherson, 1985; Robbins, 1993 p312). For pen-fed animals additional costs above basal metabolism are expressed as the basal rate divided by efficiency in use of consumed metabolizable energy (k_m , ARC, 1980; NRC, 2007) and for consumed metabolizable protein-N (k_{pm} , NRC, 2007). Although these estimates are likely to underestimate maintenance energy and protein-N requirements for free existence, they are nevertheless valuable for comparison with model output.

There is some speculation over whether basal energy metabolism (basal metabolic rate - BMR, sensu Kleiber, 1975) is responsive to seasonal effects in *Rangifer* (Nilssen *et al.*, 1984; Feist & White, 1989; Tyler & Blix, 1990). For modeling we have assumed that BMR is constant year-round at $293 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, which gives a classic maintenance requirement of a sedentary animal in winter of $493 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ and $560 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ for reindeer and caribou respectively, using an efficiency in use of ME in forage (q_m , ARC, 1980) of 0.59 for reindeer and of 0.52 for caribou. To these estimates must be added those for moving through and foraging through snow. Likewise, basic requirement for N is assumed to be that associated with BMR and is given by endogenous urinary N loss ($121 \text{ mgN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, NRC, 2007) plus metabolic fecal N produced with a basal fecal output of $\sim 15 \text{ gDM} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, which is equivalent to $326 \text{ mgN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ for caribou and reindeer (NRC, 2007). For a 75 kg animal this amounts to $11.4 \text{ gN} \cdot \text{d}^{-1}$. Black & Griffiths (1975) show the dynamic nature of interdependence of energy and N requirements for growth in lambs and the ratio of N to energy requirement approximates $1 \text{ gN} \cdot \text{MJ}^{-1}$ in the growing animal but is lower for adults at maintenance.

As season exerts an effect on maintenance energy and protein requirements (Feist & White, 1989; Tyler & Blix, 1990) we calculate classic summer maintenance requirements for energy ($660 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) and N ($\sim 484 \text{ mgN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) by adding seasonal production of hair-wool production ($50 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ and $54 \text{ mgN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) plus support of parasite burdens (5-15% MER [$\sim 99 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$] and 20% MNR [$\sim 65 \text{ mgNkg}^{-0.75} \cdot \text{d}^{-1}$], NRC, 2007) and antler growth (Moen & Pastor, 1998: $18 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ and $50 \text{ mgN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ for females and $88 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ and $145 \text{ mgN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ for males, NRC, 2007). These estimates give a N/energy ratio of $\sim 0.73 \text{ gN} \cdot \text{MJ}^{-1}$ for maintenance in summer and these estimates are the bases of setting target metabolic energy and N requirements to initiate a model run.

Daily energy requirement for basal metabolism is calculated as a function of the metabolic weight of the animal:

$$\text{ERBASE}_d = \text{EBMRCO} \cdot \text{WTEMPY}_{d-1}^{0.75} \quad (101)$$

where:

- | | | |
|-----------------------|---|--|
| ERBASE_d | = | net energy requirement for basal metabolism on day d ($\text{kJ} \cdot \text{day}^{-1}$) |
| EBMRCO | = | coefficient for calculating basal metabolic rate ($\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$):
by default set to 293 |
| WTEMPY_{d-1} | = | empty body weight on previous day $d-1$ (kg) |
| 0.75 | = | scaling of cow weight to metabolic weight |

Note that this energy requirement for basal metabolism includes energy associated with endogenous urinary N loss and fecal N loss.

Total base requirement for N each day is calculated based upon the previous day's metabolic fecal N and endogenous urinary N losses:

$$\text{NRBASE}_d = \text{MFN}_{d-1} + \text{EUN}_{d-1} \quad (102)$$

where:

- NRBASE_d = base net nitrogen requirement on day d ($\text{g} \cdot \text{day}^{-1}$)
- MFN_{d-1} = daily fecal nitrogen loss on previous day $d-1$ ($\text{g} \cdot \text{day}^{-1}$)
- EUN_{d-1} = daily endogenous urinary nitrogen loss on previous day $d-1$ ($\text{g} \cdot \text{day}^{-1}$)

Summer coat production

Daily net N requirement for summer coat production is calculated as (NRC, 2007 p97):

$$\text{NRCOAT}_d = \text{NCOATCO} \cdot \text{WTBODY}_{d-1}^{0.75} \quad \text{if } \text{STDAYCT} \leq d \leq \text{ENDAYCT} \quad (103)$$

$$= 0 \quad \text{otherwise}$$

where:

- NRCOAT_d = daily nitrogen requirement for summer coat production on day d ($\text{g} \cdot \text{day}^{-1}$)
- NCOATCO = user-specified coefficient converting body weight to daily metabolizable nitrogen requirement for coat production ($\text{g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$) – by default set to $0.054 \text{ g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$ (NRC, 2007 p97)
- WTBODY_{d-1} = body weight of animal on previous day $d-1$ (kg)
- STDAYCT = user-specified start day of the period during which summer coat production occurs (Julian day)
- ENDAYCT = user-specified end day of the period during which summer coat production occurs (Julian day)

Energy requirement associated with summer coat production is calculated as:

$$\text{ERCOAT}_d = \text{NRCOAT} \cdot \text{ECONPRO} / \text{NCONPRO} \quad \text{if } \text{STDAYCT} \leq d \leq \text{ENDAYCT} \quad (104)$$

$$= 0 \quad \text{otherwise}$$

where:

- ERCOAT_d = daily energy requirement for summer coat production on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- NRCOAT_d = daily nitrogen requirement for summer coat production on day d ($\text{g} \cdot \text{day}^{-1}$)
- ECONPRO = user-specified energy content of dry protein ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $23.6 \text{ kJ} \cdot \text{g}^{-1}$ (Robbins, 1993 p10)
- NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)

Winter scurf production

Net N requirement for winter scurf production is calculated as:

$$\text{NRSCRF}_d = \text{NSCRFCO} \cdot \text{WTBODY}_{d-1}^{0.6} \quad \text{if } \text{STDAYSC} \leq d \leq \text{ENDAYSC} \quad (105) \\ = 0 \quad \text{otherwise}$$

where:

- NRSCRF_d = daily nitrogen requirement for winter scurf production on day d ($\text{g} \cdot \text{day}^{-1}$)
 NSCRFCO = user-specified coefficient converting body weight to daily nitrogen requirement for winter scurf production ($\text{g} \cdot \text{kg}^{-0.6} \cdot \text{day}^{-1}$) – by default, set to $5.3 \cdot 10^{-4} \text{ g} \cdot \text{kg}^{-0.6} \cdot \text{day}^{-1}$ (NRC, 2007 p97)
 WTBODY_{d-1} = body weight of animal on previous day $d-1$ (kg)
 STDAYSC = user-specified start day of the period during which winter scurf production occurs (Julian day)
 ENDAYSC = user-specified end day of the period during which winter scurf production occurs (Julian day)

Energy requirement associated with winter scurf production is calculated as:

$$\text{ERSCRF}_d = \text{NRSCRF}_d \cdot \text{ECONPRO} / \text{NCONPRO} \quad \text{if } \text{STDAYSC} \leq d \leq \text{ENDAYSC} \quad (106) \\ = 0 \quad \text{otherwise}$$

where:

- ERSCRF_d = daily energy requirement for winter scurf production on day d ($\text{kJ} \cdot \text{day}^{-1}$)
 NRSCRF_d = daily nitrogen requirement for winter scurf production on day d ($\text{g} \cdot \text{day}^{-1}$)
 ECONPRO = user-specified energy content of dry protein ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $23.6 \text{ kJ} \cdot \text{g}^{-1}$ (Robbins, 1993 p10)
 NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)

Animal activity

Following initiation of a model run based on target energy and N requirement, the actual daily energy requirement is calculated from activity above lying and is determined from the animal's activity budget and body weight. Activities recognized by the model include foraging, lying, standing, walking and running, with foraging further divided into eating, pawing and other. Energy costs of these activities have been documented for reindeer and caribou (White & Yousef, 1978; Luick & White, 1985; Fancy & White, 1985b; 1987; Fancy, 1986) and the factorial integration used to estimate daily energy cost compares favorably with a study of reindeer (Gotaas *et al.*, 2000). Modeled daily costs also can be compared with other estimates of total energy expenditure measure with the doubly labelled water technique (Fancy *et al.*, 1986; Parker *et al.*, 1990; Haggarty *et al.*, 1998; Gotaas *et al.*, 2000; Haggarty, 2000).

Added cost of locomotion in snow

Before calculating costs of each activity, the model calculates snow depth and the cow's sinking depth in the snow to determine added cost of locomotion in snow (Fancy & White, 1985a; 1987):

$$\text{SINKDEP}_d = \text{SDPROP} \cdot \text{SNODEP}_d \quad (107)$$

where:

SINKDEP_d = animal's sinking depth in the snow on Julian day d (cm)

SDPROP = user-specified proportion of the snow depth to which the cow sinks (proportion)

SNODEP_d = user-specified snow depth on day d (cm)

Added cost of locomotion in snow is determined as follows (Fancy & White, 1985a,b; Fancy 1986) – see Figure 13:

$$\text{SNOWX}_d = 1 + 0.0241623 \cdot e^{(0.0635 \cdot \text{SINKDEP}_d \cdot 1.587)} \quad (108)$$

where:

SNOWX_d = change in energy requirement associated with locomotion in snow on Julian day d (proportion)

SINKDEP_d = animal's sinking depth in the snow on Julian day d (cm)

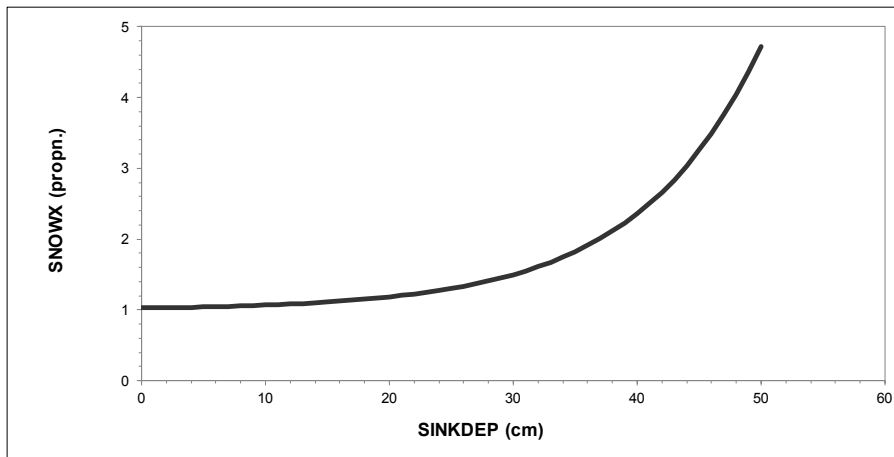


Figure 13. Relationship between the proportional increase in energy requirement associated with locomotion (SNOWX) and the animal's sinking depth in snow (SINKDEP)

Energy requirements of activity

$$\text{ERSTD}_d = \text{PSTD}_d \cdot \text{HRESTD} \cdot \text{WTBODY}_{d-1} \cdot 24 \quad (109)$$

where:

- ERSTD_d = energy requirement of standing on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- PSTD_d = user-specified proportion of day d spent standing (proportion)
- HRESTD = user-specified hourly energy requirement of standing ($\text{kJ} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$)
- WTBODY_{d-1} = weight of the animal on previous day $d-1$ (kg)
- 24 = hours in a day ($\text{h} \cdot \text{day}^{-1}$)

$$\text{ERRUN}_d = \text{PRUN}_d \cdot \text{SNOWX}_d \cdot \text{HRERUN} \cdot \text{WTBODY}_{d-1} \cdot 24 \quad (110)$$

where:

- ERRUN_d = energy requirement of running on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- PRUN_d = user-specified proportion of day d spent running (proportion)
- SNOWX_d = change in requirement associated with locomotion in snow on day d (unitless)
- HRERUN = user-specified hourly energy requirement of running ($\text{kJ} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$)
- WTBODY_{d-1} = weight of the animal on previous day $d-1$ (kg)
- 24 = hours in a day ($\text{h} \cdot \text{day}^{-1}$)

$$\text{ERPAW}_d = \text{PFOR}_d \cdot \text{PFORPAW}_d \cdot \text{HREPAW} \cdot \text{WTBODY}_{d-1} \cdot 24 \quad (111)$$

where:

- ERPAW_d = energy requirement of pawing on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- PFOR_d = user-specified proportion of day d spent foraging (proportion)
- PFORPAW_d = user-specified proportion of foraging period spent pawing on day d (proportion)
- HREPAW = user-specified hourly energy requirement of pawing ($\text{kJ} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$)
- WTBODY_{d-1} = weight of the animal on previous day $d-1$ (kg)
- 24 = hours in a day ($\text{h} \cdot \text{day}^{-1}$)

$$\text{ERWLK}_d = (\text{PWLK}_d + (\text{PFOR}_d \cdot (1 - \text{PFOREAT}_d - \text{PFORPAW}_d))) \cdot \text{SNOWX}_d \cdot \text{HREWLK} \cdot \text{WTBODY}_{d-1} \cdot 24 \quad (112)$$

where:

- ERWLK_d = energy requirement of walking on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- PWLK_d = user-specified proportion of day d spent walking (proportion)
- PFOR_d = user-specified proportion of day d spent foraging (proportion)
- PFOREAT_d = user-specified proportion of foraging period spent eating on day d (proportion)
- PFORPAW_d = user-specified proportion of foraging period spent pawing on day d (proportion)
- SNOWX_d = change in requirement associated with locomotion in snow on day d (unitless)
- HREWLK = user-specified hourly energy requirement of walking ($\text{kJ} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$)
- WTBODY_{d-1} = weight of the animal on previous day $d-1$ (kg)
- 24 = hours in a day ($\text{h} \cdot \text{day}^{-1}$)

$$\text{EREAT}_d = (\text{PFOR}_d \cdot \text{PFOREAT}_d \cdot \text{HRESTD} \cdot \text{WTBODY}_{d-1} \cdot 24) \quad (113)$$

where:

- EREAT_d = energy requirement of eating on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- PFOR_d = user-specified proportion of day d spent foraging (proportion)
- PFOREAT_d = user-specified proportion of foraging period spent eating on day d (proportion)
- HRESTD = user-specified hourly energy requirement of walking ($\text{kJ} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$)
- WTBODY_{d-1} = weight of the animal on previous day $d-1$ (kg)
- 24 = hours in a day ($\text{h} \cdot \text{day}^{-1}$)

Total energy requirement of activity (i.e. above lying) is then calculated as:

$$\text{ERACT}_d = \text{ERSTD}_d + \text{ERRUN}_d + \text{ERPAW}_d + \text{ERWLK}_d + \text{EREAT}_d \quad (114)$$

where:

- ERACT_d = energy requirement of activity (including lying) on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERSTD_d = energy requirement of standing on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERRUN_d = energy requirement of running on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERPAW_d = energy requirement of pawing on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERWLK_d = energy requirement of walking on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- EREAT_d = energy requirement of eating on day d ($\text{kJ} \cdot \text{day}^{-1}$)

Summer Protein Deposition

A new aspect of modeling protein metabolism is inclusion of a “labile (mobilizable) protein reserve” in *Rangifer* (Huot, 1989; Allaye-Chan, 1991; Gerhart *et al.*, 1996b; Russell & White, 2000; Barboza & Parker, 2006; 2008; Barboza *et al.*, 2009). This proposed lability of reserves is probably adaptive (Fauchald *et al.*, 2004). Evidence is based on the way a newly lactating female allocates her reserves when nutrition is limiting. Evidence includes limitation of milk production in favor to body condition (White, 1983; White & Luick, 1984), early weaning and a nutritionally based weaning strategy (Fig. 12), the way females regain body weight and protein reserves to meet targets (Cameron & White, 1996; Russell *et al.*, 2000) and the finding that most fetal protein is derived from maternal protein (Barboza & Parker, 2006; Barboza *et al.*, 2009). We have termed a female that weans a calf prematurely, or reduces milk production, in order to protect protein reserves a “selfish cow” (Russell *et al.*, 1996; 2000; 2005; Russell & White, 2000); the “selfish cow” strategy also is reported for bighorn sheep (*Ovis canadensis*, Festa-Bianchet & Jorgenson, 1998), evidence suggesting a reproductive strategy of large mammals in the wild.

Nitrogen requirement for the “selfish cow” protein deposition each year is calculated as a function of the user-set target protein gain for each day during the summer period:

$$\text{NRSUM}_d = \text{PTARSUM} \cdot \text{NCONPRO} \quad \text{if } \text{STDAYSUM} \leq d \leq \text{ENDAYSUM} \quad (115)$$

$$= 0 \quad \text{otherwise}$$

where:

- NRSUM_d = daily nitrogen requirement for summer protein deposition on day d ($\text{g} \cdot \text{day}^{-1}$)
- PTARSUM = user-specified target summer protein deposition ($\text{g} \cdot \text{day}^{-1}$)
- NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)
- STDAYSUM = user-specified start day of the period during which summer protein deposition occurs (Julian day)
- ENDAYSUM = user-specified end day of the period during which summer protein deposition occurs (Julian day)

Corresponding energy required in order to deposit this protein is calculated as:

$$\text{ERSUM}_d = \text{NRSUM}_d \cdot (\text{ECONPRO} / \text{NCONPRO}) \quad (116)$$

where:

- ERSUM_d = daily energy requirement for summer protein deposition on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- NRSUM_d = daily nitrogen requirement for summer protein deposition on day d ($\text{g} \cdot \text{day}^{-1}$)
- ECONPRO = user-specified energy content of dry protein ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $23.6 \text{ kJ} \cdot \text{g}^{-1}$ (Robbins, 1993 p10)
- NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)

Gestation

The following section describes the calculations incorporated in the model regarding gestation.

Target fetus weight

The model first calculates how many days the animal has been pregnant:

$$\begin{aligned} \text{DAYSGES}_d &= d - \text{STDAYGES} + 1 && \text{if } \text{STDAYGES} \leq d \leq \text{ENDAYGES} \\ \text{DAYSGES}_d &= 0 && \text{otherwise} \end{aligned} \quad (117)$$

where:

DAYSGES_d = days the animal has been pregnant on day d (days)
 STDAYGES = user-specified start day of gestation period (Julian day)
 ENDAYGES = user-specified end day of gestation period (Julian day)

This is then used to calculate the daily maximum fetus weight for reindeer (Roine *et al.*, 1982):

$$\begin{aligned} \text{MAXWTFET}_d &= 0 && \text{if } \text{DAYSGES}_d = 0 \\ &= 1.075 && \text{if } 1 \leq \text{DAYSGES}_d \leq 25 \end{aligned} \quad (118)$$

$$\begin{aligned} \text{MAXWTFET}_d &= (0.00036 \cdot \text{DAYSGES}_d^3) + (0.053 \cdot \text{DAYSGES}_d^2) - (1.58 \cdot \text{DAYSGES}_d) \\ &- 0.000096 && \text{if } 26 \leq \text{DAYSGES}_d \leq 76 \end{aligned}$$

$$\begin{aligned} \text{MAXWTFET}_d &= (6.05254 \cdot 10^{-8} \cdot \text{DAYSGES}_d^4) - (3.06828 \cdot 10^{-5} \cdot \text{DAYSGES}_d^3) \\ &+ (0.05719 \cdot \text{DAYSGES}_d^2) - (0.44743 \cdot \text{DAYSGES}_d) + 64.152 && \text{otherwise} \end{aligned} \quad (119)$$

where:

MAXWTFET_d = maximum fetus weight for reindeer on Julian day d (g)
 DAYSGES_d = number of days, on day d , the cow has been pregnant (days)

Equations above for target fetus weight were developed for reindeer. To convert results to caribou and to allow for variation in fetal growth, an algorithm that linked fetal weight (y , kg) predicted at gestation day 235 according to Bergerud *et al.* (2008, $y = (0.0487 \cdot x) - 5.653$, where x = age of fetus) is used as a correction factor adapted from Fancy (1986) – see Figure 14:

$$\text{TWTFET}_d = (\text{MAXWTFET}_d / 1000) \cdot (\text{TWTBIR} / 2.9) \quad (120)$$

where:

TWTFET_d = target fetus weight on day d (kg)
 MAXWTFET_d = maximum fetus weight for reindeer on day d (g)
 TWTBIR = user-specified target birth weight of calf (kg) – currently set to 6.5 kg
1000 = conversion coefficient ($\text{g} \cdot \text{kg}^{-1}$)
5.79 = predicted birth weight of caribou after a gestation period of 235 days (kg, Bergerud *et al.*, 2008 p188)

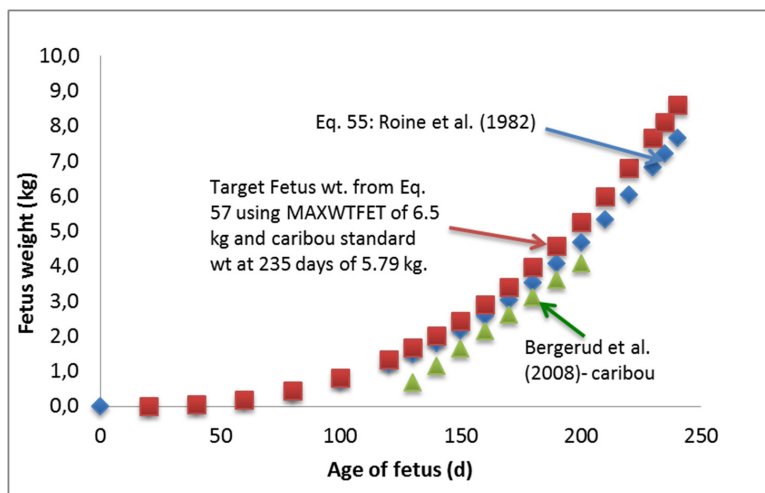


Figure 14. Target fetus weight used in the model compared to estimate from Roine *et al.* (1982) for reindeer and Bergerud *et al.* (2008) for caribou as a function of fetus age

Target growth rate of the fetus can be calculated each day as:

$$\text{TGRFET}_d = \text{TWTFET}_d - \text{TWTFET}_{d-1} \quad (121)$$

where:

TGRFET_d = target growth rate of fetus on day d ($\text{kg} \cdot \text{day}^{-1}$)

TWTFET_d = target fetus weight on day d (kg)

TWTFET_{d-1} = target fetus weight on the previous day $d-1$ (kg)

Nitrogen required to sustain the target fetus weight is calculated as:

$$\text{NRFET}_d = \text{NFETCO} \cdot (1 + \text{TGRFET}_d) \cdot \text{WTFET}_{d-1} \quad (122)$$

where:

NRFET_d = daily nitrogen requirement for the fetus on day d ($\text{g} \cdot \text{day}^{-1}$)

NFETCO = user-specified coefficient converting fetus weight to daily nitrogen requirement ($\text{g} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$) – by default, set to $0.63 \text{ g} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ (NRC, 2007 p99)

TGRFET_d = target growth rate of fetus on day d ($\text{kg} \cdot \text{day}^{-1}$)

WTFET_{d-1} = actual fetus weight on previous day $d-1$ (kg)

Nitrogen requirement for the entire conceptus, also termed gravid uterus, can be calculated from the fetus requirement as:

$$\text{NRGES}_d = \text{NRFET}_d / \text{PCONFET} \quad (123)$$

where:

NRGES_d = daily nitrogen requirement for gestation on day d ($\text{g} \cdot \text{day}^{-1}$)

NRFET_d = daily nitrogen requirement for sustaining the target fetus weight on day d ($\text{g} \cdot \text{day}^{-1}$)

PCONFET = user-specified proportion of the conceptus weight that is the fetus (proportion) – by default, set to 0.55 (range is 0.21 fetal age 100 to 0.58 near term, Robbins & Moen (1975 p686))

Energy requirements for gestation consist of two components: energy required supporting the protein portion of the fetus (as calculated previously through the nitrogen requirement for gestation), and that required depositing fetal fat.

Energy requirement for fetal fat is calculated as:

$$\text{ERGESFAT}_d = \text{PFETFAT} \cdot \text{TGRFET}_d \cdot \text{ECONFAT} \quad (124)$$

where:

ERGESFAT_d = daily energy requirement for the fat component of gestation on day d ($\text{kJ} \cdot \text{day}^{-1}$)

PFETFAT = user-specified proportion of the fetus weight that is fat (proportion) – by default, set to 0.021 (Gerhart *et al.*, 1996b)

TGRFET_d = target growth rate of fetus on day d ($\text{kg} \cdot \text{d}^{-1}$)

ECONFAT = user-specified energy content of fat ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $39.5 \text{ kJ} \cdot \text{g}^{-1}$ (Robbins, 1993 p10)

Total energy requirement for the fetus is then calculated as:

$$\text{ERFET}_d = (\text{NRFET}_d \cdot (\text{ECONPRO} / \text{NCONPRO})) + \text{ERGESFAT}_d \quad (125)$$

where:

ERFET_d = daily energy requirement for the fetus on day d ($\text{kJ} \cdot \text{day}^{-1}$)

NRFET_d = daily nitrogen requirement for the fetus on day d ($\text{g} \cdot \text{day}^{-1}$)

ECONPRO = user-specified energy content of dry protein ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $23.6 \text{ kJ} \cdot \text{g}^{-1}$ (ARC, 1980 p3; Robbins, 1993 p10)

NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)

ERGESFAT_d = daily energy requirement for the fat component of gestation on day d ($\text{kJ} \cdot \text{day}^{-1}$)

The corresponding total energy requirement for gestation (i.e. the requirement for the entire conceptus) can be calculated from the fetus requirement as:

$$\text{ERGES}_d = \text{ERFET}_d / \text{PCONFET} \quad (126)$$

where:

- ERGES_d = daily energy requirement for gestation on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERFET_d = daily energy requirement for the fetus on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- PCONFET = user-specified proportion of the conceptus weight that is the fetus (proportion) – by default, set to 0.55 (range is 0.21 fetal age 100 to 0.58 near term, Robbins & Moen (1975 p686))

Lactation

The following section outlines the steps and equations incorporated in the model regarding lactation.

Target milk production

The model first calculates how many days the animal has been lactating:

$$\begin{aligned} \text{DAYSLAC}_d &= d - \text{STDAYLAC} && \text{if } \text{STDAYLAC} \leq d \leq \text{ENDAYLAC} \\ &= 0 && \text{otherwise} \end{aligned} \quad (127)$$

where:

- DAYSLAC_d = age of the calf on day d (days)
- STDAYLAC = user-specified start day of lactation period (Julian day)
- ENDAYLAC = user-specified end day of lactation period (Julian day)

The target milk production for the cow is calculated each day during lactation as a function of the age of the calf (White & Luick, 1984; Parker *et al.*, 1990) – see Figure 15:

$$\begin{aligned} \text{TMLKPR}_d &= 0 && \text{if } \text{DAYSLAC}_d = 0 \\ \text{TMLKPR}_d &= 0.731 && \text{if } \text{DAYSLAC}_d = 1 \\ \text{TMLKPR}_d &= 1.91 && \text{if } \text{DAYSLAC}_d = 2 \\ \text{TMLKPR}_d &= 1.606 \cdot e^{-0.0072 \cdot \text{DAYSLAC}_d} + 0.374 \cdot e^{-0.0617 \cdot \text{DAYSLAC}_d} && \text{if } \text{DAYSLAC}_d > 2 \end{aligned} \quad (128)$$

where:

- TMLKPR_d = target milk production on day d ($\text{l} \cdot \text{day}^{-1}$)
- DAYSLAC_d = age of the calf on day d (days)

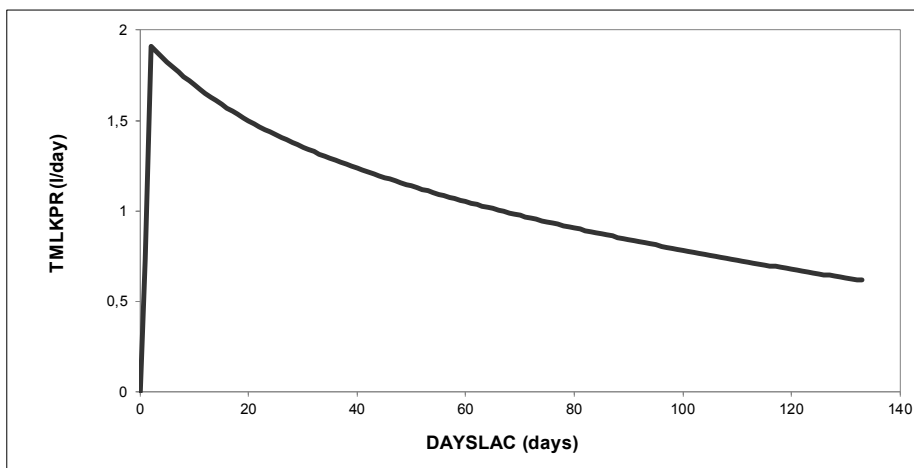


Figure 15. Relationship between the target milk production (TMLKPR) and the age of the calf (DAYSLAC)

This target milk production can also be expressed on a per unit weight basis as:

$$\text{TMLKPRWT}_d = (\text{TMLKPR}_d \cdot 1000) / \text{WTBODY}_{d-1} \quad (129)$$

where:

TMLKPRWT_d = target milk production per unit weight on day d ($\text{ml} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$)

TMLKPR_d = target milk production on day d ($\text{l} \cdot \text{day}^{-1}$)

WTBODY_{d-1} = body weight of animal on previous day $d-1$ (kg)

1000 = coefficient for converting from liters to milliliters ($\text{ml} \cdot \text{l}^{-1}$)

Protein content of milk each day is estimated as a function of the target milk production (White & Luick, 1984; NRC, 2007 100):

$$\text{PCONMLK}_d = 0.14 - (0.0034 \cdot \text{TMLKPRWT}_d) \quad (130)$$

where:

PCONMLK_d = protein content of milk (proportion)

TMLKPRWT_d = target milk production per unit weight on day d ($\text{ml} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$)

Net N requirement for lactation is calculated for each day during lactation as a function of the target milk production and the protein content of the milk:

$$\text{NRLAC}_d = \text{TMLKPR}_d \cdot 1000 \cdot \text{PCONMLK}_d \cdot \text{NCONPRO} \quad (131)$$

where:

- NRLAC_d = net nitrogen requirement for lactation on day d ($\text{g} \cdot \text{day}^{-1}$)
- TMLKPR_d = target milk production on day d ($\text{l} \cdot \text{day}^{-1}$)
- 1000 = coefficient for converting from liters to ml ($\text{ml} \cdot \text{l}^{-1}$)
- PCONMLK_d = protein content of milk on day d (proportion)
- NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)

Energy content of milk each day is estimated as a function of the target milk production (Parker *et al.*, 1990):

$$\text{ECONMLK}_d = 12.24 - (0.00323 \cdot \text{TMLKPR}_d \cdot 1000) \quad (132)$$

where:

- ECONMLK_d = energy content of milk on day d ($\text{kJ} \cdot \text{ml}^{-1}$)
- TMLKPR_d = target milk production on day d ($\text{l} \cdot \text{day}^{-1}$)
- 1000 = coefficient for converting from liters to milliliters ($\text{ml} \cdot \text{l}^{-1}$)

The corresponding energy requirement associated with lactation can then be calculated as:

$$\text{ERLAC}_d = \text{TMLKPR}_d \cdot 1000 \cdot \text{ECONMLK}_d \quad (133)$$

where:

- ERLAC_d = net energy requirement for lactation on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- TMLKPR_d = target milk production on day d ($\text{l} \cdot \text{day}^{-1}$)
- 1000 = coefficient for converting from liters to ml ($\text{ml} \cdot \text{l}^{-1}$)
- ECONMLK_d = energy content of milk on day d ($\text{kJ} \cdot \text{ml}^{-1}$)

Antler Production

Allocation of N and energy to antler growth is based on the simulation model of Moen & Pastor (1998). Currently this aspect of the model grows antlers at the rates used by Moen & Pastor (1998) based on the body weight of the animal, or production can be turned off at the discretion of the user.

Daily net N requirement for antler production is calculated as:

$$\text{NRANTL}_d = \text{NANTLCO} \cdot \text{WTBODY}_{d-1}^{0.75} \quad \text{if } \text{STDAYAN} \leq d \leq \text{ENDAYAN} \quad (134)$$

$$= 0 \quad \text{otherwise}$$

where:

- NRANTL_d = daily nitrogen requirement for antler production on day d ($\text{g} \cdot \text{day}^{-1}$)
- NANTLCO = user-specified coefficient converting body weight to daily nitrogen requirement for antler production ($\text{g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$) – by default set to $0.02 \text{ g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$ for cows and $0.105 \text{ g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$ for bulls (Moen & Pastor, 1998; NRC, 2007)
- WTBODY_{d-1} = body weight of animal on previous day $d-1$ (kg)
- STDAYAN = user-specified start day of the period during which antler production occurs (Julian day)
- ENDAYAN = user-specified end day of the period during which antler production occurs (Julian day)

Daily net energy requirement for antler production is calculated as:

$$\text{ERANTL}_d = \text{EANTLCO} \cdot \text{WTBODY}_{d-1}^{0.75} \quad \text{if } \text{STDAYAN} \leq d \leq \text{ENDAYAN} \quad (135)$$

$$= 0 \quad \text{otherwise}$$

where:

- ERANTL_d = daily energy requirement for antler production and skin (i.e. scurf) loss on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- EANTLCO = user-specified coefficient converting body weight to daily energy requirement for antler production ($\text{g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$) – by default set to $18 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$ for cows and $88 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$ for bulls (Moen & Pastor, 1998; NRC, 2007)
- WTBODY_{d-1} = body weight of animal on previous day $d-1$ (kg)
- STDAYAN = user-specified start day of the period during which antler production occurs (Julian day)
- ENDAYAN = user-specified end day of the period during which antler production occurs (Julian day)

Additional Protein Deposition

Independent of the N reserve of the “selfish cow” the animal deposits protein and energy as N and energy becomes available in excess of requirements, and this set of algorithms are important to simulate daily increases in body weight and condition.

$$\text{NRPDEP}_d = \text{PROMOBRT} \cdot \text{NCONPRO} \quad (136)$$

where:

- NRPDEP_d = daily nitrogen requirement for additional protein deposition on day d ($\text{g} \cdot \text{day}^{-1}$)
- PROMOBRT = user-specified maximum rate at which protein can be mobilized ($\text{g} \cdot \text{day}^{-1}$) – by default this value is $40 \text{ g} \cdot \text{day}^{-1}$
- NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)

The corresponding energy required to deposit this protein is calculated as:

$$\text{ERPDEP}_d = \text{NRPDEP}_d \cdot (\text{ECONPRO} / \text{NCONPRO}) \quad (137)$$

where:

- ERPDEP_d = daily energy requirement for the additional protein deposition on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- NRPDEP_d = daily nitrogen requirement for additional protein deposition on day d ($\text{g} \cdot \text{day}^{-1}$)
- ECONPRO = user-specified energy content of dry protein ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $23.6 \text{ kJ} \cdot \text{g}^{-1}$ (ARC, 1980 p3; Robbins, 1993 p10)
- NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)

Fat Deposition

Energy required for fat deposition is set according to the upper limit on the amount of fat that can be mobilized each day.

$$\text{ERFDEP}_d = \text{FATMOBRT} \cdot \text{ECONPRO} \quad (138)$$

where:

- ERPDEP_d = daily energy requirement for fat deposition on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- FATMOBRT = user-specified maximum rate at which fat can be mobilized ($\text{g} \cdot \text{day}^{-1}$) – by default this value is $250 \text{ g} \cdot \text{day}^{-1}$ (See energy available)
- ECONPRO = user-specified energy content of fat ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $39.3 \text{ kJ} \cdot \text{g}^{-1}$ (ARC, 1980 p3)

Finally, no N is required to deposit fat:

$$\text{NRFDEP}_d = 0 \quad (139)$$

where:

- NRPDEP_d = daily nitrogen requirement for fat deposition on day d ($\text{g} \cdot \text{day}^{-1}$)

Availability and Use of Energy and Nitrogen

When energy and protein requirements are calculated (see Energy and Nitrogen Requirements and Animal Activity), the next step is to allocate available energy and protein to attempt to meet those requirements. Thus, for each day of a simulation the model calculates N and energy available to the animal for each specific allocation stage – this availability is a function of both the day's intake and the portion of the animal's fat and protein stores that is potentially available for mobilization. Allocation stages represent all of the processes for which N and/or energy are required each day, ordered by allocation priority (see Table 5). In general, the model distinguishes

between three sources of available N and energy for each allocation stage: N and energy available from intake (and not already used by higher priority stages); remaining fat or protein reserves available to be mobilized in response to the requirements of this particular stage; and incidental N released, yet not required, through the mobilization of protein reserves to meet the energy requirements of higher priority stages on the same day.

Table 5. Allocation stages represented in the model, listed in default order of allocation priority, including the possible pathways through which body reserves can be used to meet each stage’s N and energy requirements. Note that the order of priority can be set by the user. Mobilization includes re-deposition and oxidation that meets metabolic requirements

Allocation Stage		Body Reserve Pathways			
Index	Name	Protein Mobilization	Protein Deposition	Fat Mobilization	Fat Deposition
1	Base Metabolism	X		X	
2	Parasites	X		X	
3	Activity	X		X	
4	Summer Protein Deposition		X		
5	Gestation	X		X	
6	Lactation	X		X	
7	Antler Production	X		X	
8	Additional Protein Deposition		X		
9	Fat Deposition				X

In general each allocation stage has a maximum N and energy requirement, both of which the model tries to meet each day (as calculated in the previous section). The model begins each day by assuming that the total available N and energy can be used first to meet requirements of the highest priority allocation stage, as shown in Table 5. The model then calculates how much of this available N and energy is actually used by this first stage, with any remaining N and/or energy then made available to meet the requirements of the next highest priority stage. This iterative process of calculating availability and use of both N and energy for each stage continues, in order of stage priority, with the N and energy available to each stage decreasing in response to use calculated for prior stages.

Nitrogen available

The first source of available N for each allocation stage is any N available from protein reserves mobilized (but not used) in order to meet energy requirements of higher priority allocation stages that same day. For all but the highest priority stage available N from this source is reduced to reflect any N used by higher priority stages.

$$\begin{aligned} \text{NAPRORE}_{a,d} &= 0 & \text{if } a = 1 \\ \text{NAPRORE}_{a,d} &= \text{NAPRORE}_{a-1,d} - \text{NUPRORE}_{a-1,d} & \text{otherwise} \end{aligned} \quad (140)$$

where:

- $\text{NAPRORE}_{a,d}$ = daily nitrogen available for allocation stage a on day d , as a result of protein reserves catabolized, but not used, in order to meet the energy requirements of higher priority allocation stages the same day ($\text{g} \cdot \text{day}^{-1}$)
- $\text{NAPRORE}_{a-1,d}$ = daily nitrogen available for allocation stage $a-1$ on day d , as a result of protein reserves catabolized, but not used, in order to meet the energy requirements of higher priority allocation stages the same day ($\text{g} \cdot \text{day}^{-1}$)
- $\text{NUPRORE}_{a-1,d}$ = daily nitrogen used by the previous allocation stage $a-1$ on day d , from protein reserves mobilized, but not used, in order to meet the energy requirements of higher priority allocation stages the same day ($\text{g} \cdot \text{day}^{-1}$)

The next source of N available for each allocation stage is any N available from intake. For the highest priority stage (i.e. $a=1$) this available N is set to the total MNI for the day, while for subsequent stages N available from intake is reduced to reflect any N used by higher priority stages.

$$\begin{aligned} \text{NAINT}_{a,d} &= \text{MNI}_d & \text{if } a = 1 \\ \text{NAINT}_{a,d} &= \text{NAINT}_{a-1,d} - \text{NUINT}_{a-1,d} & \text{otherwise} \end{aligned} \quad (141)$$

where:

- $\text{NAINT}_{a,d}$ = daily nitrogen available from intake for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
- MNI_d = daily metabolizable nitrogen intake on day d , as calculated by the intake submodel ($\text{g} \cdot \text{day}^{-1}$)
- $\text{NAINT}_{a-1,d}$ = daily nitrogen available from intake for allocation stage $a-1$ on day d ($\text{g} \cdot \text{day}^{-1}$)
- $\text{NUINT}_{a-1,d}$ = daily nitrogen used from intake by the previous allocation stage $a-1$ on day d ($\text{g} \cdot \text{day}^{-1}$)

Finally, the model makes N available from protein reserves for each allocation stage. For N reserves, maximum protein available to be mobilized is limited by the size of the mobilizable protein reserve, the maximum rate at which protein can be mobilized, and the minimum weight of protein (3.5 kg dry protein or 0.56 kg N) in order to support life processes. All body protein in excess of 3.5 kg is considered a mobilizable protein reserve.

$$\text{WTPROMIN}_d = \text{Minimum} \{ (\text{PPROMIN} \cdot \text{WTBODYIN}), \text{WTPRO}_{d-1} \} \quad (142)$$

where:

- WTPROMIN_d = minimum allowable body dry protein weight of the animal on day d (kg)
- PPROMIN = user-specified minimum proportion of initial body weight that must be dry protein (proportion) – by default this is set to 0.20 (Gerhart *et al.*, 1996b)
- WTBODYIN = initial body weight of animal (kg)
- WTPRO_{d-1} = dry protein weight of animal on previous day $d-1$ (kg)

Next the maximum amount of protein that can be mobilized each day is calculated. It is assumed that the average amount of protein mobilized overwinter by the pregnant female (~5 kg, Gerhart *et al.*, 1996b; White *et al.*, 2013b) over approximately 3 mo. is $40 \text{ g} \cdot \text{d}^{-1}$, but that this rate could be 4 times higher at the extreme, $200 \text{ g} \cdot \text{d}^{-1}$. Actual rate of mobilization of protein at term gestation is $26 \text{ g} \cdot \text{d}^{-1}$ based on data of Barboza & Parker (2008).

$$\text{PMMAX}_d = \text{Minimum} \{ (\text{PROMOBRT}, (1000 \cdot (\text{WTPRO}_{d-1} - \text{WTPROMIN}_d)) \} \quad (143)$$

where:

- PMMAX_d = maximum amount of dry protein that can be mobilized on day d ($\text{g} \cdot \text{day}^{-1}$)
- PROMOBRT = user-specified maximum rate at which protein can be mobilized ($\text{g} \cdot \text{day}^{-1}$) – by default this value is $40 \text{ g} \cdot \text{day}^{-1}$ (See above)
- 1000 = coefficient for converting from kg to g ($\text{g} \cdot \text{kg}^{-1}$)
- WTPRO_{d-1} = dry protein weight of animal on previous day $d-1$ (kg)
- WTPROMIN_d = minimum allowable dry protein weight of the animal on day d (kg)

Finally the maximum N available to be mobilized from protein reserves is calculated for each allocation stage as:

$$\begin{aligned} \text{NAPRO}_{a,d} &= \text{PMMAX}_d \cdot \text{NCONPRO} && \text{if } a = 1 \\ &= \text{NAPRO}_{a-1,d} - \text{NUPRO}_{a-1,d} && \text{otherwise} \end{aligned} \quad (144)$$

where:

- $\text{NAPRO}_{a,d}$ = nitrogen available from protein reserves for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
- PMMAX_d = maximum amount of dry protein that can be mobilized on day d ($\text{g} \cdot \text{day}^{-1}$)
- NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)
- $\text{NAPRO}_{a-1,d}$ = nitrogen available from protein reserves for allocation stage $a-1$ on day d ($\text{g} \cdot \text{day}^{-1}$)
- $\text{NUPRO}_{a-1,d}$ = nitrogen used from protein reserves for previous allocation stage $a-1$ on day d ($\text{g} \cdot \text{day}^{-1}$)

Energy available

Similar to the calculation above for N, the model determines the maximum amount of energy available to each allocation stage every day.

The first source of available energy for each allocation stage is any energy available from protein reserves catabolized, in order to meet the N requirements of higher priority allocation stages that same day. For all but the highest priority stage the available energy from this source is reduced to reflect any energy used by higher priority stages.

$$\begin{aligned} \text{EAPRORE}_{a,d} &= 0 & \text{if } a = 1 \\ \text{EAPRORE}_{a,d} &= \text{EAPRORE}_{a-1,d} - \text{EUPRORE}_{a-1,d} & \text{otherwise} \end{aligned} \quad (145)$$

where:

- $\text{EAPRORE}_{a,d}$ = daily energy available for allocation stage a on day d , as a result of protein reserves catabolized in order to meet the nitrogen requirements of higher priority allocation stages the same day ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{EAPRORE}_{a-1,d}$ = daily energy available for allocation stage $a-1$ on day d , as a result of protein reserves catabolized in order to meet the nitrogen requirements of higher priority allocation stages the same day ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{EUPRORE}_{a-1,d}$ = daily energy used by the previous allocation stage $a-1$ on day d , from protein reserves mobilized, but not used, in order to meet the nitrogen requirements of higher priority allocation stages the same day ($\text{kJ} \cdot \text{day}^{-1}$)

The next source of energy available for each allocation stage is any energy available from intake. For the highest priority stage (i.e. $a = 1$) this available energy is set to the total MEI for the day, while for subsequent stages the energy available from intake is reduced to reflect any energy used by higher priority stages.

$$\begin{aligned} \text{Eaint}_{a,d} &= \text{MEI}_d & \text{if } a = 1 \\ \text{Eaint}_{a,d} &= \text{Eaint}_{a-1,d} - \text{Euint}_{a-1,d} & \text{otherwise} \end{aligned} \quad (146)$$

where:

- $\text{Eaint}_{a,d}$ = daily energy available from intake for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- MEI_d = daily metabolizable energy intake on day d , as calculated by the intake submodel ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{Eaint}_{a-1,d}$ = daily energy available from intake for allocation stage $a-1$ on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{Euint}_{a-1,d}$ = daily energy used from intake by the previous allocation stage $a-1$ on day d ($\text{kJ} \cdot \text{day}^{-1}$)

The third source of energy is that available from fat reserves. For fat reserves, maximum energy available to be mobilized is limited by the size of the fat reserve, the maximum rate at which fat can be mobilized, and the minimum proportion of body weight that must be retained as fat in

order to support life processes. Analysis of the fat content of animals apparently starving to death is approximately 3% of body weight and this is the default value assumed as the minimum (Gerhart *et al.*, 1996b). All fat reserves greater than 3% of body weight are considered to constitute a mobilizable fat reserve.

First, the minimum allowable fat weight is calculated once each day as:

$$\text{WTFATMIN}_d = \text{Minimum} \{ (\text{PFATMIN} \cdot \text{WTBODY}_{d-1}), \text{WTFAT}_{d-1} \} \quad (147)$$

where:

- WTFATMIN_d = minimum allowable fat weight of the animal on day d (kg)
- PFATMIN = user-specified minimum proportion of body weight that must be fat (proportion) – by default this is set to 0.03 (Gerhart *et al.*, 1996b)
- WTBODY_{d-1} = body weight of animal on previous day $d-1$ (kg)
- WTFAT_{d-1} = fat weight of animal on previous day $d-1$ (kg)

Next, the amount of fat that can be mobilized each day is calculated. The actual rate of fat mobilization is estimated as that needed to satisfy the energy budget up to a maximum possible that is set by the user. A default value of $250 \text{ g} \cdot \text{d}^{-1}$ for fat mobilization is estimated from maximum overwinter fat loss of females of the PCH (Gerhart *et al.*, 1996b), calculated as 7.0 kg (9.0 kg in Nov. – 2.0 kg in May) assuming the loss occurred over 1 mo. at the end of winter. If the duration of loss occurred evenly over the final trimester of pregnancy, then the loss rate is $80 \text{ g} \cdot \text{d}^{-1}$. A more general overwinter fat loss is 2.6 kg (White *et al.*, 2013b) resulting in a loss rate of $25\text{--}90 \text{ g} \cdot \text{d}^{-1}$ is based on a time period of 1–3 mo. In late gestation Barboza & Parker (2008) determined that a female mobilizing protein at $26 \text{ g} \cdot \text{d}^{-1}$ also mobilizes fat at $8 \text{ g} \cdot \text{d}^{-1}$ (See White *et al.*, 2013b). Thus, given this extremely wide range in loss rates, the user has the option of constraining maximum mobilization below the default value.

$$\text{FMMAX}_d = \text{Minimum} \{ \text{FATMOBRT}, (1000 \cdot (\text{WTFAT}_{d-1} - \text{WTFATMIN}_d)) \} \quad (148)$$

where:

- FMMAX_d = maximum amount of fat that can be catabolized on day d ($\text{g} \cdot \text{day}^{-1}$)
- FATMOBRT = user-specified maximum rate at which fat can be mobilized ($\text{g} \cdot \text{day}^{-1}$)
– by default this is set to $250 \text{ g} \cdot \text{day}^{-1}$ (See above)
- 1000 = coefficient for converting from kg to g ($\text{g} \cdot \text{kg}^{-1}$)
- WTFAT_{d-1} = fat weight of animal on previous day $d-1$ (kg)
- WTFATMIN_d = minimum allowable fat weight of the animal on day d (kg)

Maximum metabolizable energy available from the mobilization of fat reserves is then calculated as:

$$\begin{aligned} \text{EAFAT}_{a,d} &= \text{FMMAX}_d \cdot \text{ECONFAT} & \text{if } a = 1 \\ &= \text{EAFAT}_{a-1,d} - \text{EUFAT}_{a-1,d} & \text{otherwise} \end{aligned} \quad (149)$$

where:

- $\text{EAFAT}_{a,d}$ = energy available from fat reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- FMMAX_d = maximum amount of fat that can be catabolized on day d ($\text{g} \cdot \text{day}^{-1}$)
- ECONFAT = user-specified energy content of fat ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $39.3 \text{ kJ} \cdot \text{g}^{-1}$ (ARC, 1980 p3)
- $\text{EAFAT}_{a-1,d}$ = energy available from fat reserves for allocation stage $a-1$ on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{EUFAT}_{a-1,d}$ = energy used from fat reserves for previous allocation stage $a-1$ on day d ($\text{kJ} \cdot \text{day}^{-1}$)

The final source of energy is that available from protein reserves. Given the previously calculated maximum for the amount of dry protein that can be mobilized each day, the daily maximum energy available from protein reserves is then calculated as:

$$\begin{aligned} \text{EAPRO}_{a,d} &= \text{PMMAX}_d \cdot \text{ECONPRO} & \text{if } a = 1 \\ &= \text{EAPRO}_{a-1,d} - \text{EUPRO}_{a-1,d} & \text{otherwise} \end{aligned} \quad (150)$$

where:

- $\text{EAPRO}_{a,d}$ = energy available to be mobilized from protein reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- PMMAX_d = maximum amount of dry protein that can be catabolized on day d ($\text{g} \cdot \text{day}^{-1}$)
- ECONPRO = user-specified energy content of dry protein ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $23.6 \text{ kJ} \cdot \text{g}^{-1}$ (ARC, 1980 p3)
- $\text{EAPRO}_{a-1,d}$ = energy available to be mobilized from protein reserves for allocation stage $a-1$ on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{EUPRO}_{a-1,d}$ = energy used from protein reserves for previous allocation stage $a-1$ on day d ($\text{kJ} \cdot \text{day}^{-1}$)

Nitrogen used

Based on the calculations of N required and available for a particular allocation stage, the model then determines how much N is actually used for this stage. The model distinguishes between two types of allocation stages: those that involve fat or protein deposition (referred to here as “deposition” stages), and all others (including gestation). A simplifying assumption in the model is that, with the exception of fetal growth associated with gestation, on any given day the animal’s fat reserves cannot be catabolized to support the deposition of body protein; similarly, protein reserves cannot be catabolized to support the deposition of body fat.

The first source of N used to meet requirements of each non-deposition allocation stage is any N available from protein reserves mobilized (but not used) in order to meet the energy requirements of higher priority allocation stages that same day.

$$\text{NUPRORE}_{a,d} = \text{Minimum} \{ (\text{NR}_{a,d} / \text{KNPRO}_a), \text{NAPRORE}_{a,d} \} \quad (151)$$

where:

- $\text{NUPRORE}_{a,d}$ = daily nitrogen used for allocation stage a on day d , from protein reserves mobilized, but not used, in order to meet the energy requirements of higher priority allocation stages the same day ($\text{g} \cdot \text{day}^{-1}$)
- $\text{NR}_{a,d}$ = daily nitrogen requirement for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
- KNPRO_a = efficiency in use of nitrogen derived from catabolizing body protein directed towards allocation stage a
- $\text{NAPRORE}_{a,d}$ = daily nitrogen available for allocation stage a on day d , as a result of protein reserves catabolized, but not used, in order to meet the energy requirements of higher priority allocation stages the same day ($\text{g} \cdot \text{day}^{-1}$)

The next source of N used by each non-deposition allocation stage is any N available from intake. First, the remaining N requirement from intake, after accounting for N used from previously mobilized protein reserves, is calculated:

$$\text{NRINT}_{a,d} = \text{NR}_{a,d} - (\text{NUPRORE}_{a,d} \cdot \text{KNPRO}_a) \quad (152)$$

where:

- $\text{NRINT}_{a,d}$ = daily nitrogen requirement from intake for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
- $\text{NR}_{a,d}$ = daily nitrogen requirement for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
- $\text{NUPRORE}_{a,d}$ = daily nitrogen used for allocation stage a on day d , from protein reserves mobilized, but not used, in order to meet the energy requirements of higher priority allocation stages the same day ($\text{g} \cdot \text{day}^{-1}$)
- KNPRO_a = efficiency in use of nitrogen derived from catabolizing body protein and directed towards allocation stage a

Next N used from intake is calculated:

$$\text{NUINT}_{a,d} = \text{Minimum} \{ (\text{NRINT}_{a,d} / \text{KNINT}_a), \text{NAINT}_{a,d} \} \quad (153)$$

where:

- $\text{NUINT}_{a,d}$ = daily nitrogen used from intake for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
- $\text{NRINT}_{a,d}$ = daily nitrogen requirement from intake for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
- KNINT_a = efficiency in use of nitrogen derived from intake and directed towards allocation stage a
- $\text{NAINT}_{a,d}$ = daily nitrogen available from intake for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)

The next source of N used by each non-deposition allocation stage is any N available from body protein reserves. First, the remaining N requirement from body protein reserves, after accounting for the N used from intake, is calculated:

$$NRPRO_{a,d} = NRINT_{a,d} - (NUINT_{a,d} \cdot KNINT_a) \quad (154)$$

where:

- $NRPRO_{a,d}$ = daily nitrogen requirement from newly catabolized protein reserves for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
 $NRINT_{a,d}$ = daily nitrogen requirement from intake for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
 $NUINT_{a,d}$ = daily nitrogen used from intake for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
 $KNINT_a$ = efficiency in use of nitrogen derived from intake and directed towards allocation stage a

Next N used from body protein reserves is calculated:

$$NUPRO_{a,d} = \text{Minimum} \{ ((NRPRO_{a,d} / KNPRO_a), NAPRO_{a,d}) \} \quad (155)$$

where:

- $NUPRO_{a,d}$ = daily nitrogen used from newly catabolized protein reserves for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
 $NRPRO_{a,d}$ = daily nitrogen requirement from newly catabolized protein reserves for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
 $KNPRO_a$ = efficiency in use of nitrogen derived from catabolizing body protein and directed towards allocation stage a
 $NAPRO_{a,d}$ = nitrogen available from protein reserves for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)

The only source of N used for protein deposition stages is that available from intake:

$$NDPRO_{a,d} = (NUINT_{a,d} \cdot KNINT_a) \quad (156)$$

where:

- $NDPRO_{a,d}$ = daily nitrogen deposited to body protein reserves for protein deposition stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
 $NUINT_{a,d}$ = daily nitrogen used from intake for protein deposition stage a on day d ($\text{g} \cdot \text{day}^{-1}$)
 $KNINT_a$ = efficiency in use of nitrogen derived from intake and directed towards protein deposition stage a

Energy used

Similar to calculations above for N, the model determines the amount of energy that is actually used by each allocation stage. Again, a simplifying assumption in the model is that the animal's

protein reserves cannot be catabolized to support the deposition of body fat.

The first source of energy used to meet the requirements of each non-deposition allocation stage is any energy available from protein reserves catabolized in order to meet the N requirements of higher priority allocation stages that same day.

$$\text{EUPRORE}_{a,d} = \text{Minimum} \{ (\text{ER}_{a,d} / \text{KEPRO}_a), \text{EAPRORE}_{a,d} \} \quad (157)$$

where:

$\text{EUPRORE}_{a,d}$ = daily energy used for allocation stage a on day d , from protein reserves mobilized, but not used, in order to meet the nitrogen requirements of higher priority allocation stages the same day ($\text{kJ} \cdot \text{day}^{-1}$)

$\text{ER}_{a,d}$ = daily energy requirement for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

KEPRO_a = efficiency in use of energy derived from catabolizing body protein directed towards allocation stage a

$\text{EAPRORE}_{a,d}$ = daily energy available for allocation stage a on day d , as a result of protein reserves catabolized, but not used, in order to meet the nitrogen requirements of higher priority allocation stages the same day ($\text{kJ} \cdot \text{day}^{-1}$)

The next source of energy used by each non-deposition allocation stage is that available from intake. First, the remaining energy requirement from intake, after accounting for the energy used from previously catabolized protein reserves, is calculated:

$$\text{ERINT}_{a,d} = \text{ER}_{a,d} - (\text{EUPRORE}_{a,d} \cdot \text{KEPRO}_a) \quad (158)$$

where:

$\text{ERINT}_{a,d}$ = daily energy requirement from intake for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$\text{ER}_{a,d}$ = daily energy requirement for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$\text{EUPRORE}_{a,d}$ = daily energy used for allocation stage a on day d , from protein reserves mobilized, but not used, in order to meet the nitrogen requirements of higher priority allocation stages the same day ($\text{kJ} \cdot \text{day}^{-1}$)

KEPRO_a = efficiency in use of energy derived from catabolizing body protein and directed towards allocation stage a

Next energy used from intake is calculated:

$$EUINT_{a,d} = \text{Minimum} \{ (ERINT_{a,d} / KEINT_a), EAINT_{a,d} \} \quad (159)$$

where:

$EUINT_{a,d}$ = daily energy used from intake for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$ERINT_{a,d}$ = daily energy requirement for intake for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$KEINT_a$ = efficiency in use of energy derived from intake and directed towards allocation stage a

$EAINT_{a,d}$ = daily energy available from intake for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

The next source of energy used by each non-deposition allocation stage is any energy available from body fat reserves. First, the remaining energy requirement from body fat reserves, after accounting for the energy used from intake, is calculated:

$$ERFAT_{a,d} = ERINT_{a,d} - (EUINT_{a,d} \cdot KEINT_a) \quad (160)$$

where:

$ERFAT_{a,d}$ = daily energy requirement from newly catabolized fat reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$ERINT_{a,d}$ = daily energy requirement from newly catabolized fat reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$EUINT_{a,d}$ = daily energy used from newly catabolized fat reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$KEINT_a$ = efficiency in use of energy derived from catabolizing body fat and directed towards allocation stage a

$$EUFAT_{a,d} = \text{Minimum} \{ ((ERFAT_{a,d} / KEFAT_a), EAFAT_{a,d}) \} \quad (161)$$

where:

$EUFAT_{a,d}$ = energy available from fat reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$ERFAT_{a,d}$ = daily energy requirement from intake for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$KEFAT_a$ = efficiency in use of energy derived from intake and directed towards allocation stage a

$EAFAT_{a,d}$ = daily energy used from intake for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

The last source of energy used by each non-deposition allocation stage is any energy available from body protein reserves. First the remaining energy requirement from body protein reserves, after accounting for the energy used from fat reserves, is calculated:

$$\text{ERPRO}_{a,d} = \text{ERFAT}_{a,d} - (\text{EUFAT}_{a,d} \cdot \text{KEFAT}_a) \quad (162)$$

where:

- $\text{ERPRO}_{a,d}$ = daily energy requirement from newly catabolized protein reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{ERFAT}_{a,d}$ = daily energy requirement from newly catabolized fat reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{EUFAT}_{a,d}$ = daily energy used from newly catabolized fat reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- KEFAT_a = efficiency in use of energy derived from catabolizing body fat directed towards allocation stage a

Next the energy used from body protein reserves is calculated:

$$\text{EUPRO}_{a,d} = \text{Minimum} \{ ((\text{ERPRO}_{a,d} / \text{KEPRO}_a), \text{EAPRO}_{a,d}) \} \quad (163)$$

where:

- $\text{EUPRO}_{a,d}$ = daily energy used from newly catabolized protein reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{ERPRO}_{a,d}$ = daily energy requirement from newly catabolized protein reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- KEPRO_a = efficiency in use of energy derived from catabolizing body protein and directed towards allocation stage a
- $\text{EAPRO}_{a,d}$ = energy available from protein reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

There are two possible sources of energy used for the fat deposition stage: energy available from protein reserves catabolized (but not used) in order to meet the nitrogen requirements of higher priority allocation stages and energy available from intake. The energy deposited to body fat reserves is thus calculated as:

$$\text{EDFAT}_{a,d} = (\text{EUPRORE}_{a,d} \cdot \text{KEPRO}_a) + (\text{EUINT}_{a,d} \cdot \text{KEINT}_a) \quad (164)$$

where:

- $\text{EDFAT}_{a,d}$ = daily energy deposited to body fat reserves for fat deposition stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- $\text{EUPRORE}_{a,d}$ = daily energy used for allocation stage a on day d , from protein reserves mobilized, but not used, in order to meet the nitrogen requirements of higher priority allocation stages the same day ($\text{kJ} \cdot \text{day}^{-1}$)
- KEPRO_a = efficiency in use of energy derived from catabolizing body protein directed towards allocation stage a
- $\text{EUINT}_{a,d}$ = daily energy used from intake for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- KEINT_a = efficiency in use of energy derived from intake and directed towards allocation stage a

The only source of energy used for protein deposition stages is available from intake:

$$\text{EDPRO}_{a,d} = \text{EUINT}_{a,d} \cdot \text{KEINT}_a \quad (165)$$

where:

$\text{EDPRO}_{a,d}$ = daily energy deposited to body protein reserves for the fat deposition stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$\text{EUINT}_{a,d}$ = daily energy used from intake for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

KEINT_a = efficiency in use of energy derived from intake and directed towards allocation stage a

Proportion of energy deposited as fat

The final calculation in the allocation of energy is to adjust the proportion of energy deposited as fat and protein each day. When running the model the user specifies a target for the proportion of the energy available, over and above the requirements of all non-deposition allocation stages, which should be deposited as fat – the remainder is deposited as protein (assuming sufficient nitrogen is also available). Based on calculations in the previous section of how much fat and protein is used and deposited each day, the model then recalculates the daily change in fat and protein weight of the animal.

Fat weight

First, the change in energy content of the fat reserves is calculated:

$$\text{EFATCHG}_d = \sum_a (\text{EDFAT}_{a,d}) - \sum_a (\text{EUFAT}_{a,d}) \quad (166)$$

where:

EFATCHG_d = daily change in the energy content of body fat reserves on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$\text{EDFAT}_{a,d}$ = daily energy deposited to body fat reserves for fat deposition stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

$\text{EUFAT}_{a,d}$ = daily energy used from fat reserves for allocation stage a on day d ($\text{kJ} \cdot \text{day}^{-1}$)

This energy content is then converted to a change in fat weight:

$$\text{WTFATCHG}_d = \text{EFATCHG}_d / (\text{ECONFAT} \cdot 1000) \quad (167)$$

where:

WTFATCHG_d = daily change in the weight of body fat reserves on day d ($\text{kg} \cdot \text{day}^{-1}$)

EFATCHG_d = daily change in the energy content of body fat reserves on day d ($\text{kJ} \cdot \text{day}^{-1}$)

ECONFAT = user-specified energy content of fat ($\text{kJ} \cdot \text{g}^{-1}$) – by default this is set to $39.3 \text{ kJ} \cdot \text{g}^{-1}$ (ARC, 1980 p3)

1000 = conversion coefficient ($\text{g} \cdot \text{kg}^{-1}$)

Finally, the fat weight of the animal is updated each day:

$$\text{WTFAT}_d = \text{WTFAT}_{d-1} + \text{WTFATCHG}_d \quad (168)$$

where:

WTFAT_d = fat weight of animal at the end of day d (kg)

WTFATCHG_d = daily change in the weight of body fat reserves on day d ($\text{kg} \cdot \text{day}^{-1}$)

Protein weight

Similarly, the change in N content of the protein reserves is calculated:

$$\text{NPROCHG}_d = \sum_a (\text{NDPRO}_{a,d}) - \sum_a (\text{NUPRO}_{a,d}) \quad (169)$$

where:

NPROCHG_d = daily change in the nitrogen content of body protein reserves on day d ($\text{g} \cdot \text{day}^{-1}$)

$\text{NDPRO}_{a,d}$ = daily nitrogen deposited to body protein reserves for protein deposition stage a on day d ($\text{g} \cdot \text{day}^{-1}$)

$\text{NUPRO}_{a,d}$ = daily nitrogen used from newly catabolized protein reserves for allocation stage a on day d ($\text{g} \cdot \text{day}^{-1}$)

This N content is then converted to a change in protein weight:

$$\text{WTPROCHG}_d = \text{NPROCHG}_d / (\text{NCONPRO} \cdot 1000) \quad (170)$$

where:

WTPROCHG_d = daily change in the weight of body protein reserves on day d ($\text{kg} \cdot \text{day}^{-1}$)

NPROCHG_d = daily change in the nitrogen content of body protein reserves on day d ($\text{g} \cdot \text{day}^{-1}$)

NCONPRO = user-specified nitrogen content of dry protein (proportion) – by default the value is 0.16 (Robbins, 1993 p17)

1000 = conversion coefficient ($\text{g} \cdot \text{kg}^{-1}$)

Finally, the protein weight of the animal is updated each day:

$$\text{WTPRO}_d = \text{WTPRO}_{d-1} + \text{WTPROCHG}_d \quad (171)$$

where:

WTPRO_d = protein weight of animal at the end of day d (kg)

WTPRO_{d-1} = protein weight of animal at the end of day $d-1$ (kg)

WTPROCHG_d = daily change in the weight of body protein reserves on day d ($\text{kg} \cdot \text{day}^{-1}$)

Additional Indicators

A number of additional indicators are calculated in the model:

Net nitrogen requirement for maintenance

The net (i.e. metabolic) N requirement for maintenance each day is calculated as:

$$\text{NRMA}_d = \text{NRBASE}_d + \text{NRCOAT}_d + \text{NRSCRF}_d + \text{NRPARA}_d \quad (172)$$

where:

- NRMA_d = net nitrogen requirement for maintenance on day d ($\text{g} \cdot \text{day}^{-1}$)
- NRBASE_d = net base nitrogen requirement on day d ($\text{g} \cdot \text{day}^{-1}$)
- NRCOAT_d = net nitrogen requirement for coat production on day d ($\text{g} \cdot \text{day}^{-1}$)
- NRSCRF_d = net nitrogen requirement for scurf production on day d ($\text{g} \cdot \text{day}^{-1}$)
- NRPARA_d = user-specified net nitrogen requirement for parasites on day d ($\text{g} \cdot \text{day}^{-1}$)

Net energy requirement for maintenance

$$\text{ERMA}_d = \text{ERBASE}_d + \text{ERCOAT}_d + \text{ERSCRF}_d + \text{ERPARA}_d \quad (173)$$

where:

- ERMA_d = net energy requirement of maintenance on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERBASE_d = net base energy requirement on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERCOAT_d = daily energy requirement for summer coat production and skin (i.e. scurf) loss on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERSCRF_d = daily energy requirement for winter scurf production on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERPARA_d = user-specified net energy requirement for parasites on day d ($\text{kJ} \cdot \text{day}^{-1}$)

Net energy requirement for a non-productive animal

The net energy requirement for maintenance and activity of a non-productive animal (excluding antler growth) is calculated as:

$$\text{ERNP}_d = \text{ERMA}_d + \text{ERACT}_d \quad (174)$$

where:

- ERNP_d = net energy requirement of a non-productive animal (excluding antlers) on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERMA_d = net energy requirement of maintenance on day d ($\text{kJ} \cdot \text{day}^{-1}$)
- ERACT_d = energy requirement of activity (including lying) on day d ($\text{kJ} \cdot \text{day}^{-1}$)

Muscle weight

$$\text{WTMUS}_d = \text{WTPRO}_d / \text{PMUSPRO} \quad (175)$$

where:

WTMUS_d = muscle weight of the animal on day d (kg)

WTPRO_d = dry protein weight of the animal on day d (kg)

PMUSPRO = user-specified proportion of muscle weight that is dry protein (unitless) – by default this is set to 0.29 (van Es 1978)

Water weight

In late winter (April-June) and if the cow is not pregnant, a water conversion mechanism proposed by Cameron *et al.* (1975; see also Fancy, 1986) is used where water replaces catabolized body fat and protein. The water is assumed to be a component of the alimentary tract and most likely the rumen (Cameron *et al.*, 1975). This mechanism is not invoked for the pregnant cow. When the non-pregnant cow catabolizes fat, the weight of fat that is replaced by water is calculated as follows:

$$\text{WTWATFAT}_d = \begin{cases} \text{Maximum } \{-\text{WTFATCHG}_d \cdot \text{PFATWAT}, 0\} & \text{if } \text{PREG}_d = 1 \\ 0 & \text{otherwise} \end{cases} \quad (176)$$

where:

WTWATFAT_d = fat weight that is replaced by water on day d (kg)

WTFATCHG_d = change in fat weight on day d (kg)

PFATWAT = user-specified proportion of fat that is replaced by water (unitless) – by default this is set to 0.18 (Farrell *et al.*, 1972)

Similarly, when protein is catabolized in the non-pregnant cow, the muscle weight that is replaced by water is calculated as:

$$\text{WTWATMUS}_d = \begin{cases} \text{Maximum } \{(-\text{WTPROCHG}_d \cdot \text{PMUSWAT} / \text{PMUSPRO}), 0\} & \text{if } \text{PREG}_d = 1 \\ 0 & \text{otherwise} \end{cases} \quad (177)$$

where:

WTWATMUS_d = muscle weight that is replaced by water on day d (kg)

WTPROCHG_d = change in protein weight on day d (kg)

PMUSWAT = user-specified proportion of muscle that is replaced by water (unitless) – by default this is set to 0.71 (van Es 1978)

PMUSPRO = user-specified proportion of muscle weight that is dry protein (unitless) – by default this is set to 0.29 (van Es 1978)

This water conversion mechanism only occurs when the animal is not pregnant. The mechanism is not implemented once the animal is depositing either fat or protein:

$$\begin{aligned}
 \text{WTWAT}_d &= \text{Maximum} \{ (\text{WTWAT}_{d-1} + \text{WTWATFAT}_d + \text{WTWATMUS}_d), \\
 &\quad (\text{PWATMAX} \cdot \text{WTBODY}_d) \} & (178) \\
 &= 0 & \text{if } \text{PREG}_d = 0 \\
 & & \text{if } \text{PREG}_d = 0 \text{ and} \\
 & & (\text{WTFATCHG}_d > 0 \text{ or} \\
 & & \text{WTPROCHG}_d > 0) \\
 &= \text{WTWAT}_{d-1} & \text{otherwise}
 \end{aligned}$$

where:

- WTWAT_d = cow water weight on Julian day d (kg)
- WTWAT_{d-1} = cow water weight on previous Julian day d (kg)
- WTWATFAT_d = fat weight that is replaced by water on day d (kg)
- WTWATMUS_d = muscle weight that is replaced by water on day d (kg)
- PWATMAX = user-specified maximum proportion of body water that is due to muscle and fat catabolism – by default this value is set to 0.15 (Cameron *et al.*, 1975)
- WTBODY_d = body weight of the animal on Julian day d (kg)

Rumen wet weight

Alimentary and rumen contents fill, measured as wet weight, can vary considerably between seasons (Reimers & Ringberg, 1983; Tyler *et al.*, 1999), with age (Adamczewski *et al.*, 1987b; Knott *et al.*, 2005; Munn & Barboza 2008) and with diet (Cameron *et al.*, 1975; Staaland *et al.*, 1979). However, wet weight of rumen-reticulum is highly correlated with alimentary fill (Reimer & Ringberg, 1983) and as a fraction of total alimentary fill it approximates 0.75 (range 0.70 - 0.85, Staaland *et al.*, 1979). Dry matter content of rumen contents also is variable and although a mean fractional dry matter of 0.166 is the default, the user can adjust the value. Hence, the model keeps track of rumen dry matter, which is updated to give rumen wet weight and total alimentary fill.

Wet weight of the rumen is calculated as:

$$\text{WTRUMWET}_d = \text{WTRUM}_d / (\text{PRUMDRY} \cdot 1000) \quad (179)$$

where:

- WTRUMWET_d = weight of wet forage in the rumen at the end of day d (kg)
- WTRUM_d = total rumen contents at the end of day d (g)
- PRUMDRY = user-specified ratio of dry to wet rumen contents (proportion) – by default this value is set to 0.166 (Staaland *et al.*, 1984)
- 1000 = coefficient for converting from kg to g ($\text{g} \cdot \text{kg}^{-1}$)

Gut content weight

Weight of the cow's gut contents is then calculated as:

$$\text{WTGUT}_d = \text{WTRUMWET}_d / \text{PRUMGUT} \quad (180)$$

where:

WTGUT_d = weight of the gut contents at the end of Julian day d (kg)
 WTRUMWET_d = weight of wet forage in the rumen at the end of Julian day d (kg)
 PRUMGUT = user-specified ratio of weight of wet rumen contents to the total gut weight (proportion) – by default this value is set to 0.75 (Staaland *et al.*, 1979).

Calf weight

Target calf growth rates are calculated from the following age specific equations relating growth to milk production (White & Luick, 1984; Parker *et al.*, 1990; White, 1992):

$$\begin{aligned} \text{TGRCALF}_d &= ((\text{TMLKPR}_d \cdot 1000) - 653) / (2.79 \cdot 1000) && \text{if } \text{DAYSLAC}_d \leq 21 \\ &= \text{TMLKPR}_d / 3.13 && \text{if } 21 < \text{DAYSLAC}_d \leq 42 \\ &= \text{TMLKPR}_d / 2 && \text{otherwise} \end{aligned} \quad (181)$$

where:

TGRCALF_d = target calf growth rate on Julian day d ($\text{kg} \cdot \text{day}^{-1}$)
 TMLKPR_d = target milk production on day d ($\text{l} \cdot \text{day}^{-1}$)
1000 = conversion coefficient ($\text{ml} \cdot \text{l}^{-1}$)
 DAYSLAC_d = age of the calf on day d (days)

This target calf growth rate is then converted into a target calf weight:

$$\text{TWTCALF}_d = \text{WTCALF}_{d-1} + \text{TGRCALF}_d \quad (182)$$

where:

TWTCALF_d = target calf weight on Julian day d (kg)
 WTCALF_{d-1} = calf weight at the end of the previous Julian day $d-1$ (kg)
 TGRCALF_d = target calf growth rate on Julian day d ($\text{kg} \cdot \text{day}^{-1}$)

Finally, the actual weight gain of the calf each day is calculated as a function of the proportion of the overall energy and N requirement for lactation met that day; note that this overall proportion is set to whichever proportion, either energy or N, is lowest.

$$\text{WTCALF}_d = \text{WTCALF}_{d-1} + (\text{TGRCALF}_d \cdot \text{PRTARLAC}_d) \quad (183)$$

where:

WTCALF_d = calf weight at the end of Julian day d (kg)

WTCALF_{d-1} = calf weight at the end of Julian day $d-1$ (kg)

TGRCALF_d = target calf growth rate on Julian day d ($\text{kg} \cdot \text{day}^{-1}$)

PRTARLAC_d = proportion of the energy/nitrogen requirement for lactation met on Julian day d

Fetus and conceptus weight

Similar to the calculation of calf weight, the weight gain of the fetus each day is calculated as a function of the proportion of the overall energy and N requirement for gestation that day:

$$\text{WTFET}_d = \text{WTFET}_{d-1} + (\text{TGRFET}_d \cdot \text{PRTARGES}_d) \quad (184)$$

where:

WTFET_d = fetus weight at the end of Julian day d (kg)

TGRFET_d = target fetus growth rate on Julian day d ($\text{kg} \cdot \text{day}^{-1}$)

PRTARGES_d = proportion of the energy/nitrogen requirement for gestation met on Julian day d

Finally, the weight of the conceptus is calculated as:

$$\text{WTCON}_d = \text{WTFET}_d / \text{PCONFET} \quad (185)$$

where:

WTCON_d = weight of the conceptus at the end of Julian day d (kg)

WTFET_d = weight of fetus at the end of Julian day d (kg)

PCONFET = user-specified proportion of conceptus that is fetus – by default this value is set to 0.55 (range is 0.21 fetal age 100 to 0.58 near term, Robbins & Moen (1975 p686))

Fat-free, ingesta-free body weight

The fat-free, ingesta-free body weight is calculated using the approach of Reimers *et al.*, (1982) for Svalbard reindeer and based on the dominance of protein as shown by Gerhart *et al.*, (1996b) for caribou of the Porcupine herd.

$$\begin{aligned} \text{WTFFIF}_d &= (4.184 \cdot \text{WTPRO}_d) + 0.343 && \text{Svalbard reindeer} \\ \text{WTFFIF}_d &= (4.065 \cdot \text{WTPRO}_d) + 1.40 && \text{Porcupine herd caribou} \end{aligned} \quad (186)$$

where:

WTFFIF_d = fat-free, ingesta-free body weight at the end of Julian day d (kg)

WTPRO_d = dry protein weight of the cow at the end of Julian day d (kg)

Body weight, empty body weight, maternal weight

These weights are then combined to estimate the total weight of the cow, the empty body weight, and the maternal weight:

$$\text{WTBODY}_d = \text{WTFFIF}_d + \text{WTFAT}_d + \text{WTGUT}_d + \text{WTWAT}_d + \text{WTCON}_d \quad (187)$$

$$\text{WTEMPY}_d = \text{WTFFIF}_d + \text{WTFAT}_d + \text{WTWAT}_d \quad (188)$$

$$\text{WTMAT}_d = \text{WTBODY}_d - \text{WTWAT}_d - \text{WTCON}_d \quad (189)$$

where:

WTBODY_d	=	body weight of the animal on Julian day d (kg)
WTFFIF_d	=	fat-free, ingesta-free body weight on Julian day d (kg)
WTFAT_d	=	fat weight of the cow on Julian day d (kg)
WTGUT_d	=	weight of the contents of the gut on Julian day d (kg)
WTWAT_d	=	cow water weight on Julian day d (kg)
WTCONC_d	=	weight of the conceptus on Julian day d (kg)
WTEMPY_d	=	empty body weight on Julian day d (kg)
WTMAT_d	=	maternal weight of the cow on Julian day d (kg)

Prediction of actual carcass and animal composition is based on the above calculations and checked against the marked linearity and interrelations of muscle, fat and bone and the amount of chemical protein and fat estimated by the model (Ringberg *et al.*, 1981a; 1981b; Reimers *et al.*, 1982; Reimers & Ringberg, 1983; Adamczewski *et al.*, 1987a; 1987b; Huot 1989; Gerhart *et al.*, 1996b).

Rumen capacity

Although weight of rumen contents varies greatly, the maximum quantity is 16 kg for a mature female caribou of 84 kg (0.25 kg per kg empty body weight, from Adamczewski *et al.*, 1987b 1151). This wet weight at 0.166 fractional dry matter gives a maximum fractional dry matter per kg empty body weight (PRCAP) of 0.041 ($0.25 \cdot 0.166$).

Thus, rumen capacity is calculated each day as:

$$\text{RCAP}_d = (\text{WTEMPY}_d - \text{WTWAT}_d) \cdot \text{PRCAP} \cdot 1000 \quad (190)$$

where:

RCAP_d	=	capacity of the rumen on Julian day d (g)
WTEMPY_d	=	empty body weight on Julian day d (kg)
NWTWAT_d	=	cow water weight on Julian day d (kg)
PRCAP	=	user-specified rumen dry matter capacity as a proportion of empty body weight (proportion) – by default this value is set to 0.041 (See above)
1000	=	coefficient for converting from kg to g ($\text{g} \cdot \text{kg}^{-1}$)

Model Applications

In this manuscript we provide the detailed description of an energy-protein model for caribou. In large part the model was derived from data collected while the first two authors were conducting research on the Porcupine Caribou Herd. As the model progressed and as there was a need to expand the application of the model to herds across the circumpolar north, data from other herds were assembled and applied to specific projects. Concurrent with these applications, new research, insights and the need for more detail (e.g. the incorporation of the protein dynamics) resulted in examples of model applications that do not reflect the current model description. Although we realize typically modeling publications confine applications to the model described in the manuscript, we think it is instructive to provide an accounting of model applications, even in its earlier versions.

In their monograph, Russell *et al.* (1993) described how the model could integrate reported activity budgets, diet, plant quantity and quality for the range of the Porcupine Caribou Herd to examine energy requirements and resultant weight and fat change under good and bad environmental conditions. As well, Russell *et al.* (1993) used the model to compare spring migration strategies of bulls versus cows. Luick *et al.* (1994) used the model to estimate the effect of low flying military jet aircraft on the productivity of the Delta Caribou Herd in central Alaska. For the George River Herd, Manseau (1996) also used the model to integrate habitat and animal data she collected to report on the energetic implications of environmental change. For the Central Arctic Herd in Alaska, Murphy *et al.* (2000) used the model to examine the implications to fall pregnancy rates under different insect harassment and development exposure near the Prudhoe Bay oilfields. A similar approach to Murphy *et al.*, (2000) was used to assess the implications from fall body weight and probability of pregnancy under variable insect harassment and exposure to proposed Diavik diamond mine infrastructure within the range of the Bathurst Caribou Herd. The Bathurst Herd was also the focus of a pilot project to assess the utility of the energetics model to incorporate results of Resource Selection Function (RSF) models on the summer range (Gunn *et al.*, 2011).

The only application of the model with the protein component incorporated was for assessing the impacts on North Baffin Caribou herd of a proposed iron mine on Baffin Island (Russell 2011). In that application, we tested scenarios with respect to potential disturbance and displacement for a 50-year time frame while the herd was recovering. Although the scenarios were considered beyond what we would predict to happen if the mine project were to proceed, we felt that it was important to test the outside bounds and compare with baseline conditions. Output of body condition variables that link directly to rates of herd productivity were used to compare scenarios. These were: 1) birth weight (calf survival), 2) late June growth rate of the calf (post-natal weaning, calf dies), 3) mid-summer protein gain of the cow (summer weaning, calf dies), late summer fat weight of the cow (early weaning, calf survival reduced, cow increases probability of pregnancy), cow weight at rut (pregnancy rate, cow overwinter survival), and calf weight at rut (normal or extended lactation, calf survival, age of first reproduction). Figure 16 provides an output example for three increasingly severe scenarios with respect to a decline in probability of pregnancy over a 50-year recovery period.

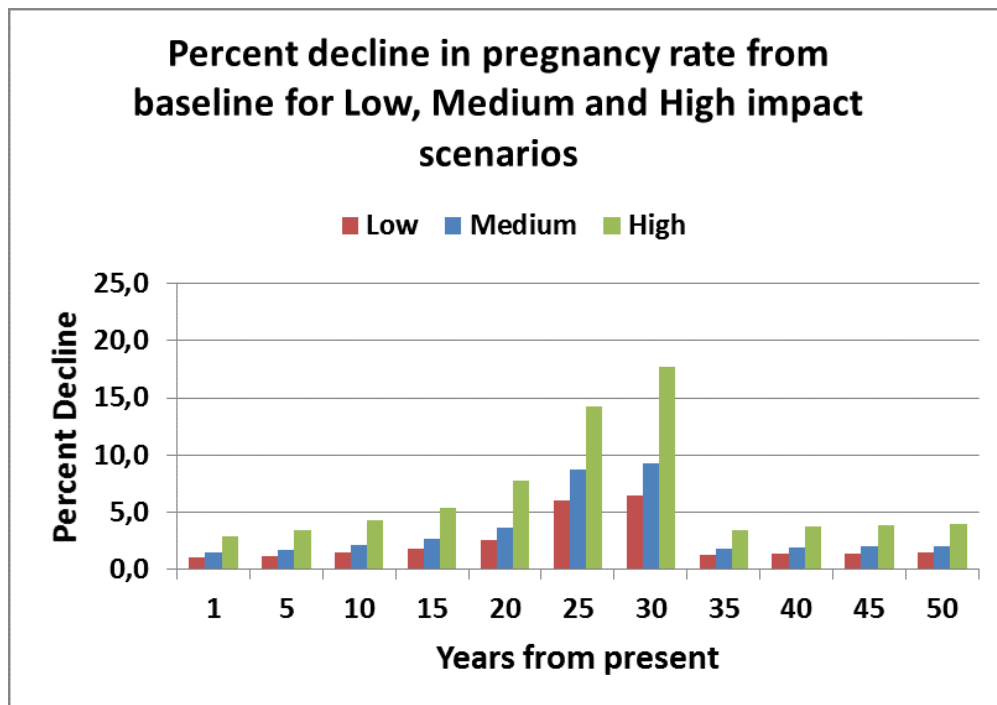


Figure 16. Potential impact of three scenarios on pregnancy rate of the North Baffin Caribou Herd, simulated over a 50-year recovery period. (Data from Russell, 2011)

Conclusions

Testing this model is an ongoing process. Components of the original energy model were assessed through sensitivity analyses (White *et al.*, 1991) that continues to date. Throughout model building an objective has been to verify sections of the model through spreadsheet models using relevant sets of algorithms and data sets that were not used to derive the algorithms. At a higher level, seasonal outputs of body weight and body composition were used to derive changes in caribou herds other than the Porcupine Caribou Herd. More widespread use of the model will likely test its universality, particularly where the user alters variables to ask questions of the model that we have not addressed. We view the model as part of a dynamic process to better understand the energy-protein relationships of *Rangifer*; we anticipate that periodic modifications in logic and perhaps algorithm expression will be necessary.

The model described is complex which has its advantages and disadvantages. The most obvious disadvantage is the data requirements needed to run the model. However, complexity allows the user to ask more detailed “what if” questions. Many factors influence the annual energy and protein balance and the productivity of individual *Rangifer*. Simulation of energy and protein in separate but integrated pathways allows the user to ask questions about the relative importance of plant quality and biomass availability in seasonal, regional and long-term trends in variability of the food base. Heretofore models have addressed only energy implications for analysis of population responses. As we have outlined in the body of this report protein status and the recognition of

a mobilizable protein reserve adds a new dimension to simulation modeling. The model allows the proposal and testing of evolutionary strategies (Sibley *et al.*, 2012) such as the extent of plasticity and the trade-offs between reproduction and survival.

A limitation of the model is that it does not simulate the mineral balance and metabolism of the individual. Given the recognized role of sodium, calcium, phosphorus and copper as regulated components of metabolism (Hove *et al.*, 1986; Moen & Pastor 1998; Barboza *et al.*, 2009) and the ability of individuals to respond in deficiency situations, the user of the model must be aware of this set of limitations. Given the model generates diet and intake on a dry matter basis, the user can formulate an intake analysis outside the model simulation, which could be used to test if a mineral becomes limiting.

Currently we have modified the model structure to allow up to 1000 animals to be run through the model concurrently under the same scenario. This modification will enable the user to examine the implications of a scenario for a cross section of the population, which may represent an array of body weights, ages, and reproductive histories. An obvious advantage of multi-animal simulations is the ability to summarize results, with mean and variance, to be utilized in a population model. This approach has been applied in the latest assessment (i.e. Russell, 2011) of the effects of a proposed iron ore mine on the North Baffin Caribou Herd, although a report on that application isn't public as of the writing of this document.

Although still untested, the model now allows the user to simulate an animal for up to 10 years. Users therefore may wish to compare model outputs for time periods when their herds were increasing or declining or to compare decades, or simply explore the implications of a series of good or bad years that may provide a better understanding of, for example, breeding pauses (Cameron 1994).

Assembling data sets to drive the model has been done for most Arctic herds in North America and a few in Russia. This process was facilitated through the CircumArctic Rangifer Monitoring and Assessment (CARMA) program and is discussed by Russell *et al.* (2013). In addition, a population dynamics model that uses local population demography has been developed to link with the energy-protein model and will be the subject of a future manuscript. Thus, the user has the ability to ask questions at the population level, the region level and in relation to trends in climate and human activity. This paper addresses for the reader and potential user, how and why the model was structured in this highly mechanistic framework, and how it facilitates many levels of questioning.

Acknowledgements

This current document has built upon earlier technical reports describing the initial computer simulation models for the Porcupine Caribou Herd. The energetics model description in this report is based upon previous model documentation originally provided in Kremsater *et al.* (1989) and Hovey *et al.* (1989). The authors wish to thank Dr. Fred Bunnell, UBC, for guiding the group through those initial workshops. At those workshops a number of researchers and managers helped to conceptualize the structure of the model. Among those were Art Martell, Steve Fancy, Ray Cameron, Ken Whitten, Rick Farnell and David Klein. As well, this write-up builds on the Canadian Wildlife Service technical report (Russell *et al.*, 2005) that described the second version of the model, especially equations used in the energy portion of the model. In addition, attendees at the annual CARMA Network included community members, biologists

and managers, provided feedback and ideas. Many attendees reviewed stages of the model as energy and protein became integrated. To make comparisons of herds possible, a free- exchange between circum-polar groups at the CARMA workshops improved monitoring of data that became available for accessing local trends that drive modeling runs. Feedback from participants was used to modify the capabilities of the model. We particularly recognize the special input from our colleagues Perry Barboza, Ray Cameron, Christine Cuyler, Brad Griffith, Anne Gunn, Gary Kofinas, Susan Kutz, Craig Nicholson, Kathy Parker, and Don Spalinger. We acknowledge critical input from Dr. Anne Gunn and two anonymous reviewers that improved a previous version of the manuscript.

The modeling project was initially funded by Environment Canada (Canadian Wildlife Service) and the Canadian Department of Indian and Northern Affairs, Canada. Subsequently, funding has been provided by Environment Canada, U. S. Man and the Biosphere Program (High Latitude Directorate), the Canadian Climate Change Action Fund, and the U. S. National Science Foundation ("Sustainability of Arctic Communities" project). The Canadian International Polar Program provided funding to develop the protein section of the model and thus played a major role in this current document. Developments and refinements of the model were also funded by the Porcupine Caribou Management Board. Finally, credit is given to the Minerals and Metals Group (MMG, Ltd) through Environmental Dynamics Inc. (EDI) who provided funding to help with final push to ensure this manuscript was completed, and to Environment Canada who covered the publication costs.

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Appendix 1

Variable name is associated with current value in model together with its unit and description.

Variable Name	Current Value (Read-only)	Units	Description
DEBY	20	kJ/g	Digestible energy associated with bypass
DECC	20	kJ/g	Digestible energy associated with cell content
DECW	13	kJ/g	Digestible energy associated with cell wall
EANTLCO	18	kJ / (kg ^{0.75} - day)	Coefficient converting body weight to daily energy requirement for antler production
EBMRCO	293	kJ / (kg ^{0.75} - day)	Coefficient for calculating basal metabolic rate
ECONCOAT	0		[Not used?]
ECONFAT	37.7	kJ/g	Energy content of fat
ECONFI	20.5	kJ/g	Gross energy content of forage intake
ECONPRO	23.6	kJ/g	Energy content of protein
ENDAYAN	244	Julian Day	End day of the period during which antler production occurs
ENDAYCT	244	Julian Day	End day of the period during which coat production occurs
ENDAYGES	153	Julian Day	End day of gestation period
ENDAYLAC	287	Julian Day	End day of lactation period
ENDAYSC	152	Julian Day	End day of the period during which winter scurf production occurs
ENDAYSUM	212	Julian Day	End day of the period during which summer protein gain occurs
ESCRFCO	50.2		[Not used?]
FATMOBRT	250	g/day	Rate at which fat can be mobilized
HREEAT	1.88	kJ/(kg-h)	Hourly net energy requirement of eating
HRELIE	0	kJ/(kg-h)	Hourly net energy requirement of lying
HREPAW	4	kJ/(kg-h)	Hourly net energy requirement of pawing
HRERUN	15.36	kJ/(kg-h)	Hourly net energy requirement of running
HRESTD	0.45	kJ/(kg-h)	Hourly net energy requirement of standing
HREWLK	4.22	kJ/(kg-h)	Hourly net energy requirement of walking
KPNDMIN	0.02	Propn	Minimum hourly passage rate of non-digestible material from the rumen
LACTIN	0	0/1	Specifies whether or not the animal is lactating at the start of the run (0-no, 1=yes)
LACTYR	1	0/1	Specifies whether animal lactates during the lactation period (0-no, 1=yes)

Variable Name	Current Value (Read-only)	Units	Description
MFNCO	0.2	g N / (g-day)	Coefficient converting fecal production to daily fecal nitrogen loss
NANTLCO	0.02	g N / (kg0.75- day)	Coefficient converting body weight to daily nitrogen requirement for antler production
NCOATCO	0.054	g N / (kg0.75- day)	Coefficient converting body weight to daily nitrogen requirement for coat production
NCONPRO	0.16	Propn	Nitrogen content of protein
NEUNCO	0.115	g N / (kg0.75- day)	Coefficient converting metabolic body weight to daily endogenous nitrogen
NFETCO	0.63	g N / (kg0.75- day)	Coefficient converting fetus weight to daily nitrogen requirement
NSCRFCO	0.00053	g N / (kg0.75- day)	Coefficient converting body weight to daily nitrogen requirement for winter scurf production
PBYN	0.95	Propn	Proportion of bypass nitrogen that can be absorbed
PCONFET	0.55	Propn	Proportion of the conceptus weight that is the fetus
PCONIN	0		[Not used]
PCWN	0.8	Propn	Proportion of cell wall nitrogen that can be absorbed
PDOM	0.88	Propn	Proportion of the digestible material that is dry organic matter
PDPN	0.85	Propn	Proportion of degradable protein nitrogen that can be absorbed
PFATDEP	0.4	Propn	Target proportion of energy deposited as fat
PFATIN	0.066	Propn	Proportion of body weight that is fat at the start of the run
PFATMIN	0.03	Propn	Minimum proportion of body weight that must be fat
PFATWAT	0.18	Propn	Proportion of fat that is replaced by water
PFETFAT	0.021	Propn	Proportion of the fetus weight that is fat
PMCDOM	0.035	Propn/h	Ratio of microbial nitrogen to dry organic matter in the rumen
PMCN	0.8	Propn	Proportion of microbial nitrogen that can be absorbed
PMEBY	0.9	Propn	Proportion of bypass that can be absorbed and metabolized
PMECC	0.9	Propn	Proportion of digestible energy of cell content that can be metabolized
PMECW	0.82	Propn	Proportion of digestible energy of cell wall that can be metabolized
PMUSPRO	0.29	Propn	proportion of muscle weight that is dry protein
PMUSWAT	0.71	Propn	proportion of muscle that is replaced by water

Variable Name	Current Value (Read-only)	Units	Description
PPROIN	0		[Not used]
PPROMIN	0.15	Propn	Minimum proportion of body weight that must be dry protein
PRCAP	0.045	Propn	Rumen dry matter capacity as proportion of empty body weight
PREGIN	1	0/1	Specifies whether or not the animal is pregnant at the start of the run (0-no, 1=yes)
PREGYR	1	0/1	Specifies whether animal lactates during the gestation period (0-no, 1=yes)
PROMOVRT	200	g/day	Rate at which protein can be mobilized
PRUMDRY	0.166	Unitless	Ratio of dry to wet rumen contents
PRUMGUT	0.83	Unitless	Ratio of weight of wet rumen contents to the total gut weight
PTPCWXMAX	0.055	Propn	nitrogen content where proportion of true-protein N intake in cell wall reaches a maximum
PTPCWXMIN	0.015	Propn	nitrogen content where proportion of true-protein N intake in cell wall reaches a minimum
PTPCWYMAX	0.3	Propn	maximum proportion of true-protein nitrogen intake that is cell wall
PTPCWYMIN	0.1	Propn	minimum proportion of true-protein nitrogen intake that is cell wall
PTPNDIG	0.92	g/h	true-protein nitrogen digestibility
PUPN	0.95	Propn	proportion of undegradable protein nitrogen that can be absorbed
PWATIN	0		[Not used]
PWATMAX	0.15	Propn	[Not used]
RNCCTANX-MAX	0.7	Propn	BSA level where reduction in cell contents N digestibility is maximum due to tannins
RNCCTANX-MIN	0.006	Propn	BSA level where reduction in cell contents N digestibility is minimum due to tannins
RNCCTANY-MAX	0.013	Propn	Maximum reduction in nitrogen digestibility of cell content due to tannins
RNCCTANY-MIN	0	Propn	Minimum reduction in nitrogen digestibility of cell content due to tannins
SDPROP	0.75	Propn	Proportion of snow depth to which cow sinks
STDAYAN	153	Julian Day	Start day of the period during which antler production occurs
STDAYCT	153	Julian Day	Start day of the period during which coat production occurs
STDAYGES	283	Julian Day	Start day of gestation period
STDAYLAC	154	Julian Day	Start day of lactation period

Variable Name	Current Value (Read-only)	Units	Description
STDAYSC	245	Julian Day	Start day of the period during which winter scurf production occurs
STDAYSUM	182	Julian Day	Start day of the period during which summer protein gain occurs
WTBODYIN	90	kg	Body weight of animal at the start of the run
WTTBIR	6.13	kg	Target birth weight

