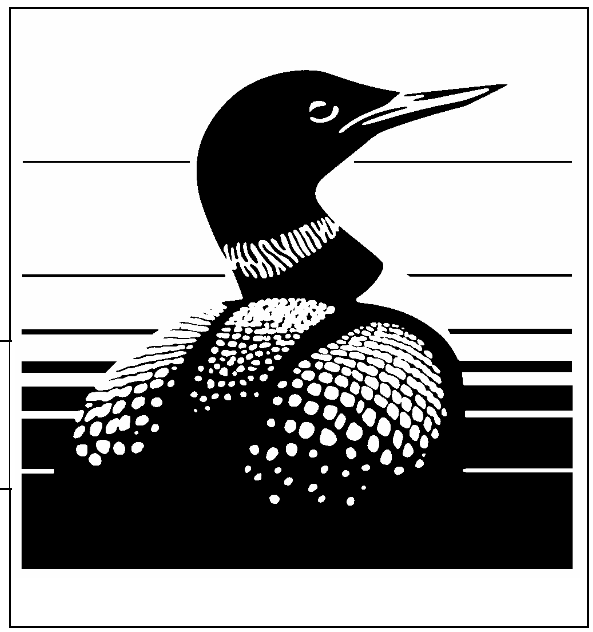
Energetics of the Porcupine Caribou Herd: A Computer Simulation Model

D. E. Russell, R. G. White and C. J. Daniel

Pacific and Yukon Region 2005

Canadian Wildlife Service

Environmental Conservation Branch



Technical Report Series Number 431

Environment Canada
Environnement Canada

Canadian Wildlife Service
Service canadien de la faune

Canada

TECHNICAL REPORT SERIES

CANADIAN WILDLIFE SERVICE

This series of reports, established in 1986, contains technical and scientific information from projects of the Canadian Wildlife Service. The reports are intended to make available material that either is of interest to a limited audience or is too extensive to be accommodated in scientific journals or in existing CWS series.

Demand for these Technical Reports is usually confined to specialists in the fields concerned. Consequently, they are produced regionally and in small quantities; they can be obtained only from the address given on the back of the title page. However, they are numbered nationally. The recommended citation appears on the title page.

Technical Reports are available in CWS libraries and are listed in the catalogue of the National Library of Canada in scientific libraries across Canada. They are printed in the official language chosen by the author to meet the language preference of the likely audience, with a résumé in the second official language. **To determine whether there is significant demand for making the reports available in the second official language, CWS invites users to specify their official language preference. Requests for Technical Reports in the second official language should be sent to the address on the back of the title page.**

SÉRIE DE RAPPORTS TECHNIQUES DU SERVICE CANADIEN

DE LA FAUNE

Cette série de rapports donnant des informations scientifiques et techniques sur les projets du Service canadien de la faune (SCF) a démarré en 1986. L'objet de ces rapports est de promouvoir la diffusion d'études s'adressant à un public restreint ou trop volumineuses pour paraître dans une revue scientifique ou l'une des séries du SCF.

Ordinairement, seuls les spécialistes des sujets traités demandent ces rapports techniques. Ces documents ne sont donc produits qu'à l'échelon régional et en quantités limitées; ils ne peuvent être obtenus qu'à l'adresse figurant au dos de la page titre. Cependant, leur numérotage est effectué à l'échelle nationale. La citation recommandée apparaît à la page titre.

Ces rapports se trouvent dans les bibliothèques du SCF et figurent aussi dans la liste de la Bibliothèque nationale du Canada utilisée dans les principales bibliothèques scientifiques du Canada. Ils sont publiés dans la langue officielle choisie par l'auteur en fonction du public visé, avec un résumé dans la deuxième langue officielle. **En vue de déterminer si la demande est suffisamment importante pour produire ces rapports dans la deuxième langue officielle, le SCF invite les usagers à lui indiquer leur langue officielle préferée. Il faut envoyer les demandes de rapports techniques dans la deuxième langue officielle à l'adresse indiquée au verso de la page titre.**

Energetics of the Porcupine Caribou Herd: A Computer Simulation Model

D. E. Russell[1], R. G. White[2], and C. J. Daniel[3]

[1] Canadian Wildlife Service, Pacific and Yukon Region, 91780 Alaska Hwy, Whitehorse, YT Y1A 5B7
[2] Institute of Arctic Biology, University of Alaska, Fairbanks, Fairbanks, AK 99775 USA
[3] ESSA Technologies, Suite 300, 222 Somerset Street West, Ottawa, ON K2P 2G3

Technical Report Series No. 431
Pacific and Yukon Region 2005
Canadian Wildlife Service

Issued under the Authority of the
Minister of the Environment
Canadian Wildlife Service

Catalogue No. CW69-5/431E
ISBN 0-662-39676-6

This report may be cited as:

D.E. Russell, R.G. White and C. J. Daniel. 2005. Porcupine Caribou Herd Energetics: A Computer Simulation Model. Technical Report Series No. 431. Canadian Wildlife Service, Ottawa, Ontario, 64 pp.

ABSTRACT

The Porcupine caribou herd has been the focus of considerable research over the last three decades, spurred on by potential large-scale developments within the international range of the herd. The interest in the herd and depth of knowledge gained enabled researchers to initiate energetics modeling to address the “what if” questions regarding impacts of development and climate change. This report details the structure of the model developed over the last 15 years.

The energetics model predicts the daily growth of a caribou cow and her calf as a function of activity budgets, forage quality, and forage quantity. The energetics model consists of two sub-models. The first is the energy sub-model, which predicts daily changes in a cow's metabolizable energy intake (MEI) by calculating the cow's food intake and then simulating the functioning of the cow's rumen and her digestive kinetics on an hourly basis. The MEI predicted by the energy sub-model is then fed into a growth sub-model, which calculates the cow's energy balance and the subsequent change in weight of both the cow and her calf on a daily basis based on the differential allocation of energy to gestation, lactation, and deposition and/or depletion of fat and protein reserves.

RÉSUMÉ

La possibilité de développement industriel à grande échelle dans l’aire de répartition de caribous de la Porcupine a abouti à la recherche scientifique de ce troupeau pendant trois décennies. Les connaissances fournies par ces études ont initié un programme d’informatique qui adresse les questions des effets de développement et des changements climatiques sur le bilan énergique de caribous. Ce rapport précise le développement du programme au cours des 15 années précédentes.

« Le programme énergétique » prédit la croissance quotidienne d’une femelle caribou et son faon dans le cadre des bilans d’activités, de la qualité et la quantité de fourrage. Le programme énergétique comprend deux parties : la première, « le modèle énergique », prédit les changements quotidiens de l’ingestion de l’énergie métabolisable (IEM) en calculant l’ingestion de nourriture par la femelle et en simulant ensuite la fonction du rumen de la femelle et la cinétique digestive horaire. L’IEM prédite par le modèle énergique est utilisée dans « le modèle de croissance » qui calcule le bilan d’énergie et donc les changements de poids et de la femelle et de son faon. Ce calcul est exécuté quotidiennement et est basé sur la répartition différentielle de l’énergie à la gestation, la lactation, le dépôt et/ou l’épuisement des réserves de protéines et de graisse.

ACKNOWLEDGEMENTS

The model as presented in this report culminates a 20 year development period during which time many changes have been made with sections added to reflect new research findings. We do not view the development of this model as final but at some point it is necessary to document the current state of the model. Our desire was to have the basic structure and detailed calculations in the model clearly spelt out in this document, with follow-up reports and publications providing results of gaming runs, sensitivity analysis and validation exercises.

The basis for this 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.* (1989a). 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 conceptualized the structure of the model. Among those were Art Martell, Steve Fancy, Ray Cameron, Ken Whitten and Rick Farnell. Philippa McNeil took the report to the final stages for publication.

The modelling project was initially funded by Environment Canada (Canadian Wildlife Service) and the Canadian Department of Indian and Northern Affairs. Subsequent 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), and Canada's Northern Ecosystem Initiative.

TABLE OF CONTENTS

LIST OF FIGURES

1.0 INTRODUCTION

The Porcupine caribou herd is a herd of Grant's caribou (*Rangifer tarandus granti)* that migrates from wintering grounds south of treeline to tundra calving and summer ranges in northwestern Yukon and northeastern Alaska (Figure 1). Because the area also contains potential hydrocarbon resources, the region has received a lot of attention from industry, government, native organizations and special interest groups. As a result beginning in the early 1970s the herd and its range have been the subject of a number of research and monitoring studies and is now probably the most studied *Rangifer* herd in the world (Russell *et al.* 2000).

Since 1970 the research has progressively focused on:

- distribution and movements (Russell *et al.* 1992a)
- range conditions — vegetation, snow, insects (Russell *et al.* 1992b; Russell *et al.* 1993; Cameron *et al.* 2002)
- population monitoring and productivity (Cameron 1994; Fancy *et al.* 1994; Walsh *et al.* 1995)
- energetic relations - diet, activity (Luick and White 1983, 1985; Duquette 1984; Fancy and White 1985a,b, 1987; Allaye-Chan *et al.* 1990; Russell *et al.* 1993;)
- energetic relations – lactation, calf growth (White and Luick 1984; Parker *et al.* 1990; White 1992; Chan-McLeod *et al.* 1994; White *et al.* 2000)
- assessment of body condition (Allaye-Chan 1991; Chan-McLeod *et al.* 1995, 1999; Gerhart *et al.* 1996b; Kofinas *et al.* 2002)
- linkage between body condition, energetics, and range (Russell *et al.* 1993; Gerhart *et al.* 1996a)
- energy allocation and weaning strategies (Russell *et al.* 1991, 2000; Russell and White 2000)
- linkage between population parameters and body condition (Gerhart *et al.* 1996a,b; Gerhart *et al.* 1997; Russell *et al.* 1998)
- assessing characteristics of calving grounds and linking population performance to climate/range (Russell *et al.* 1993; Griffith *et al.* 2001a, 2002; Cameron *et al.* 2002, 2005; Russell *et al.* 2002).

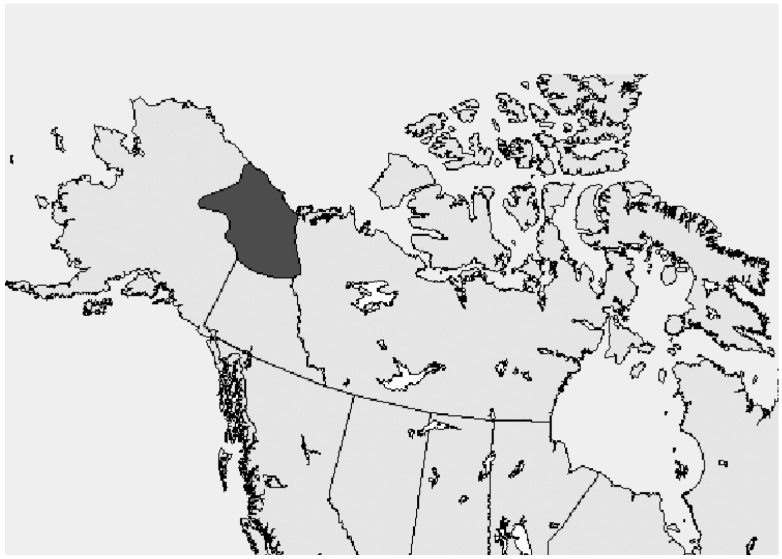


FIGURE 1: RANGE OF THE PORCUPINE CARIBOU HERD IN NORTH AMERICA

Because of increasing attention to the range of the herd by industry, and the amount of research that had been conducted, the Porcupine Caribou Technical Committee requested that scientists involved in research and management of the Porcupine Caribou Herd (PCH) develop computer simulation models to “aid in evaluating present data, help guide future research, and provide some insights into the potential impact of alternate development scenarios” (Kremsater *et al.* 1989). In response to this request, researchers from the Canadian Wildlife Service, the University of Alaska Fairbanks, and the University of British Columbia initiated the development of three models:

- an energy model (Kremsater *et al.* 1989) to simulate the metabolizable energy intake (MEI) of a female caribou over 15 life cycle periods, using a simplified rumen function model and various input data (e.g., diet, biomass and nutrient content of major forage types, activity time budgets);
- a growth model (Hovey *et al.* 1989a) to evaluate effects of changing activity budgets and MEI on the energetics, reproductive status, and reproductive success of a female caribou; and
- a harvest model to simulate the demographics of the herd over several years (Hovey *et al.* 1989b).

The growth and energy models were designed to explore various questions, such as:

- what are the effects of different environmental conditions (quantity and quality of forage, activity budgets, insect harassment, winter severity) on the MEI of female caribou?
- what are the impacts of changing activity costs, maintenance costs and MEI on a cow's energy balance and growth?
- how do changes in a cow's energy balance affect the growth of her fetus during pregnancy and of her calf during lactation?

The harvest model was designed to run independently of the other two models, predicting the effects of caribou migration patterns on harvest and population dynamics of the herd.

In 1993, a second generation of these computer simulation models was developed. This work was undertaken by ESSA Technologies, in conjunction with the Canadian Wildlife Service and the University of Alaska Fairbanks. This version of the models included a number of enhancements to the original energy and growth models:

- the energy and growth models were combined into a single energetics model, so that predicted values for daily values for MEI (from the original energy model) are used to drive the growth of the cow; and
- a new population dynamics model was developed linking the fecundity and survival of the population to the weight of cows, as predicted by the energetics model. The population model is not reported here.

Finally, a third generation of the model has now been developed and is described in this report. This latest version has been further enhanced to reflect new research findings on the biology of the PCH. The model has been refined to reflect the current understanding of PCH and arctic caribou strategies for reproduction (based on Cameron 1994, Gerhart *et al.* 1996b and Russell *et al.* 1998) and weaning (based on Russell and White 2000), and their allocation of energy to gestation, lactation, and fat and protein deposition. These allocations allow rational simulation of breeding pauses reported for arctic caribou (Cameron 1994; Cameron and Ver Hoef 1994; Cameron *et al.* 2002, 2005).

In this report we present the relationships and equations that are incorporated into the energetics model structure. Validation, gaming runs, sensitivity analysis, discussion of output and generalized across-herd simulations will be reported in separate publications.

2.0 MODEL DESCRIPTION

The energetics model predicts the daily body weight and body composition change of a caribou cow, her milk production and the daily body weight change of her calf as a function of milk intake. Variables driving these outcomes include daily activity budgets, forage quality, and forage quantity. The energetics model consists of two submodels. The first is the energy submodel, which predicts daily changes in a cow's metabolizable energy intake (MEI) by calculating the cow's food intake and then simulating the functioning of the cow's rumen and her digestive kinetics on an hourly basis. The MEI predicted by the energy submodel is then transferred to a growth submodel, which calculates the cow's energy expenditure, her energy balance, and the subsequent daily change in her weight, milk production and hence the daily change in the weight of her calf.

The energy submodel asks the question: how do changes in activity budgets, forage quality, and forage quantity affect the energy intake of a female caribou? In particular, it is designed to predict effects of environmental conditions on metabolizable energy intake (MEI). Specific objectives of the energy submodel are:

- to show effects of environmental conditions and movement patterns (as reflected by changes in activity budgets, forage quality, and forage quantity) on MEI;
- to evaluate effects of human and natural disturbance (e.g., oil development, insect harassment) on MEI; and
- to evaluate winter severity (as reflected by snow depth) on MEI.

The broad purpose of the growth submodel is to evaluate effects of changes in seasonal activity budgets and metabolizable energy intake (MEI) on the energetic and reproductive status of a female caribou.

The growth submodel has two specific objectives:

- to evaluate the impact of changing activity costs, maintenance costs, and MEI on the cow's energy balance and subsequent change in body composition and growth; and
- to evaluate effects of the cow's energy balance on the growth of her fetus during pregnancy and of her calf during lactation.

Figure 2 provides an overview of the energetics model structure, and the relationship between the energy and growth submodels.

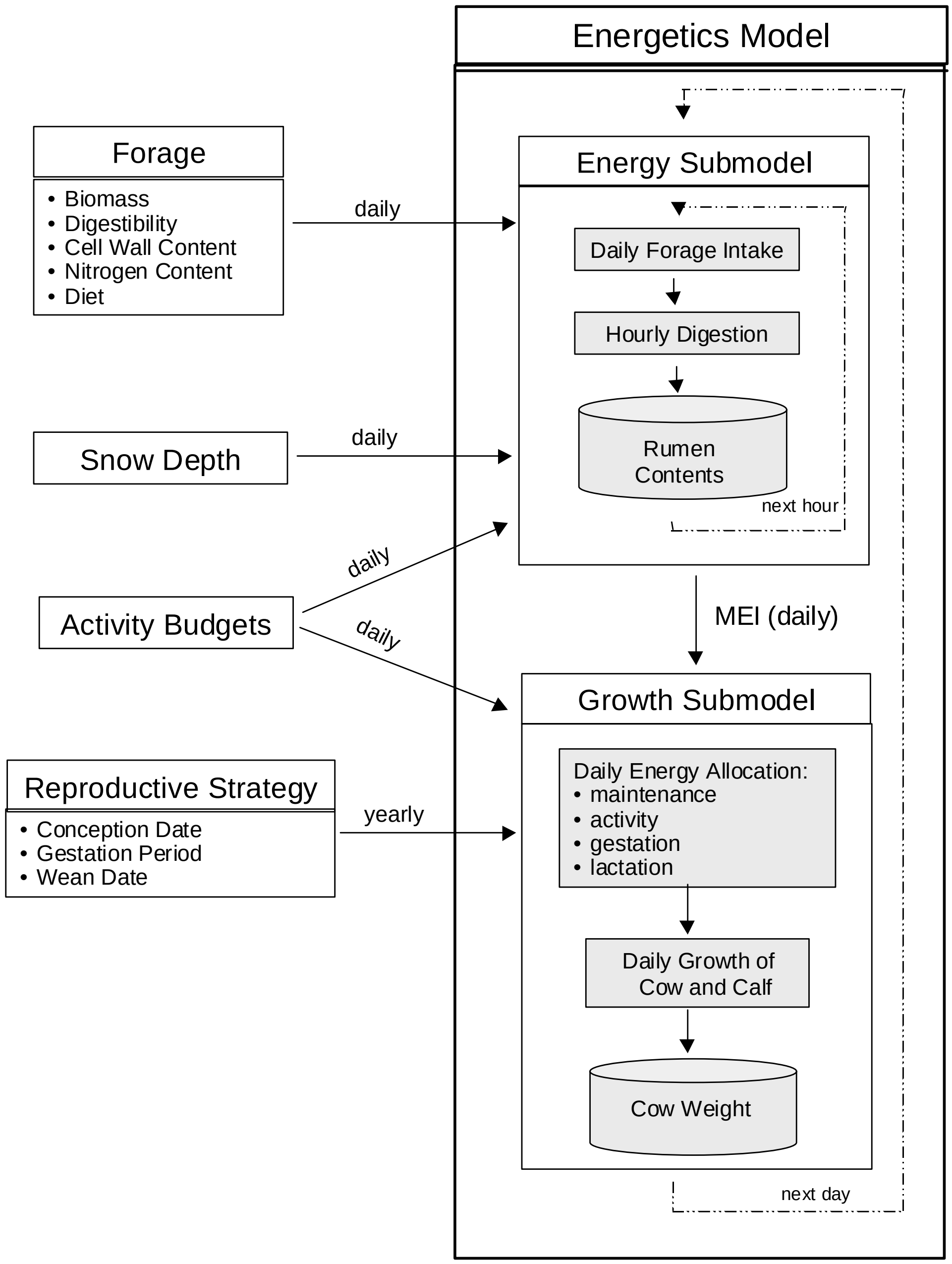


FIGURE 2: STRUCTURE OF THE ENERGETICS MODEL

2.1 ENERGY SUBMODEL

The energy submodel operates on an hourly timestep, although the inputs and outputs of the submodel are specified on a daily basis. The energy submodel has two major parts: first it calculates forage intake in specific environments; it then simulates the functioning of the rumen of a female caribou and her digestive kinetics to predict metabolizable energy from forage intake.

Calculating forage intake, the model's first step, requires specification of the environment in which the caribou cow is feeding. This environment is characterized empirically according to the temporal pattern of biomass availability for various plant types at different locations, the quality of this biomass (specified as digestibility, cell wall and nitrogen content), and the diet of the caribou cow. Empirical activity budgets are also used to estimate the time spent feeding each day.

Forage intake in each environment is governed by three broad constraints:

- availability of forage and time available for the caribou to ingest that forage (logistic constraint);
- capacity of the rumen (rumen constraint); and
- energy needs of the caribou (metabolic constraint).

In the model, four simple logistic factors determine the maximum amount of forage a caribou can ingest: available biomass of each forage group, proportion of the diet made up by each forage group, the rate at which the caribou encounters each forage group, and time spent eating.

Rumen capacity may limit forage intake below the intake determined by logistic factors. For example, a caribou foraging on poorly digestible forage may fill its rumen so that it cannot ingest more forage until digestion has reduced forage in the rumen.

Energy needs of the caribou are calculated daily by the growth submodel from empirical daily activity budgets and snow depth estimates, with an allowance for maximum growth and fattening. If the caribou meets its maximum energy requirement while foraging, then it does not ingest any more forage.

The model begins by calculating the logistic constraint and compares this intake with those intakes calculated by the other two constraints. The model assumes intake is governed by the logistic constraint unless overridden by one of the other two constraints. Food intake calculated using the logistic constraint is digested to determine rumen fill and energy intake. Rumen fill is then compared to rumen capacity to determine if food intake should be limited by rumen capacity. Energy intake is compared to energy requirements to see if food intake should be limited by the metabolic constraint. For the metabolic constraint to operate, food intake under the logistic constraint must yield more energy than the caribou needs. The minimum constraint, whether logistic, rumen capacity or metabolic, is specified as forage intake.

Because factors controlling the logistic constraint operate on a daily basis, the logistic constraint is calculated daily. To accommodate for different rates of digestion and passage, the model calculates the rumen capacity and metabolic constraints on food intake on an hourly basis (*sensu* Hudson and White 1985).

During the second step of the model, forage intake specified by the minimum constraint is digested to determine MEI.

Activity budgets

Activity budgets are set empirically for every day of a model run. They are estimated as proportions (0-1) of time spent each day at five activities: foraging, lying, standing, walking and running. When caribou are foraging in winter, not all of the time spent foraging is spent actually consuming food. Often, the caribou must paw through snow to uncover forage buried beneath. The model accounts for time spent pawing and eating while foraging by separating the foraging activity into two components: 1) eating intensity, which is the proportion of the foraging period spent consuming food, and 2) pawing intensity, which is the proportion of the foraging period spent cratering for forage.

To generate forage intake, the model uses the product of foraging time and eating intensity from the activity budget data to estimate the time spent eating each day.

Forage characteristics

Diets are set empirically for every day of a model run, with dietary components estimated as proportions (0-1) of up to 10 different plant groups. For example, the plant groups used for the PCH model runs included: moss, lichens, mushrooms, horsetails, graminoids, deciduous shrubs, evergreen shrubs, forbs, standing dead material and *Eriophorum vaginatum* heads. Alternative groups could be specified for other herds.

In addition to the diet information, forage quantity and quality are also specified on a daily basis by the user for each plant group. Input variables include: total available biomass (g live green dry matter (DM).m^{-2}), dry matter digestibility (proportion), cell wall content (proportion) and nitrogen content (g.100 g^{-1} DM).

The following sections describe calculations for the energy submodel. First, equations are presented for the logistic, rumen capacity, and metabolic constraints on food intake. After the constraints are calculated, food intake is specified and digested to produce MEI.

Logistical constraint on forage intake

The first task of the model is to determine the potential forage intake and resulting MEI based solely on the logistic constraints imposed by available biomass, the rate at which the caribou finds the forage (plant encounter rates), known grazing time, and known dietary composition.

Determining biomass available and forage intake

Available forage biomass data are recorded as the mean available biomass (g DM. m^{-2}) plus two standard deviations for each habitat considered in each season. This allowance considers that caribou within a vegetative community select higher biomass microsites but still restrict biomass within the confines of that community. Available forage biomass is converted in the model from dry matter, measured as g.m^{-2}, to kg.ha^{-1} for use in equations calculating forage intake. Although a number of factors including chewing (Spalinger *et al.* 1988) and spatial factors (Spalinger and Hobbs 1992; Shipley *et al*. 1999; Hobbs *et al.* 2003) are involved in the functional foraging and eating response in ruminants, we limited the functional response to plant biomass. Available dry matter biomass influences the rate at which caribou encounter their forage (White *et al.*1975; White and Trudell 1980; Trudell and White 1981; Wickstrom *et al.* 1984).

Together, available biomass and known plant encounter rates for each forage group determine potential forage intake.

The potential amount of forage that can be ingested per minute for each forage group is calculated daily from plant encounter rates and available biomass as (see Figure 3):

$$PFIP_{p,d} = \frac{AR_p \times FB_{p,d}}{1 + \left(\frac{AR_p \times FB_{p,d}}{PCMAX_{p,d}} \right)} \qquad [1]$$

where:

- $PFIP_{p,d}$ = potential forage intake rate of plant group *p* on Julian day *d* ($g \cdot min^{-1}$)
- 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 ($m^2 \cdot min^{-1}$)
- $FB_{p,d}$ = user-specified available forage biomass for plant group *p* on Julian day *d* ($g.m^{-2}$)
- $PCMAX_{p,d}$ = user-specified maximum consumption rate for plant group *p* on Julian day *d* ($g \cdot min^{-1}$)

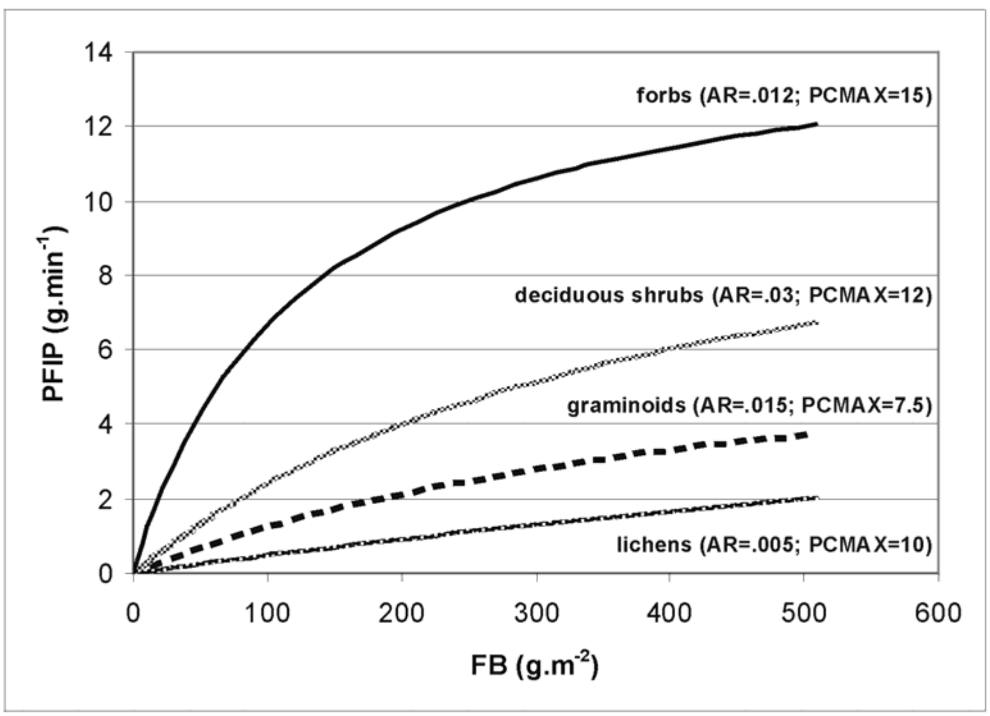


FIGURE 3: POSSIBLE RELATIONSHIPS BETWEEN POTENTIAL FORAGE INTAKE (PFIP) AND AVAILABLE FORAGE BIOMASS (FB) FOR DIFFERENT PLANT SPECIES

Actual forage intake of each forage group is constrained by the amount of time actually spent eating and the proportion of each plant group making up the daily diet. Although forage intake under the logistic constraint is calculated only once a day, forage intake is described as forage intake per hour ($g.h^{-1}$). The proportion of each day spent eating is calculated from the proportion of the day spent foraging and the eating intensity (which indicates the proportion of the foraging time actually spent eating). The proportion of the day spent eating is assigned to each hour of the day, which results in every hour of the day having the same proportion of time spent eating. Actual forage intake during each hour, as determined by logistic constraint, is calculated as:

$$FIP_{p,d} = PFIP_{p,d} \times DPDP_{p,d} \times 60 \times EATINT_d \times ACTIVEFOR_d \qquad [2]$$

where:

$FIP_{p,d}$	=	actual forage intake rate for plant group *p* on Julian day *d* ($g \cdot h^{-1}$)
$PFIP_{p,d}$	=	potential forage intake rate of plant group *p* on Julian day *d* ($g \cdot min^{-1}$)
$DPDP_{p,d}$	=	user-specified fraction of time spent eating plant group *p* on Julian day *d* (proportion) – note that this generally approximates the diet
60	=	coefficient to convert units of potential forage intake rate from $g \cdot min^{-1}$ to $g \cdot h^{-1}$
$EATINT_d$	=	user-specified proportion of foraging period spent eating on Julian day *d* (proportion)
$ACTIVEFOR_d$	=	user-specified proportion of Julian day *d* spent foraging (proportion)

Logistic constraint

Total daily forage intake over all plant groups is calculated by summing the actual forage intake of each plant group. This is the forage intake determined by the logistic constraint; it is the same for every hour of the day:

$$CONSTR2_h = \sum_p FIP_{p,d} \qquad \text{for all } h \in d \qquad [3]$$

where:

$CONSTR2_h$	=	forage ingested in hour *h*, as constrained by forage availability (g)
$FIP_{p,d}$	=	actual forage intake rate for plant group *p* on Julian day *d* ($g \cdot h^{-1}$)
h	=	hour of the model run
d	=	Julian day of the model run

Rumen constraint on forage intake

To determine if forage intake is limited by rumen capacity, the amount of fill in the rumen must be calculated every hour. The model assumes that the daily rate of forage intake can be applied to all hours of the day:

$$FIPHR_{p,h} = FIP_{p,d} \qquad \text{for all } h \in d \qquad [4]$$

where:

$FIPHR_{p,h}$	=	actual forage intake rate for plant group p in hour h ($g \cdot h^{-1}$)
$FIP_{p,d}$	=	actual forage intake rate for plant group p on Julian day d ($g \cdot h^{-1}$)
h	=	hour of the model run
d	=	Julian day of the model run

Digesting forage

Ingested forage is composed of both digestible and non-digestible material. Both components are subject to different rates of digestion and passage. To determine the digestible component of forage intake, the actual forage intake rate is multiplied by its dry matter digestibility:

$$DFI_{p,h} = FIPHR_{p,h} \times DPDIG_{p,d} \qquad \text{for all } h \in d \qquad [5]$$

where:

$DFI_{p,h}$	=	digestible forage intake for plant group p in hour h ($g \cdot h^{-1}$)
$FIPHR_{p,h}$	=	actual forage intake rate for plant group p in hour h ($g \cdot h^{-1}$)
$DPDIG_{p,d}$	=	user-specified dry matter digestibility for plant group p on Julian day d (proportion)
h	=	hour of the model run
d	=	Julian day of the model run

In the model, the digestible portion of forage intake is composed of nitrogen intake, cell content intake, and digestible cell wall intake. Partitioning digestible forage intake into cell wall, cell content, and nitrogen components allows the assumption of constant digestibilities for these components; using broad forage components is a simplification for modelling purposes (Figure 4).

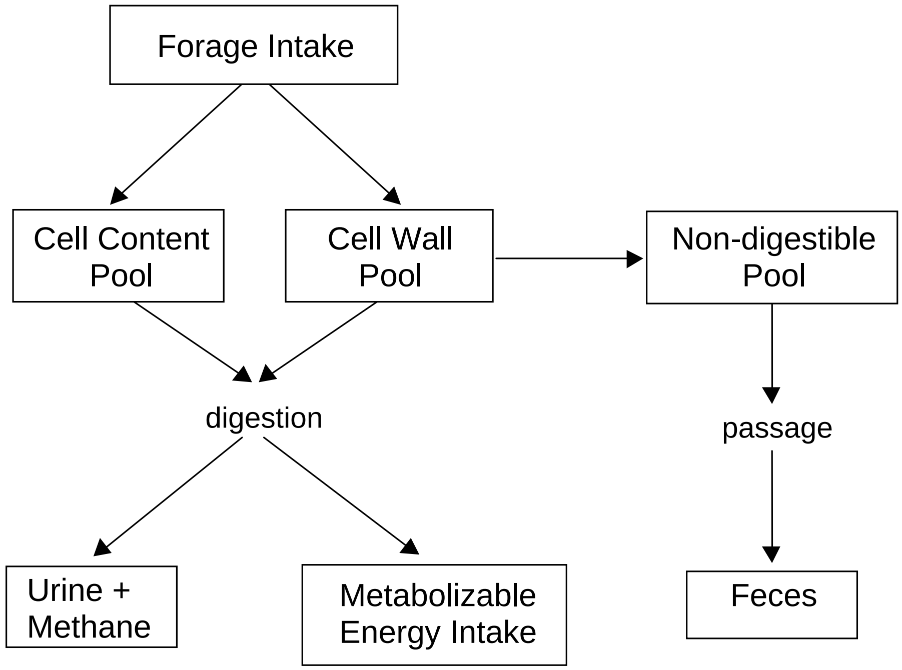


FIGURE 4: HOURLY DIGESTION OF FORAGE IN THE ENERGY SUBMODEL

An approximation of digestible nitrogen intake is determined simply from the percent nitrogen in each plant group times the digestibility of DM of the plant group. Currently the model only accumulates digestible nitrogen intake, although nitrogen could influence digestive kinetics in later versions of the model.

Digestible nitrogen intake is calculated as:

$$NIT_{p,h} = DFI_{p,h} \times \frac{DPNIT_{p,d}}{100} \qquad \text{for all } h \in d \qquad [6]$$

where:

$NIT_{p,h}$	=	digestible nitrogen intake for plant group p in hour h ($g \cdot h^{-1}$)
$DFI_{p,h}$	=	digestible forage intake for plant group p in hour h ($g \cdot h^{-1}$)
$DPNIT_{p,d}$	=	user-specified percent nitrogen content for plant group p on Julian day d ($g \cdot 100g^{-1}$)
100	=	a coefficient to convert units of nitrogen content from $g \cdot 100g^{-1}$ to $g \cdot g^{-1}$.
h	=	hour of the model run
d	=	Julian day of the model run

Digestible nitrogen intake each hour, combined over all plant groups, is then calculated as:

$$NITRO_h = \sum_p NIT_{p,h} \tag{7}$$

where:

$NIT_{p,h}$	=	digestible nitrogen intake for plant group p in hour h (g · h^{-1})
$NITRO_h$	=	rumen digestible nitrogen pool in hour h (g)

Cell content intake is calculated as:

$$\begin{aligned} CCI_{p,h} &= FIPHR_{p,h} \times \left(1 - DPCWAL_{p,d}\right) \quad \text{for all } h \in d,\ CCI_{p,h} < DFI_{p,h} \\ CCI_{p,h} &= DFI_{p,h} \quad \text{otherwise} \end{aligned} \tag{8}$$

where:

$CCI_{p,h}$	=	cell content intake for plant group p in hour h (g · h^{-1})
$FIPHR_{p,h}$	=	actual forage intake rate for plant group p in hour h (g · h^{-1})
$DPCWAL_{p,d}$	=	user-specified proportion of cell wall in plant group p on Julian day d, as calculated from neutral detergent fibre analysis (unitless)
h	=	hour of the model run
d	=	Julian day of the model run

Digestible cell wall intake is calculated as the remaining component of digestible forage intake:

$$CWI_{p,h} = DFI_{p,h} - CCI_{p,h} \tag{9}$$

where:

$CWI_{p,h}$	=	digestible cell wall intake for plant group p in hour h (g · h^{-1})
$DFI_{p,h}$	=	digestible forage intake for plant group p in hour h (g · h^{-1})
$CCI_{p,h}$	=	cell content intake for plant group p in hour h (g · h^{-1})

Digestible forage intake values are added to pools of digestible forage already existing in the rumen. After digesting forage in the rumen, the rumen pools must be reduced by the amount of each pool digested. The cell content pool is calculated as:

$$CELCON_h = \left(CELCON_{h-1} + \sum_p CCI_{p,h}\right) \times \left(1 - CCK\right) \tag{10}$$

where:

$CELCON_h$	=	rumen cell content pool in hour h (g)
$CCI_{p,h}$	=	cell content intake for plant group p in hour h (g · h^{-1})
CCK	=	user-specified digestion rate of cell contents (proportion · h^{-1})

The cell wall pool is calculated as:

$$CELWAL_h = \left(CELWAL_{h-1} + \sum_p CWI_{p,h}\right) \times (1 - CWK) \qquad [11]$$

where:

$CELWAL_h$	=	rumen cell wall pool in hour h (g)
$CWI_{p,h}$	=	digestible cell wall intake for plant group p in hour h (g • h^{-1})
CWK	=	user-specified digestion rate of cell wall (proportion • h^{-1})

Non-digestible material

The non-digestible forage intake of each plant group is calculated from the digestibility of each plant group:

$$NONDIGFI_{p,h} = FIPHR_{p,h} - DFI_{p,h} \qquad [12]$$

where:

$NONDIGFI_{p,h}$	=	non-digestible forage intake for plant group p in hour h (g • h^{-1})
$FIPHR_{p,h}$	=	actual forage intake rate for plant group p in hour h (g • h^{-1})
$DFI_{p,h}$	=	digestible forage intake for plant group p in hour h (g • h^{-1})

The hourly passage rate of non-digestible material of each plant group from the rumen is calculated each day as a function of the daily digestibility:

$$KNDIG_{p,d} = \frac{1}{50 - (50 \times DPDIG_{p,d})} \qquad [13]$$

where:

$KNDIG_{p,d}$	=	rate of passage of non-digestible material from the rumen for plant group p on Julian day d (proportion • h^{-1})
$DPDIG_{p,d}$	=	user-specified dry matter digestibility for plant group p on Julian day d (proportion)

Together, non-digestible forage intake and passage rates determine the amount of non-digestible material in the rumen for each plant group:

$$NRFP_{p,h} = (NRFP_{p,h-1} + NONDIGFI_{p,h}) \times (1 - KNDIG_{p,d}) \qquad \textit{where } h \in d \qquad [14]$$

where:

$NRFP_{p,h}$	=	non-digestible material in the rumen for plant group p in hour h (g)
$NONDIGFI_{p,h}$	=	non-digestible forage intake of plant group p in hour h (g • h^{-1})
$KNDIG_{p,d}$	=	rate of passage of non-digestible material from the rumen for plant group p on Julian day d (proportion • h^{-1})
h	=	hour of the model run
d	=	Julian day of the model run

The total non-digestible pool in the rumen, combined over all plant groups, is calculated hourly as the sum of the non-digestible rumen pools for each plant group:

$$TNRF_h = \sum_p NRFP_{p,h} \qquad [15]$$

where:

$TNRF_h$ = total non-digestible pool in hour h (g)

$NRFP_{p,h}$ = non-digestible material in the rumen for plant group p in hour h (g)

The amount of feces output is calculated as the amount of non-digestible material in the rumen multiplied by its passage rate. It is accumulated to provide a daily total and can be used to check if passage rates are reasonable:

$$FECES_d = \sum_{p,h \in d} \left(NRFP_{p,h-1} + NONDIGFI_{p,h} \right) \times KNDIG_{p,d} \qquad [16]$$

where:

$FECES_d$ = output of non-digestible material from the rumen on Julian day d (g · day^{-1})

$NRFP_{p,h}$ = non-digestible material in the rumen for plant group p in hour h (g)

$NONDIGFI_{p,h}$ = non-digestible forage intake of plant group p in hour h (g · h^{-1})

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

Calculating rumen fill

The rumen fill is calculated in three steps. Firstly, each of the individual rumen pools is constrained to be no greater than the total capacity of the rumen:

$$TNRF_h = RCAP_{d-1} \quad \text{if } TNRF_h > RCAP_{d-1} \text{ and } h \in d \qquad [17]$$

$$CELCON_h = RCAP_{d-1} \quad \text{if } CELCON_h > RCAP_{d-1} \text{ and } h \in d \qquad [18]$$

$$CELWAL_h = RCAP_{d-1} \quad \text{if } CELWAL_h > RCAP_{d-1} \text{ and } h \in d \qquad [19]$$

where:

$TNRF_h$ = total non-digestible pool in hour h (g)

$RCAP_d$ = capacity of the rumen on Julian day d (g), as calculated by the growth submodel

$CELCON_h$ = rumen cell content pool in hour h (g)

$CELWAL_h$ = rumen digestible cell wall pool in hour h (g)

h = hour of the model run

d = Julian day of the model run

Secondly, the total rumen fill is calculated as the sum of reduced pools of digestible forage and non-digestible material:

$$RFILL_h = CELCON_h + CELWAL_h + TNRF_h \qquad [20]$$

where:

$RFILL_h$	=	amount of forage in the rumen in last hour *h* of Julian day *d* (g)
$CELCON_h$	=	rumen cell content pool in hour *h* (g)
$CELWAL_h$	=	rumen digestible cell wall pool in hour *h* (g)
$TNRF_h$	=	total non-digestible pool in hour *h* (g)

Finally, the total rumen pool each hour ($RFILL_h$) is constrained to be no greater than the daily total capacity of the rumen ($RCAP_{d-1}$). If $RFILL_h > RCAP_{d-1}$, then the excess forage is removed from each of the three individual pools (i.e. $CELCON_h$, $CELWAL_h$ and $TNRF_h$) according to the initial proportions of each individual pool at the start of the model run. For example, if the cell content pool contained 20% of the forage at the start of the model run, then 20% of the excess forage would be removed from this pool.

Rumen capacity constraint on forage intake

The rumen capacity constraint on forage intake is calculated hourly as the difference between rumen capacity and rumen fill:

$$CONSTR3_h = RCAP_{d-1} - RFILL_h \qquad [21]$$

where:

$CONSTR3_h$	=	forage ingested in hour *h*, as constrained by rumen capacity (g)
$RCAP_d$	=	capacity of the rumen on Julian day *d*, as calculated by the growth submodel (g)
$RFILL_h$	=	amount of forage in the rumen in last hour *h* of Julian day *d* (g)

Metabolic constraint on forage intake

The metabolic constraint on forage intake is calculated by comparing the potential energy obtained from the caribou's diet to the caribou's maximum energy requirements (as determined by the growth submodel). If the diet supplies more energy than the caribou requires, then forage intake is limited so that it provides only as much energy as the caribou can use.

Calculating energy yield from forage intake

The first step in calculating the metabolic constraint is determining energy yield from forage intake. Every hour, digestible forage in the rumen from previous hours' foraging, combined with forage ingested in the current hour, is digested to yield energy. Forage not digested in the hour constitutes the basis of the subsequent hour's rumen pool.

Metabolizable energy from the pool of cell contents in the rumen is calculated as:

$$CCNRG_h = \left(CELCON_{h-1} + \sum_p CCI_{p,h} \right) \times CCK \times CCDPNRG \times CCMEC \qquad [22]$$

where:

$CCNRG_h$	=	energy obtained in hour *h* from cell contents (kJ · h^{-1})
$CELCON_h$	=	rumen cell content pool in hour h (g)
CCK	=	user-specified digestion rate of cell contents (proportion • h-1)
$CCI_{p,h}$	=	cell content intake for plant group *p* in hour *h* (g · h^{-1})
$CCDPNRG$	=	user-specified digestible energy associated with cell contents (kJ · g^{-1})
$CCMEC$	=	user-specified proportion of digestible energy of cell contents that can be metabolized (proportion)

Metabolizable energy obtained from the pool of cell wall material in the rumen is calculated as:

$$CWNRG_h = \left(CELWAL_{h-1} + \sum_p CWI_{p,h} \right) \times CWK \times CWDPNRG \times CWMEC \qquad [23]$$

where:

$CWNRG_h$	=	energy obtained from cell wall in hour *h* (kJ · h^{-1})
$CELWAL_h$	=	rumen digestible cell wall pool in hour *h* (g)
$CWI_{p,h}$	=	digestible cell wall intake for plant group *p* in hour *h* (g · h^{-1})
CWK	=	user-specified digestion rate of cell wall (proportion · h^{-1})
$CWDPNRG$	=	user-specified digestible energy associated with the cell wall (kJ · g^{-1})
$CWMEC$	=	user-specified proportion of digestible energy of cell wall that can be metabolized (proportion)

Total metabolizable energy intake is calculated by accumulating hourly energy obtained from cell contents and cell wall:

$$MEIHR_h = CCNRG_h + CWNRG_h \qquad [24]$$

where:

$MEIHR_h$	=	total metabolizable energy intake in hour *h* (kJ · h^{-1})
$CCNRG_h$	=	energy obtained in hour *h* from cell contents (kJ · h^{-1})
$CWNRG_h$	=	energy obtained from cell wall in hour *h* (kJ · h^{-1})

Calculating energy required to meet all costs

The second step in calculating the metabolic constraint is determining how much energy is required to meet all activity and growth costs. That required energy is calculated as:

$$HACOST_h = \frac{MAINCST_d + ACTCST_d + GESTCST_d + LACTCST_d + (MAXGROW \times 39.75)}{24} \qquad \text{for all } h \in d \qquad [25]$$

where:

$HACOST_h$	=	energy requirement of all activities in hour *h* (kJ · h^{-1})
$MAINCST_d$	=	cost of maintenance on Julian day *d* (kJ · day^{-1})
$ACTCST_d$	=	metabolizable energy requirement for all activities on Julian day *d* (kJ · day^{-1})
$GESTCST_d$	=	metabolizable energy required for gestation on Julian day *d* (kJ · day^{-1})
$LACTCST_d$	=	metabolizable energy required for lactation on Julian day *d* (kJ · day^{-1})
MAXGROW	=	maximum growth rate (g • day^{-1}) – set to 240 g • day^{-1}
39.75	=	amount of energy contained in fat (kJ • g^{-1})
24	=	hours in a day (h • day^{-1})
h	=	hour of the model run
d	=	Julian day of the model run

Calculating metabolic constraint

The energy required to meet all activity and growth costs requires a specific forage intake. That food intake, the metabolic constraint, is computed as the difference between the energy required for activities and the energy supplied by the rumen pool, divided by the amount of energy available from each gram of forage ingested.

The first step in calculating the metabolic constraint is to determine the total digestible energy obtained from the rumen pool before adding forage ingested in the current hour:

$$TER_h = (CCNRG_{h-1} \times (1 - CCK)) + (CWNRG_{h-1} \times (1 - CWK)) \qquad [26]$$

where:

TER_h	=	total metabolizable energy obtained from the rumen pool before adding forage ingested in hour *h* (kJ · h^{-1})
$CCNRG_h$	=	metabolizable energy obtained in hour *h* from cell contents (kJ · h^{-1})
CCK	=	user-specified digestion rate of cell contents (proportion · h^{-1})
$CWNRG_h$	=	metabolizable energy obtained from cell wall in hour *h* (kJ · h^{-1})
CWK	=	user-specified digestion rate of cell wall (proportion · h^{-1})

Next, the metabolizable energy yield per gram of ingested forage each hour is expressed as:

$$KJPG_h = \frac{(MEIHR_h - TER_h)}{\sum_p FIPHR_h} \qquad [27]$$

where:

$KJPG_h$	=	metabolizable energy yield per gram of ingested forage in hour *h* (kJ · g^{-1})
$MEIHR_h$	=	total metabolizable energy intake in hour *h* (kJ · h^{-1})
TER_h	=	total metabolizable energy obtained from the rumen pool before adding forage ingested in hour *h* (kJ · h^{-1})
$FIPHR_h$	=	actual forage intake rate for plant group *p* in hour *h* (g · h^{-1})

The metabolic constraint is then calculated as:

$$CONSTR1_h = Maximum\ of\ \left\{ \frac{(HACOST_h - TER_h)}{KJPG_h}, 0 \right\} \qquad [28]$$

where:

$CONSTR1_h$	=	forage ingested in hour *h*, as constrained by energetic requirements (g)
$HACOST_h$	=	(metabolizable) energy requirement of all activities in hour *h* (kJ · h^{-1})
TER_h	=	total (metabolizable) energy obtained from the rumen pool before adding forage ingested in hour *h* (kJ · h^{-1})
$KJPG_h$	=	metabolizable energy yield per gram of ingested forage in hour *h* (kJ · g^{-1})

Choosing which constraint operates on food intake

The model has now calculated three different constraints on the forage intake every hour; it compares each of the constraints and selects the smallest one. That minimum constraint, whether logistic, rumen, or metabolic, is the one that specifies forage intake.

$$FOODIN_h = \text{Minimum of } \{CONSTR1_h, CONSTR2_h, CONSTR3_h\} \qquad [29]$$

where:

$FOODIN_h$	=	actual forage intake in hour *h* (g)
$CONSTR1_h$	=	metabolic constraint - forage ingested in hour *h*, as constrained by energetic requirements (g)
$CONSTR2_h$	=	logistic constraint - forage ingested in hour *h*, as constrained by forage availability (g)
$CONSTR3_h$	=	rumen constraint - forage ingested (g) in hour *h*, as constrained by rumen capacity (g)

Actual constrained forage intake, as determined by the minimum constraint, is used to recalculate digestive kinetics and produce metabolizable energy intake.

$$FIPHRCON_{p,h} = FOODIN_h \times DPDP_{p,d} \qquad \text{for all } h \in d \tag{30}$$

where:

$FIPHRCON_{p,h}$	=	actual constrained forage intake rate for plant group p in hour h (g · h^{-1})
$FOODIN_h$	=	actual forage intake in hour h (g)
$DPDP_{p,d}$	=	user-specified fraction of time spent eating plant group p on Julian day d (proportion) – note that this generally approximates the diet
h	=	hour of the model run
d	=	Julian day of the model run

This actual constrained hourly forage intake (*FIPHRCON*) is then converted into actual constrained hourly MEI (*MEIHRCON*) by repeating the calculations of equations [5] - [20] and [22] - [24], substituting *FIPHRCON* for *FIPHR* and *MEIHRCON* for *MEIHR*. The constraint operating on food intake can change rapidly, thus constraints are allowed to change on an hourly basis in the model.

At the end of each day, hourly values for MEI and forage intake are summed:

$$MEI_d = \sum_{h \in d} MEIHRCON_h \tag{31}$$

$$FOOD_d = \sum_{h \in d} FOODIN_h \tag{32}$$

where:

MEI_d	=	metabolizable energy intake on Julian day d (kJ)
$MEIHRCON_h$	=	total constrained metabolizable energy intake in hour h (kJ · h^{-1})
$FOOD_d$	=	forage intake on Julian day d (g)
$FOODIN_h$	=	actual forage intake in hour h (g· h^{-1})

Finally, the metabolizability of gross energy intake is also calculated daily as:

$$QM_d = \frac{MEI_d}{FOOD_d \times ENEDIET} \tag{33}$$

where:

QM_d	=	metabolizability coefficient of the gross energy of diet on Julian day d (unitless)
MEI_d	=	metabolizable energy intake on Julian day d (kJ)
$FOOD_d$	=	forage intake on Julian day d (g)
$ENEDIET$	=	gross energy content of diet (Robbins 1983) (kJ · g^{-1}) — set to 20.5

2.2 GROWTH SUBMODEL

The broad purpose of the growth submodel is to evaluate the effects of daily changes in metabolizable energy intake (MEI) and seasonal activity budgets on the body weight and composition, pregnancy status and milk production of a female caribou.

The submodel has two specific objectives:

- to evaluate the impact of changing MEI (as predicted by the energy submodel), together with activity and maintenance costs, on the cow's energy balance and subsequent body weight and composition; and
- to evaluate effects of the cow's energy balance on the growth of her fetus during pregnancy, her milk production and the growth of her calf.

The growth submodel allocates MEI predicted by the energy submodel into three categories: energy requirements of maintenance and activity, energy requirements of gestation and lactation, and energy requirements of growth and fattening of the cow (Figure 5).

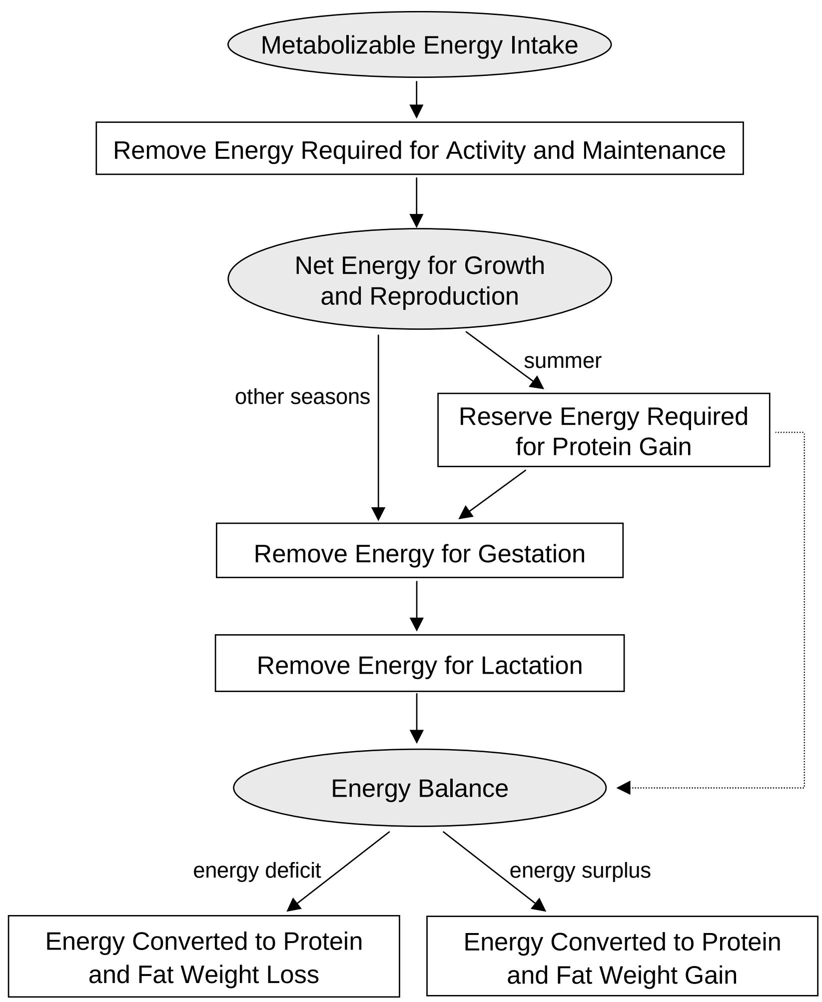


FIGURE 5: ENERGY BALANCE FOR THE GROWTH SUBMODEL

Energy requirements for maintenance are calculated from standard fasting metabolism (Kleiber 1961), adjusted for caribou in winter and summer (McEwan 1970; Fancy 1986), and scaled to metabolic body size (Kleiber 1961). The requirements for activity are derived from the cow's daily activity budget and activity costs derived from the literature (Robbins 1983, 1993), using those specifically for caribou whenever possible (White and Yousef 1978; Luick and White 1983, 1985; Fancy and White 1985a,b, 1987). The model recognizes six activities: eating, lying, standing, walking, running, and in winter, pawing (Russell *et al.* 1993). The daily cost of each activity is calculated by determining the number of hours the cow spends performing the activity multiplied by the activity's energy cost per hour. The sum of the costs of the 6 activities is the total daily activity cost.

Costs of gestation and lactation are based on a rather novel approach. The energy associated with each phase of reproduction is calculated from daily target rates of output; for gestation the output is fetus weight (Roine *et al.* 1982, see Fancy 1986; Robbins 1983) and for lactation the output is milk production (White and Luick 1984; Parker *et al.* 1990; Robbins 1983, 1993). Those rates are adjusted downwards by the cow's energy status (i.e. MEI and her fat and lean tissue reserves).

When the female has a surplus of energy, the reproductive outputs are at the target levels. However, when she does not have enough energy to meet the target demands, the output is reduced in direct proportion to the difference between what she needs for maximum production and what she actually has available (Figures 6 and 7).

Changes in the cow's body composition due to catabolism and anabolism of fat and lean tissue stores follow the methods of Fancy (1986).

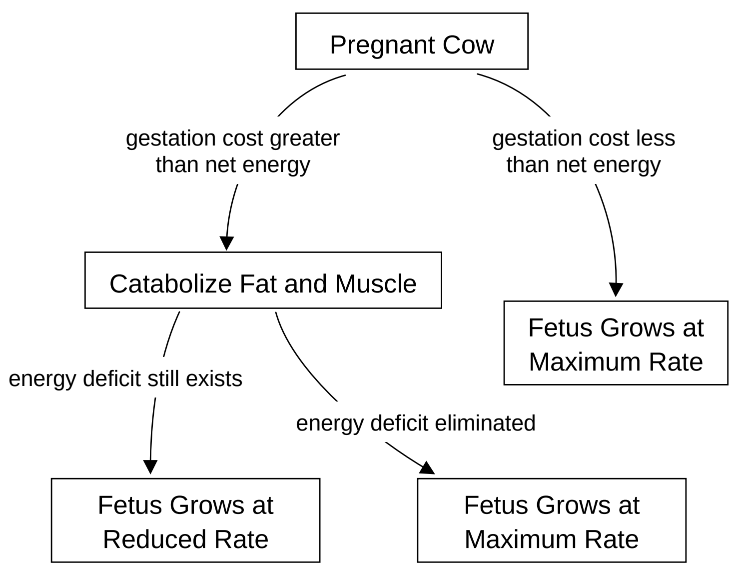


FIGURE 6: CALCULATION OF GESTATION ENERGETICS.

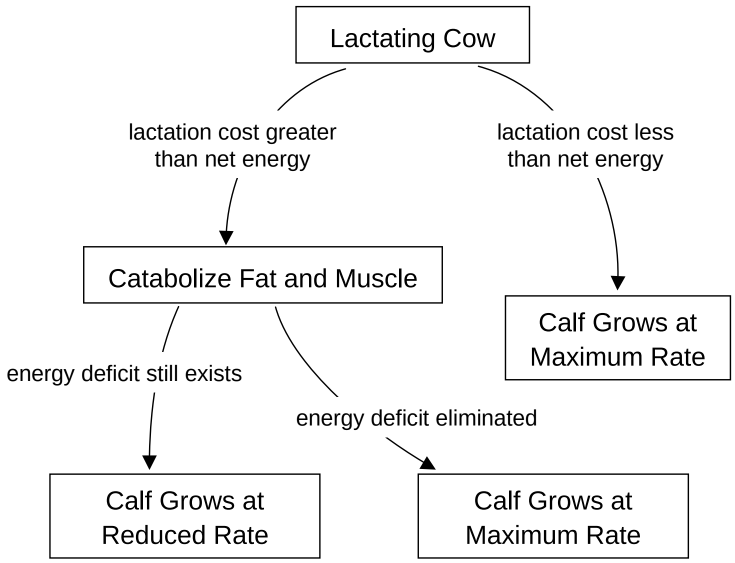


FIGURE 7: CALCULATION OF LACTATION ENERGETICS.

Calculating maintenance cost

To calculate the maintenance costs, the first step is to calculate the efficiency with which energy can be used for energy maintenance according to the following equation (ARC 1980):

$$EFMAIN_d = (0.35 \times QM_d) + 0.503 \qquad [34]$$

where:

$EFMAIN_d$	=	efficiency with which metabolizable energy can be used for energy maintenance on Julian day *d* (unitless)
QM_d	=	metabolizability coefficient of the gross energy of diet on Julian day *d* (unitless)

Next the daily heat production plus the standing cost is calculated as:

$$HP_d = 313 \times EBW_{d-1}^{0.75} \qquad [35]$$

where:

HP_d	=	heat production on Julian day *d* (kJ · day^{-1})
313	=	basal metabolic rate (kJ · kg$^{-0.75}$ · day^{-1}): calculated as 70 (kcal) × 4.187 (kJ.kcal^{-1}) plus the energy cost of standing (20 kJ · kg$^{-0.75}$ · day^{-1})
EBW_d	=	empty body weight on Julian day *d* (kg)
0.75	=	scaling of cow weight to metabolic weight

The cost of maintenance is calculated as (ARC 1980; Hudson and Christopherson 1985):

$$MAINCST_d = \frac{HP_d}{EFMAIN_d} \quad [36]$$

where:

$MAINCST_d$	=	cost of maintenance on Julian day *d* (kJ · day^{-1})
HP_d	=	heat production on Julian day *d* (kJ · day^{-1})
$EFMAIN_d$	=	efficiency with which metabolizable energy can be used for energy maintenance on Julian day *d* (unitless)

Finally, the heat increment is calculated as (ARC 1980; Fancy 1986):

$$HI_d = (1 - EFMAIN_d) \times MEI_d \quad [37]$$

where:

HI_d	=	heat increment on Julian day *d* (kJ · day^{-1})
$EFMAIN_d$	=	efficiency with which metabolizable energy can be used for energy maintenance on Julian day *d* (unitless)
MEI_d	=	metabolizable energy intake on Julian day *d* (kJ)

Calculating activity cost

The daily energy costs of activity are determined from the cow's activity budget and body weight. The activities recognized by the model include foraging, lying, standing, walking and running, with foraging further divided into eating and searching (includes “pawing” in winter). Before calculating the costs of each activity, the model calculates the snow depth and the cow's sinking depth in the snow to determine the added cost of locomotion in snow (Russell *et al.* 1993):

$$SINKDEP_d = SDPROP \times SNODEP_d \quad [38]$$

where:

$SINKDEP_d$	=	cow'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 Julian day *d* (cm)

The added cost of locomotion in snow is determined as follows (Fancy and White 1985a,b; Fancy 1986):

$$SNOWX_d = 1 + \frac{2.41623 \times e^{(0.0635 \times SINKDEP_d \times 1.587)}}{100} \quad [39]$$

where:

$SNOWX_d$	=	change in cost associated with locomotion in snow on Julian day *d* (proportion)
$SINKDEP_d$	=	cow's sinking depth in the snow on Julian day *d* (cm)
100	=	a coefficient to convert from percentage to proportion (%$^{-1}$)

The daily energy cost of each of the six recognized activities can be calculated as:

$$CSTNRGLIE_d = COSTLIE \times ACTIVELIE_d \times COWWT_d \times 24 \quad [40]$$

$$CSTNRGSTD_d = COSTSTD \times ACTIVESTD_d \times COWWT_d \times 24 \quad [41]$$

$$\begin{aligned} CSTNRGWLK_d = {} & COSTWLK \times ACTIVEWLK_d \times COWWT_d \times SNOWX_d \times 24 \\ & + COSTWLK \times ACTIVEFOR_d \times (1 - EATINT_d - PAWINT_d) \times COWWT_d \times SNOWX_d \times 24 \end{aligned} \quad [42]$$

$$CSTNRGRUN_d = COSTRUN \times ACTIVERUN_d \times COWWT_d \times SNOWX_d \times 24 \quad [43]$$

$$CSTNRGEAT_d = COSTEAT \times ACTIVEFOR_d \times EATINT_d \times COWWT_d \times 24 \quad [44]$$

$$CSTNRGPAW_d = COSTPAW \times ACTIVEFOR_d \times PAWINT_d \times COWWT_d \times 24 \quad [45]$$

where:

$CSTNRGLIE_d$	=	energy cost of lying on Julian day *d* (kJ · day^{-1})
COSTLIE	=	user-specified energy cost of lying (kJ · kg^{-1} · hour^{-1})
$ACTIVELIE_d$	=	user-specified proportion of Julian day *d* spent lying (proportion)
$COWWT_d$	=	weight of the cow on Julian day *d* (kg)
24	=	hours in a day (h · day^{-1})
$CSTNRGSTD_d$	=	energy cost of standing on Julian day *d* (kJ · day^{-1})
COSTSTD	=	user-specified energy cost of standing (kJ · kg^{-1} · hour^{-1})
$ACTIVESTD_d$	=	user-specified proportion of Julian day *d* spent standing (proportion)
$CSTNRGWLK_d$	=	energy cost of walking on Julian day *d* (kJ · day^{-1})
COSTWLK	=	user-specified energy cost of walking (kJ · kg^{-1} · hour^{-1})
$ACTIVEWLK_d$	=	user-specified proportion of Julian day *d* spent walking (proportion)
$SNOWX_d$	=	change in cost associated with locomotion in snow on Julian day *d* (proportion)
$CSTNRGRUN_d$	=	energy cost of running on Julian day *d* (kJ · day^{-1})
COSTRUN	=	user-specified energy cost of running (kJ · kg^{-1} · hour^{-1})
$ACTIVERUN_d$	=	user-specified proportion of Julian day *d* spent running (proportion)
$CSTNRGEAT_d$	=	energy cost of eating on Julian day *d* (kJ · day^{-1})
COSTEAT	=	user-specified energy cost of feeding, includes cost of both eating plus standing while eating (kJ · kg^{-1} · hour^{-1})
$ACTIVEFOR_d$	=	user-specified proportion of Julian day *d* spent foraging (proportion)
$EATINT_d$	=	user-specified proportion of foraging period spent eating on Julian day *d* (proportion)
$CSTNRGPAW_d$	=	energy cost of pawing on Julian day *d* (kJ · day^{-1})
COSTPAW	=	user-specified energy cost of pawing (kJ · kg^{-1} · hour^{-1})
$PAWINT_d$	=	user-specified proportion of foraging period spent pawing on Julian day *d* (proportion)

The model sums the daily costs of all activities to produce the total daily activity cost:

$$EACTIVE_d = CSTNRGLIE_d + CSTNRGSTD_d + CSTNRWLK_d + CSTNRGRUN_d + CSTNRGEAT_d + CSTNRGPAW_d \quad [46]$$

where:

$EACTIVE_d$ = total activity cost on Julian day *d* (kJ · day^{-1})
$CSTNRGLIE_d$ = energy cost of lying on Julian day *d* (kJ · day^{-1})
$CSTNRGSTD_d$ = energy cost of standing on Julian day *d* (kJ · day^{-1})
$CSTNRGWLK_d$ = energy cost of walking on Julian day *d* (kJ · day^{-1})
$CSTNRGRUN_d$ = energy cost of running on Julian day *d* (kJ · day^{-1})
$CSTNRGEAT_d$ = energy cost of eating on Julian day *d* (kJ · day^{-1})
$CSTNRGPAW_d$ = energy cost of pawing on Julian day *d* (kJ · day^{-1})

Using the total activity cost, the model calculates the daily net energy available for growth and reproduction:

$$NETNRG_d = MEI_d - \frac{EACTIVE_d + HP_d}{EFMAIN_d} \quad [47]$$

where:

$NETNRG_d$ = net energy available for growth and reproduction on Julian day *d* (kJ)
MEI_d = metabolizable energy intake on Julian day *d* (kJ)
$EACTIVE_d$ = total activity cost on Julian day *d* (kJ · day^{-1})
HP_d = heat production on Julian day *d* (kJ · day^{-1})
$EFMAIN_d$ = efficiency at which metabolizable energy can be used for energy maintenance on Julian day *d* (unitless)

Summer protein cost

During the summer months, the model assumes the cow first allocates energy to depositing protein. To calculate this energy requirement, the model first calculates the efficiency of using metabolizable energy for growth and fattening (ARC 1980):

$$EFPROD_d = (0.78 \times QM_d) + 0.006 \quad [48]$$

where:

$EFPROD_d$ = efficiency of using metabolizable energy for growth and fattening on Julian day *d* (unitless)
QM_d = metabolizability coefficient of the gross energy of diet on Julian day *d* (unitless)

The daily energy required for summer protein deposition (Russell and White 2000) is then calculated as:

$$SUMPRTCST_d = \text{Minimum of } \left\{ \frac{SUMTRGPRT_d \times 23.85}{EFPROD_d}, NETNRG_d \right\} \quad \text{if } STPRT \le d \le ENDPRT \text{ and } NETNRG_d > 0 \qquad [49]$$

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

where:

$SUMPRTCST_d$	=	energy required to deposit target summer protein on Julian day *d* (kJ)
$SUMTRGPRT_d$	=	user-specified target for summer protein deposition on Julian day *d* ($g \cdot day^{-1}$)
23.85	=	energy content of dry protein ($kJ \cdot g^{-1}$)
$EFPROD_d$	=	efficiency of using metabolizable energy for growth and fattening on Julian day *d* (unitless)
$NETNRG_d$	=	net energy available for growth and reproduction on Julian day *d* (kJ)
STPRT	=	user-specified start date for summer protein gain (Julian day)
d	=	Julian day of the model run
ENDPRT	=	user-specified end date for summer protein gain (Julian day)

This energy requirement is then removed from the daily net energy available for reproduction:

$$ADJNETNRG_d = NETNRG_d - SUMPRTCST_d \qquad [50]$$

where:

$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$NETNRG_d$	=	net energy available for growth and reproduction on Julian day *d* (kJ)
$SUMPRTCST_d$	=	energy required to deposit target summer protein on Julian day *d* (kJ)

Reproduction costs

The model tracks both the pregnancy and lactation status of the cow on each day of a model run. A cow can become pregnant once a year on the user-set conception date each fall, and will remain pregnant until it gives birth to a calf the following spring. Similarly, a pregnant cow can begin lactating once a year when it gives birth to a calf in the following spring, and will continue to lactate until it reaches its weaning date.

There are two possible ways for the pregnancy and lactation status of a cow to be updated as the cow moves from day to day in the model: "user-controlled", where the user explicitly specifies when changes in pregnancy and lactation occur; and "modelled", 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 "modelled" is selected, the model predicts changes in pregnancy and lactation status of the cow each year based upon the weight of the cow and calf at various times of the year.

The possible reproductive strategies represented in the model, when the changes in reproductive status are "modelled", are shown in Figure 8 (Russell *et al*. 1996, 2000; Russell and White 2000). The model determines whether or not the cow becomes pregnant each year based upon whether or not the cow has reached a threshold minimum fat weight in the fall. Similarly, the model determines the weaning strategy of a pregnant cow, based upon whether or not the calf and/or cow reach a series of other weight-related thresholds through the spring, summer and fall. The model provides a rational framework to study and simulate breeding pauses (Cameron 1994; Cameron and Ver Hoef 1994). Details of these calculations are presented in the following sections.

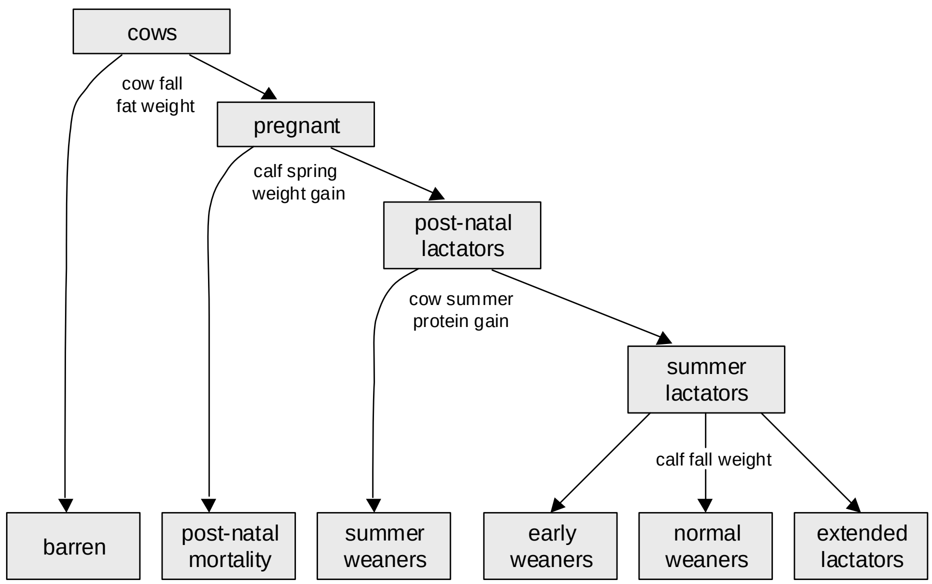


FIGURE 8: REPRODUCTIVE STRATEGIES IN THE GROWTH SUBMODEL.

Determining pregnancy status

Pregnancy status is represented using the state variable $PREG_d$, which is set to 1 for those days of the simulation when the cow is pregnant, and 0 for those days when she is barren.

If the pregnancy status is "user-controlled", then pregnancy is determined as follows:

$$
\begin{aligned}
PREG_d &= 1 && \text{if } PREG_{d-1} = 0 \text{ and} \\
& && d = CDATE \text{ and} \\
& && USERPREG_y = 1, \text{ for } d \in y \\
PREG_d &= 1 && \text{if } PREG_{d-1} = 1 \text{ and} \\
& && DPREG_d < GESLEN \\
PREG_d &= 0 && \text{otherwise}
\end{aligned}
\qquad [51]
$$

where:

$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day d (1 = pregnant, 0 = barren)
d	=	Julian day of the model run
$CDATE$	=	user-specified Julian date of conception (Julian days)
$USERPREG_y$	=	user-specified annual pregnancy status for year y (0 = barren, 1 = pregnant)
$DPREG_d$	=	number of days, on Julian day d, the cow has been pregnant (days)
$GESLEN$	=	user-specified gestation period (days)

Alternatively if the pregnancy status is "modeled" on fat reserves at conception (Gerhart *et al.* 1997), pregnancy is determined as follows:

$$\begin{aligned}
PREG_d &= 1 && \text{if } PREG_{d-1} = 0 \text{ and} \\
& && [(CDATE + PREGST) \le d \le (CDATE + PREGEND)] \text{ and} \\
& && FATWT_d \ge PREGFATWT \\
PREG_d &= 1 && \text{if } PREG_{d-1} = 1 \text{ and} \\
& && DPREG_d < GESLEN \\
PREG_d &= 0 && \text{otherwise}
\end{aligned} \qquad [52]$$

where:

$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day d (1 = pregnant, 0 = barren)
$CDATE$	=	user-specified Julian date of conception (Julian days)
$PREGST$	=	user-specified start of window for conception (days); expressed as the number of days after CDATE that conception can first occur
d	=	Julian day of the model run
$PREGEND$	=	user-specified end of window for conception (days); expressed as the number of days after CDATE that conception can last occur
$FATWT_d$	=	fat weight of the cow on Julian day d (kg)
$PREGFATWT$	=	user-specified threshold fat weight at conception above which the cow will become pregnant (kg)
$DPREG_d$	=	number of days, on Julian day d, the cow has been pregnant (days)
$GESLEN$	=	user-specified gestation period (days)

Calculating gestation costs

For those days when the cow is not pregnant, the daily cost of gestation is zero:

$$EGEST_d = 0 \qquad \text{if } PREG_d = 0 \tag{53}$$

where:

$EGEST_d$ = actual energy cost of gestation on Julian day *d* (kJ · day^{-1})
$PREG_d$ = a state variable indicating pregnancy status of cow on Julian day *d* (1 = pregnant, 0 = barren)

For those days when the cow is pregnant (i.e. $PREG_d = 1$), the model calculates the daily cost of gestation to day 76 of pregnancy (Roine *et al.* 1982) and for days 77 to 220 with a modification as proposed by Fancy (1986); the following section outlines the calculations associated with the cost of gestation for pregnant cows.

The first step is to calculate the number of days the cow has been pregnant:

$$DPREG_d = d - CDATE \tag{54}$$

where:

$DPREG_d$ = number of days, on Julian day *d*, the cow has been pregnant (days)
d = Julian day of the model run
CDATE = user-specified Julian date of conception (Julian days)

This is then used to calculate the daily target fetus weight (Roine *et al.* 1982, corrected by Fancy 1986):

$$\begin{aligned} TFETWTR_d &= \left(0.00036 \times DPREG_d^{\,3}\right) + \left(0.053 \times DPREG_d^{\,2}\right) - \left(1.58 \times DPREG_d\right) - 0.000096 \qquad \text{if } DPREG_d \le 76 \\ TFETWTR_d &= \left(6.05254 \times 10^{-8} \times DPREG_d^{\,4}\right) - \left(3.06828 \times 10^{-5} \times DPREG_d^{\,3}\right) \\ &\quad + \left(0.05719 \times DPREG_d^{\,2}\right) - \left(0.44743 \times DPREG_d\right) + 64.152 \qquad \text{otherwise} \end{aligned} \tag{55}$$

where:

$TFETWTR_d$ = target fetus weight for reindeer on Julian day *d* (g)
$DPREG_d$ = number of days, on Julian day *d*, the cow has been pregnant (days)

Note that the daily target fetus weight is constrained as:

$$TFETWTR_d = Minimum\ of\ \{1.075,\ TFETWTR_d\} \tag{56}$$

where:

$TFETWTR_d$ = target fetus weight for reindeer on Julian day *d* (g)

The equations above for target fetus weight were developed for reindeer. To convert the results to caribou, the model adjusts the daily target fetus weight by the equation (Fancy 1986):

$$TFETWT_d = \frac{TFETWTR_d}{1000} \times \frac{BIRWT}{5.89} \quad [57]$$

where:

$TFETWT_d$	=	target fetus weight on Julian day *d* (kg)
$TFETWTR_d$	=	target fetus weight for reindeer on Julian day *d* (g)
$BIRWT$	=	user-specified target birth weight (kg)
1000	=	conversion coefficient ($g \cdot kg^{-1}$)
5.89	=	predicted birth weight of reindeer assuming a gestation length of 220 days (kg)

Based on the duration of the pregnancy, the model calculates the daily energy cost of gestation as (Robbins 1983):

$$TEGEST_d = 2.4 \times 10^{-07} \times \left(\frac{DPREG_d \times 100}{GESLEN} \right)^{3.13} \times MAINCST_d \times 0.59 \quad [58]$$

where:

$TEGEST_d$	=	target energy cost of gestation on Julian day *d* ($kJ \cdot day^{-1}$)
$DPREG_d$	=	number of days, on Julian day *d*, the cow has been pregnant (days)
$GESLEN$	=	user-specified gestation period (days)
$MAINCST_d$	=	cost of maintenance on Julian day *d* ($kJ \cdot day^{-1}$)

From the energy cost of gestation, the model calculates the daily cost of maintaining the conceptus (as defined in equation [68], below) as:

$$CONCCOST_d = \frac{TEGEST_d}{TFETWT_d} \quad [59]$$

where:

$CONCCOST_d$	=	cost of maintaining the conceptus on Julian day *d* ($kJ \cdot kg^{-1}$ fetus weight $\cdot day^{-1}$)
$TEGEST_d$	=	target energy cost of gestation on Julian day *d* ($kJ \cdot day^{-1}$)
$TFETWT_d$	=	target fetus weight on Julian day *d* (kg)

The target fetus weight is then used to determine the target daily relative growth rate of the fetus:

$$TGR_d = \frac{TFETWT_d - TFETWT_{d-1}}{TFETWT_{d-1}} \quad [60]$$

where:

TGR_d	=	target daily relative growth rate on Julian day *d* (unitless)
$TFETWT_d$	=	target fetus weight on Julian day *d* (kg)

The amount of energy available for gestation is the next calculation. If the net energy available for reproduction is greater than the energy required for growing the fetus at the target rate, then the model will increase the weight of the fetus by an amount corresponding to the target growth rate; any remaining energy is deposited as fat or lean tissue:

$$FETUSWT_d = FETUSWT_{d-1} + \left(FETUSWT_{d-1} \times TGR_d\right) \qquad if \ \left(0.13 \times ADJNETNRG_d\right) \geq TEGEST_d \qquad [61]$$

where:

$FETUSWT_d$	=	weight of the fetus on Julian day *d* (kg)
TGR_d	=	target daily relative growth rate on Julian day *d* (unitless)
0.13	=	efficiency of using metabolizable energy for fetal growth (ARC 1980)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$TEGEST_d$	=	target energy cost of gestation on Julian day *d* ($kJ \cdot day^{-1}$)

If net energy available for reproduction is less than the energy required, the model will determine if the energy deficit can be accounted for by the cow's body fat reserves. The amount of energy that must be drawn from the cow's energy reserves, at 100% efficiency, to compensate for the energy deficit (kJ) is calculated as:

$$\begin{aligned} BFR_d &= TEGEST_d - ADJNETNRG_d && if \ ADJNETNRG_d < 0 \\ BFR_d &= TEGEST_d - \left(ADJNETNRG_d \times 0.13\right) && if \ 0 \leq \left(ADJNETNRG_d \times 0.13\right) < TEGEST_d \end{aligned} \qquad [62]$$

where:

BFR_d	=	amount of body fat required on Julian day *d* to meet gestation costs (kJ)
$TEGEST_d$	=	target energy cost of gestation on Julian day *d* ($kJ \cdot day^{-1}$)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
0.13	=	efficiency of using metabolizable energy for fetal growth (ARC 1980)

If the required energy from fat is less than the maximum amount available, the fetus will grow at the maximum rate:

$$FETUSWT_d = FETUSWT_{d-1} + \left(FETUSWT_{d-1} \times TGR_d\right) \qquad \begin{aligned} &if \ BFR_d < \left(FATMOB \times 39.54\right) \ and \\ &\left(0.13 \times ADJNETNRG_d\right) < TEGEST_d \end{aligned} \qquad [63]$$

where:

$FETUSWT_d$	=	weight of the fetus on Julian day *d* (kg)
TGR_d	=	target daily relative growth rate on Julian day *d* (unitless)
BFR_d	=	amount of body fat required on Julian day *d* to meet gestation costs (kJ)
FATMOB	=	user-specified maximum rate at which fat can be mobilized ($g \cdot day^{-1}$)
39.54	=	amount of energy contained in fat ($kJ \cdot g^{-1}$)
0.13	=	efficiency of using metabolizable energy for fetal growth (ARC 1980)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$TEGEST_d$	=	target energy cost of gestation on Julian day *d* ($kJ \cdot day^{-1}$)

If the required energy from fat is greater than the maximum amount available, the model reduces fetus growth rate. This adjustment involves two steps. First, the model calculates the actual energy available for gestation from both fat stores and net energy intake:

$$NEWNET_d = (ADJNETNRG_d \times 0.13) + (FATMOB \times 39.54) \qquad [64]$$

where:

$NEWNET_d$	=	actual energy available from both fat and energy intake for gestation on Julian day *d* (kJ)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
0.13	=	efficiency of using metabolizable energy for fetal growth (ARC 1980)
FATMOB	=	user-specified maximum rate at which fat can be mobilized ($g \cdot day^{-1}$)
39.54	=	amount of energy contained in fat ($kJ \cdot g^{-1}$)

This actual energy available is constrained as follows:

$$\begin{aligned} NEWNET_d &= 0 && \text{if } ADJNETNRG_d < 0 \\ NEWNET_d &= TEGEST_d && \text{if } NEWNET_d > TEGEST_d \end{aligned} \qquad [65]$$

where:

$NEWNET_d$	=	actual energy available from both fat and energy intake for gestation on Julian day *d* (kJ)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$TEGEST_d$	=	target energy cost of gestation on Julian day *d* ($kJ \cdot day^{-1}$)

The model then uses *NEWNET* to adjust the target growth rate and calculates the adjusted fetus weight as:

$$FETUSWT_d = FETUSWT_{d-1} + \left[FETUSWT_{d-1} + \left(\frac{NEWNET_d}{TEGEST_d} \right) \times TGR_d \right] \quad \text{if } BFR_d \geq (FATMOB \times 39.54) \; and \; (0.13 \times ADJNETNRG_d) < TEGEST_d \qquad [66]$$

where:

$FETUSWT_d$	=	weight of the fetus on Julian day *d* (kg)
$NEWNET_d$	=	actual energy available from both fat and energy intake for gestation on Julian day *d* (kJ)
$TEGEST_d$	=	target energy cost of gestation on Julian day *d* ($kJ \cdot day^{-1}$)
TGR_d	=	target daily relative growth rate on Julian day *d* (unitless)
BFR_d	=	amount of body fat required on Julian day *d* to meet gestation costs (kJ)
FATMOB	=	user-specified maximum rate at which fat can be mobilized ($g \cdot day^{-1}$)
39.54	=	amount of energy contained in fat ($kJ \cdot g^{-1}$)
0.13	=	efficiency of using metabolizable energy for fetal growth (ARC 1980)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)

The model then calculates the actual (as opposed to target) energy cost of gestation:

$$EGEST_d = CONCCOST_d \times FETUSWT_d \qquad [67]$$

where:

$EGEST_d$	=	actual energy cost of gestation on Julian day *d* (kJ • day^{-1})
$CONCCOST_d$	=	cost of maintaining the conceptus on Julian day *d* (kJ • kg^{-1} fetus weight • day^{-1})
$FETUSWT_d$	=	weight of the fetus on Julian day *d* (kg)

The weight of the conceptus, which includes fetus weight and maternal fluids and tissue, is determined by:

$$CONCWT_d = FETUSWT_d \times CWT \qquad [68]$$

where:

$CONCWT_d$	=	weight of the conceptus on Julian day *d* (kg)
$FETUSWT_d$	=	weight of the fetus on Julian day *d* (kg)
CWT	=	user-specified factor that relates weight of fetus to weight of conceptus (unitless)

Determining lactation status

Lactation status is modeled using the state variable $LACT_d$, which is set to 1 for those days of the simulation when the cow is lactating, and 0 for those days when she is not.

Pregnancy is completed when the number of days the cow has been pregnant ($DPREG_d$) equals the gestation length (*GESLEN*) set by the user. On this day parturition occurs, the calf is born, cow weight is reduced by the weight of the conceptus, and the cow begins lactating. Birth is reflected in the model as follows:

$$\begin{aligned} PREG_d &= 0 \\ LACT_d &= 1 \\ COWWT_d &= COWWT_d - CONCWT_d \\ CALFWT_d &= FETUSWT_d \end{aligned} \qquad [69]$$

$$if \;\; PREG_{d-1} = 1 \; and \;\; DPREG_d = GESLEN$$

where:

$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day *d* (1 = pregnant, 0 = barren)
$LACT_d$	=	state variable indicating lactation status of cow on Julian day *d* (1 = lactating, 0 = not lactating)
$COWWT_d$	=	weight of the cow on Julian day *d* (kg)
$CONCWT_d$	=	weight of the conceptus on Julian day *d* (kg)
$CALFWT_d$	=	calf body weight on Julian day *d* (kg)
$FETUSWT_d$	=	weight of the fetus on Julian day *d* (kg)
$DPREG_d$	=	number of days, on Julian day *d*, the cow has been pregnant (days)
$GESLEN$	=	user-specified gestation period (days)

Once the cow is lactating, the model must check each subsequent day to determine when the cow weans the calf. As with pregnancy, lactation can be either "user set" or "modelled".

If lactation is "user-set", then the wean date is determined as follows:

$$\begin{array}{ll} LACT_d = 1 & \text{if } LACT_{d-1} = 1 \text{ and} \\ & (BDATE + WEANDAY_y) < d,\ d \in y \\ LACT_d = 0 & \text{otherwise} \end{array} \qquad [70]$$

where:

$LACT_d$	=	state variable indicating lactation status of cow on Julian day d (1 = lactating, 0 = not lactating)
$BDATE$	=	Julian birth date (Julian day); calculated as: $CDATE + GESLEN - 365$
$WEANDAY_y$	=	user-specified annual number of days after birth when weaning occurs for calf born in year y (days)
d	=	Julian day of the model run
y	=	year of the model run

Alternatively, lactation status can be "modelled". In this case, the cow can adopt one of five weaning strategies: post-natal weaning (mortality), summer weaning, early weaning, normal weaning and extended lactation (see Russell and White 2000; Figure 8). The remainder of this section describes these five strategies and the calculations associated with each of them.

Post-natal mortality

These are cows whose calves die in the first few weeks following birth. For modelling purposes, this occurs when the average daily weight gain of the calf over the first few weeks of life is too low.

To determine if a lactating cow loses its calf in the post-natal period, the post-natal weight gain of the calf is determined once each year:

$$ACTPCALFWTGN_y = 1000 \times \frac{(CALFWT_{BDATE+PEND} - CALFWT_{BDATE+PSTD})}{(PEND - PSTD)} \qquad [71]$$

where:

$ACTPCALFWTGN_y$	=	average daily post-natal weight gain of the calf in year y (g)
1000	=	conversion coefficient ($g \cdot kg^{-1}$)
$CALFWT_d$	=	calf body weight on Julian day d (kg)
$BDATE$	=	Julian birth date (Julian day); calculated as: $CDATE + GESLEN - 365$
$PEND$	=	user-specified end averaging date for post-natal mortality calf weight gain, expressed as days after birth (days)
$PSTD$	=	user-specified start averaging date for post-natal mortality calf weight gain, expressed as days after birth (days)

This weight gain is then compared to a threshold weight gain to determine whether or not the cow stops lactating:

$$LACT_d = 0 \qquad \text{if } LACT_{d-1} = 1 \text{ and } d = BDATE + POWEAND \text{ and } ACTPCALFWTGN_y < THPCALFWTGN, \text{ for } d \in y \tag{72}$$

where:

$LACT_d$	=	state variable indicating lactation status of cow on Julian day *d* (1 = lactating, 0 = not lactating)
BDATE	=	Julian birth date (Julian day); calculated as: *CDATE* + *GESLEN* - 365
POWEAND	=	user-specified post-natal mortality wean date, expressed as days after birth (days)
ACTPCALFWTGNy	=	annual average daily post-natal weight gain of the calf in year y (g)
THPCALFWTGN	=	user-specified threshold post-natal average daily weight gain of the calf (g)
d	=	Julian day of the model run
y	=	year of the model run

Summer weaning

These are cows that wean their calves during the first summer after birth; this occurs when the average daily protein gain of the cow during the summer after birth is too low.

To determine if a lactating cow weans its calf during the summer, the summer protein gain of the cow is calculated as:

$$ACTSUMPRTGN_y = 1000 \times \frac{\left(DRYPTN_{BDATE+SUEND} - DRYPTN_{BDATE+SUSTD}\right)}{\left(SUEND - SUSTD\right)} \tag{73}$$

where:

$ACTSUMPRTGN_y$	=	average daily protein gain of the cow during the summer in year *y* (g)
1000	=	conversion coefficient (g · kg^{-1})
$DRYPTN_d$	=	dry protein weight of the cow on Julian day *d* (kg)
BDATE	=	Julian birth date (Julian day); calculated as: *CDATE* + *GESLEN* - 365
SUEND	=	user-specified end averaging date for summer weaning, expressed as days after birth (days)
SUSTD	=	user-specified start averaging date for summer weaning, expressed as days after birth (days)

This weight gain is then compared to a threshold weight gain to determine whether or not the cow stops lactating:

$$LACT_d = 0 \qquad \text{if } LACT_{d-1} = 1 \text{ and } d = BDATE + SUWEAND \text{ and } ACTSUMPRTGN_y < THSUMPRTGN, \text{ for } d \in y \qquad [74]$$

where:

$LACT_d$	=	state variable indicating lactation status of cow on Julian day *d* (1 = lactating, 0 = not lactating)
BDATE	=	Julian birth date (Julian day); calculated as: *CDATE* + *GESLEN* - 365
SUWEAND	=	user-specified summer wean date, expressed as days after birth (days)
$ACTSUMPRTGN_y$	=	average daily protein gain of the cow during the summer in year *y* (g)
THSUMPRTGN	=	user-specified threshold protein gain of the cow (g)
d	=	Julian day of the model run
y	=	year of the model run

Early, normal and extended weaning

Early, normal and extended weaning are determined based on the weight of the calf in the fall. Early weaning occurs before the rut, normal weaning during the rut, while extended weaning occurs when a cow continues lactation beyond the rut and into the following year. For extended weaning, if the cow is pregnant then the cow will wean its calf just prior to calving in the following spring; if the extended weaner cow is not pregnant, it will wean its calf during the following year's rut.

The choice between these three strategies is based upon the weight of the calf in the fall. If the fall calf weight falls below a minimum threshold, the cow weans the calf early:

$$LACT_d = 0 \qquad \text{if } LACT_{d-1} = 1 \text{ and } d = BDATE + EAWEAND \text{ and } CALFWT_{BDATE + FALLD} < THMINCALFWT \qquad [75]$$

where:

$LACT_d$	=	state variable indicating lactation status of cow on Julian day *d* (1 = lactating, 0 = not lactating)
d	=	Julian day of the model run
BDATE	=	Julian birth date (Julian day); calculated as: *CDATE* + *GESLEN* - 365
EAWEAND	=	user-specified early wean date, expressed as days after birth (days)
$CALFWT_d$	=	calf body weight on Julian day *d* (kg)
FALLD	=	user-specified fall weaning check date, expressed as days after birth (days)
THMINCALFWT	=	user-specified threshold minimum fall calf weight of extended weaner (kg)

On the other hand, if the calf weight is above a maximum threshold, then the cow weans normally:

$$LACT_d = 0 \quad \text{if } LACT_{d-1} = 1 \text{ and } d = BDATE + NOWEAND \text{ and } CALFWT_{BDATE+FALLD} \geq THMAXCALFWT \qquad [76]$$

where:

$LACT_d$	=	state variable indicating lactation status of cow on Julian day d (1 = lactating, 0 = not lactating)
d	=	Julian day of the model run
$BDATE$	=	Julian birth date (Julian day); calculated as: $CDATE + GESLEN - 365$
$NOWEAND$	=	user-specified normal wean date, expressed as days after birth (days)
$CALFWT_d$	=	calf body weight on Julian day d (kg)
$FALLD$	=	user-specified fall weaning check date, expressed as days after birth (days)
$THMAXCALFWT$	=	user-specified threshold maximum fall calf weight for extended weaner (kg)

Finally, for those calves that fall between the minimum and maximum thresholds, the cow chooses to extend lactation into the following year. If the cow is pregnant the following spring, weaning occurs in the following spring:

$$LACT_d = 0 \quad \text{if } LACT_{d-1} = 1 \text{ and } d = BDATE + EXPRWEAND \text{ and } PREG_{EXPRCHK} = 1 \text{ and } THMINCALFWT \geq CALFWT_{BDATE+FALLD} > THMAXCALFWT \qquad [77]$$

where:

$LACT_d$	=	state variable indicating lactation status of cow on Julian day d (1 = lactating, 0 = not lactating)
d	=	Julian day of the model run
$BDATE$	=	Julian birth date (Julian day); calculated as: $CDATE + GESLEN - 365$
$EXPRWEAND$	=	user-specified extended wean date for pregnant cows, expressed as days after birth in the following year (days)
$PREG_d$	=	a state variable indicating lactation status of cow on Julian day d (1 = pregnant, 0 = barren)
$EXPRCHK$	=	pregnancy check date for extended weaners (Julian day); calculated as: BDATE + EXPRWEAND – 1
$THMINCALFWT$	=	user-specified threshold minimum fall calf weight of extended weaner (kg)
$CALFWT_d$	=	calf body weight on Julian day d (kg)
$FALLD$	=	user-specified fall weaning check date, expressed as days after birth (days)
$THMAXCALFWT$	=	user-specified threshold maximum fall calf weight for extended weaner (kg)

If the cow is not pregnant in the following spring, weaning is extended to the following fall:

$$LACT_d = 0 \quad \text{if } LACT_{d-1} = 1 \text{ and } d = CDATE + EXNPWEAND \text{ and } PREG_{EXPRCHK} = 0 \text{ and } THMINCALFWT \geq CALFWT_{BDATE+FALLD} > THMAXCALFWT \qquad [78]$$

where:

$LACT_d$	=	state variable indicating lactation status of cow on Julian day d (1 = lactating, 0 = not lactating)
d	=	Julian day of the model run
$CDATE$	=	user-specified Julian date of conception (Julian days)
$EXNPWEAND$	=	user-specified extended wean date for cows that are not pregnant, expressed as days after conception in the following year (days)
$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day d (1 = pregnant, 0 = barren)
$BDATE$	=	Julian birth date (Julian day); calculated as: $CDATE + GESLEN - 365$
$EXPRCHK$	=	pregnancy check date for extended weaning (Julian day); calculated as: BDATE + EXPRWEAND – 1
$THMINCALFWT$	=	user-specified threshold minimum fall calf weight for extended weaner (kg)
$CALFWT_d$	=	calf body weight on Julian day d (kg)
$FALLD$	=	user-specified fall weaning check date, expressed as days after birth (days)
$THMAXCALFWT$	=	user-specified threshold maximum fall calf weight of extended weaner (kg)

Calculating lactation costs

For those days when the cow is not lactating, the daily cost of lactation is zero:

$$ELACT_d = 0 \quad \text{if } LACT_d = 0 \qquad [79]$$

where:

$ELACT_d$	=	energy contained in actual milk production on Julian day d ($kJ \cdot day^{-1}$)
$LACT_d$	=	state variable indicating lactation status of cow on Julian day d (1 = lactating, 0 = not lactating)

For those days when the cow is lactating (i.e. $LACT_d = 1$), the model calculates the daily cost of lactation; the following section outlines the calculations associated with the cost of lactation for lactating cows.

The first step is to update the age of the calf each day:

$$CALFAGE_d = d - BDATE + 1 \tag{80}$$

where:

$CALFAGE_d$	=	age of the calf on Julian day d (days)
$BDATE$	=	Julian birth date (Julian day); calculated as: $CDATE$ + $GESLEN$ - 365
d	=	Julian day of the model run

In a manner similar to that described for gestation, the model calculates a daily target for milk production as a function of the calf's age, based on equations of White and Luick (1984) and Parker *et al.*(1990):

$$\begin{aligned} TARMP_d &= 0.731 && \text{if } CALFAGE_d = 1 \\ TARMP_d &= 1.91 && \text{if } CALFAGE_d = 2 \\ TARMP_d &= 1.606 \times e^{-0.0072 \times CALFAGE_d} + 0.374 \times e^{-0.0617 \times CALFAGE_d} && \text{otherwise} \end{aligned} \tag{81}$$

where:

$TARMP_d$	=	target milk production on Julian day d ($l \cdot day^{-1}$)
$CALFAGE_d$	=	age of the calf on Julian day d (days)

The daily amount of energy contained in the target milk production was calculated from Parker *et al.* (1990) as:

$$TMLKNRG_d = 12.24 - (0.0032334 \times TARMP_d \times 1000) \tag{82}$$

where:

$TMLKNRG_d$	=	amount of target milk energy on Julian day d ($kJ \cdot ml^{-1}$)
$TARMP_d$	=	target milk production on Julian day d ($l \cdot day^{-1}$)

As in the gestation section described earlier, the model adjusts target milk production during periods when the cow's energy balance cannot meet target demands. The first decision is to determine if the energy cost of target lactation can be met by the available energy. Costs of target lactation are determined from the energy contained in target milk production and the efficiency of producing that energy.

$$TELACT_d = TMLKNRG_d \times TARMP_d \times 1000 \tag{83}$$

where:

$TELACT_d$	=	target energy contained in target milk production on Julian day d (kJ)
$TMLKNRG_d$	=	amount of target milk energy on Julian day d ($kJ \cdot ml^{-1}$)
$TARMP_d$	=	target milk production on Julian day d ($l \cdot day^{-1}$)
1000	=	conversion coefficient ($ml \cdot l^{-1}$)

The model then calculates the efficiency of using metabolizable energy for lactation:

$$EFLACT_d = (0.35 \times QM_d) + 0.42 \qquad [84]$$

where:

$EFLACT_d$	=	efficiency of using metabolizable energy for lactation on Julian day *d* (unitless)
QM_d	=	metabolizability coefficient of the gross energy of diet on Julian day *d* (unitless)

If there is enough available net energy for reproduction, then actual milk production will equal the target production:

$$MP_d = TARMP_d \qquad \text{if } (ADJNETNRG_d \times EFLACT_d) \geq TELACT_d \qquad [85]$$

where:

MP_d	=	actual milk production on Julian day *d* ($l \cdot day^{-1}$)
$TARMP_d$	=	target milk production on Julian day *d* ($l \cdot day^{-1}$)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$EFLACT_d$	=	efficiency of using metabolizable energy for lactation on Julian day *d* (unitless)
$TELACT_d$	=	target energy contained in target milk production on Julian day *d* (kJ)

Otherwise, if there is not enough available energy, then the model will calculate the amount of energy that must be drawn from the cow's fat reserves to compensate for the deficit:

$$BFR_d = TELACT_d - (ADJNETNRG_d \times EFLACT_d) \qquad [86]$$

where:

BFR_d	=	amount of body fat required on Julian day *d* to meet gestation costs (kJ)
$TELACT_d$	=	target energy contained in target milk production on Julian day *d* (kJ)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$EFLACT_d$	=	efficiency of using metabolizable energy for lactation on Julian day *d* (unitless)

The cow must have a critical amount of fat:

$$CHECKFAT_d = (CHKWT \times COWWT_d) + \frac{BFR_d}{39.54 \times 1000} \qquad [87]$$

where:

$CHECKFAT_d$	=	critical amount of fat on Julian day *d* (kg)
$CHKWT$	=	user-specified proportion of the cow's weight that cannot be catabolized (unitless)
$COWWT_d$	=	weight of the cow on Julian day *d* (kg)
BFR_d	=	amount of body fat required on Julian day *d* to meet gestation costs (kJ)
39.54	=	amount of energy contained in fat ($kJ \cdot g^{-1}$)
1000	=	conversion coefficient ($g \cdot kg^{-1}$)

The model then compares the critical amount of fat with the amount of fat in the body reserves. If the amount of fat in the body reserves is less than the critical amount, the cow produces milk only to the level permitted by dietary net energy and body reserves (White *et al.* 1995).

First, the body fat available for lactation is calculated:

$$BFA_d = [FATWT_d - (CHKWT \times COWWT_d)] \times 1000 \qquad [88]$$

where:

BFA_d	=	body fat available on Julian day *d* for lactation (g)
$FATWT_d$	=	fat weight of the cow on Julian day *d* (kg)
$CHKWT$	=	user-specified proportion of the cow's weight that cannot be catabolized (unitless)
$COWWT_d$	=	weight of the cow on Julian day *d* (kg)
1000	=	conversion coefficient ($g \cdot kg^{-1}$)

This body fat available is constrained as follows:

$$\begin{aligned} BFA_d &= 0 && \text{if } BFA_d < 0 \\ BFA_d &= FATMOB_d && \text{if } BFA_d > FATMOB_d \end{aligned} \qquad [89]$$

where:

BFA_d	=	body fat available on Julian day *d* for lactation (g)
$FATMOB_d$	=	user-specified maximum rate at which fat can be mobilized ($g \cdot day^{-1}$)

If fat reserves are greater than the critical amount, *CHECKFAT*, the model compares the amount of energy needed from the fat reserves for lactation (*BFR*) to the maximum amount of energy that can be taken from the reserves in a single day (*BFA*). If the required energy (*BFR*) is less than the maximum amount available (*BFA*), the cow will produce milk at the target level. If the required energy is greater than the maximum amount available, the model reduces the cow's milk production. The available energy is then calculated as:

$$NEWNET_d = \left(ADJNETNRG_d \times EFLACT_d\right) + \left(BFA_d \times 39.54\right) \qquad if\ \ FATWT_d < CHECKFAT_d \qquad [90]$$

$$NEWNET_d = \left(ADJNETNRG_d \times EFLACT_d\right) + \left(FATMOB \times 39.54\right) \qquad if\ \ FATWT_d \geq CHECKFAT_d\ \ and\ \ BFR_d \geq \left(FATMOB \times 39.54\right) \qquad [91]$$

$$NEWNET_d = TELACT_d \qquad if\ \ FATWT_d \geq CHECKFAT_d\ \ and\ \ BFR_d < \left(FATMOB \times 39.54\right) \qquad [92]$$

where:

$NEWNET_d$	=	actual energy available from both fat and energy intake for gestation on Julian day *d* (kJ)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$EFLACT_d$	=	efficiency of using metabolizable energy for lactation on Julian day *d* (unitless)
BFA_d	=	body fat available on Julian day *d* for lactation (g)
39.54	=	amount of energy contained in fat ($kJ \cdot g^{-1}$)
$FATWT_d$	=	fat weight of the cow on Julian day *d* (kg)
$CHECKFAT_d$	=	critical amount of fat on Julian day *d* (kg)
FATMOB	=	user-specified maximum rate at which fat can be mobilized ($g \cdot day^{-1}$)
BFR_d	=	amount of body fat required on Julian day *d* to meet gestation costs (kJ)
$TELACT_d$	=	target energy contained in target milk production on Julian day *d* (kJ)

Note that $NEWNET_d$ is constrained to be positive:

$$NEWNET_d = 0 \qquad \text{if}\ \ NEWNET_d < 0 \qquad [93]$$

where:

$NEWNET_d$	=	actual energy available from both fat and energy intake for gestation on Julian day *d* (kJ)

From this the actual milk production is calculated as:

$$MP_d = \frac{NEWNET_d}{TELACT_d} \times TARMP_d \qquad if \ \left(ADJNETNRG_d \times EFLACT_d\right) < TELACT_d \tag{94}$$

where:

MP_d	=	actual milk production on Julian day *d* (l · day^{-1})
$NEWNET_d$	=	actual energy available from both fat and energy intake for gestation on Julian day *d* (kJ)
$TELACT_d$	=	target energy contained in target milk production on Julian day *d* (kJ)
$TARMP_d$	=	target milk production on Julian day *d* (l · day^{-1})
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$EFLACT_d$	=	efficiency of using metabolizable energy for lactation on Julian day *d* (unitless)

The daily energy contained in the actual milk production is calculated as:

$$AMLKNRG_d = 12.24 - \left(3.2334 \times MP_d\right) \tag{95}$$

where:

$AMLKNRG_d$	=	amount of actual milk energy on Julian day *d* (kJ · ml^{-1})
MP_d	=	actual milk production on Julian day *d* (l · day^{-1})

Once the model has computed the actual milk production, it calculates the actual energy cost of lactation as:

$$ELACT_d = MP_d \times AMLKNRG_d \times 1000 \tag{96}$$

where:

$ELACT_d$	=	energy contained in actual milk production on Julian day *d* (kJ · day^{-1})
MP_d	=	actual milk production on Julian day *d* (l · day^{-1})
$AMLKNRG_d$	=	amount of actual milk energy on Julian day *d* (kJ · ml^{-1})
1000	=	conversion coefficient (ml · l^{-1})

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

$$GR_d = \frac{(MP_d \times 1000) - 653}{2.79 \times 1000} \qquad \text{if } CALFAGE_d \le 21 \tag{97}$$

$$GR_d = \frac{MP_d}{3.13} \qquad \text{if } 21 < CALFAGE_d \le 42 \tag{98}$$

$$GR_d = \frac{MP_d}{2} \qquad \text{if } CALFAGE_d > 42 \tag{99}$$

where:

GR_d	=	calf growth rate on Julian day *d* (kg · day^{-1})
MP_d	=	actual milk production on Julian day *d* (l · day^{-1})
1000	=	conversion coefficient (ml · l^{-1})
$CALFAGE_d$	=	age of the calf on Julian day *d* (days)

Calf body weight (kg) is then calculated as:

$$CALFWT_d = CALFWT_{d-1} + GR_d \tag{100}$$

where:

$CALFWT_d$	=	calf body weight on Julian day *d* (kg)
GR_d	=	calf growth rate on Julian day *d* (kg · day^{-1})

Growth and fattening

The model uses Fancy's (1986) approach to determine growth from net energy balance. The model calculates the daily energy balance by adjusting the energy requirements for activity, gestation, and lactation by their respective efficiencies. Those adjusted energy costs are added to the cost of maintenance calculated earlier (see equation [36]), and the resulting total is then subtracted from MEI to produce the cow's daily energy balance.

$$ACTCST_d = \frac{EACTIVE_d}{EFMAIN_d} \tag{101}$$

$$GESTCST_d = EGEST_d \tag{102}$$

$$LACTCST_d = \frac{ELACT_d}{EFLACT_d} \tag{103}$$

where:

$ACTCST_d$	=	metabolizable energy requirement for all activities on Julian day *d* (kJ · day^{-1})
$EACTIVE_d$	=	total activity cost on Julian day *d* (kJ · day^{-1})
$EFMAIN_d$	=	efficiency at which metabolizable energy can be used for energy maintenance on Julian day *d* (unitless)
$GESTCST_d$	=	metabolizable energy required for gestation on Julian day *d* (kJ · day^{-1})
$EGEST_d$	=	actual energy cost of gestation on Julian day *d* (kJ · day^{-1})
$LACTCST_d$	=	metabolizable energy required for lactation on Julian day *d* (kJ · day^{-1})
$ELACT_d$	=	energy contained in actual milk production on Julian day *d* (kJ · day^{-1})
$EFLACT_d$	=	efficiency of using metabolizable energy for lactation on Julian day *d* (unitless)

The net energy balance is then calculated as:

$$EB_d = MEI_d - \left(MAINCST_d + ACTCST_d + GESTCST_d + LACTCST_d\right) \qquad [104]$$

where:

EB_d	=	net energy balance on Julian day *d* (kJ · day^{-1})
MEI_d	=	metabolizable energy intake on Julian day *d* (kJ)
$MAINCST_d$	=	cost of maintenance on Julian day *d* (kJ · day^{-1})
$ACTCST_d$	=	metabolizable energy requirement for all activities on Julian day *d* (kJ · day^{-1})
$GESTCST_d$	=	metabolizable energy required for gestation on Julian day *d* (kJ · day^{-1})
$LACTCST_d$	=	metabolizable energy required for lactation on Julian day *d* (kJ · day^{-1})

Calculating fat and muscle weight

If energy balance is negative (i.e. an energy deficit), then catabolism occurs and the fat and protein reserves are reduced. If not, then energy is added to those body reserves. Because MEI is used for growth and fattening at a lower efficiency than it is for maintenance, the model reduces the energy available for growth and fattening according to the following:

$$REQPRO_d = EB_d \times EFPROD_d \qquad [105]$$

where:

$REQPRO_d$	=	energy available for growth and fattening on Julian day *d* (kJ)
EB_d	=	partial net energy balance on Julian day *d* (kJ · day^{-1})
$EFPROD_d$	=	efficiency of using metabolizable energy for growth and fattening on Julian day *d* (unitless)

Similarly, the energy available for summer protein deposition is calculated as:

$$REQSUMPRT_d = SUMPRTCST_d \times EFPROD_d \qquad [106]$$

where:

$REQSUMPRT_d$	=	energy required for protein deposition in summer on Julian day *d* (kJ)
$SUMPRTCST_d$	=	energy required to deposit target summer protein on Julian day *d* (kJ)
$EFPROD_d$	=	efficiency of using metabolizable energy for growth and fattening on Julian day *d* (unitless)

The amount of energy for growth and fattening (*REQPROD*) is either added to or subtracted from the cow's protein and fat reserves depending on whether it has a positive or negative value. The method Fancy (1986) used for adjusting those body reserves was not based on caribou. He used data from Torbit *et al.* (1985) on differential losses of fat and protein by mule deer during winter and applied the results to caribou. His approach is probably valid because composition of weight gains and losses have been shown to be similar among most adult ruminants (ARC 1980).

Fancy (1986) assumed that 27% of the energy content of weight gains or losses in caribou is contributed by the deposition or catabolism of body protein, whereas 73% of that energy is associated with fat reserves. The energy content of fat and dry protein used in the model is 39.75 $kJ.g^{-1}$ and 23.85 $kJ.g^{-1}$, respectively. Using this approach, protein and fat added or subtracted from body reserves can be determined.

First, the protein gain/loss is calculated:

$$GPRTN_d = \frac{REQSUMPRT_d}{23.85 \times 1000} \qquad \text{if } STPRT \le d \le ENDPRT \qquad [107]$$

$$GPRTN_d = \frac{PCTPRT \times REQPRO_d}{23.85 \times 1000} \qquad \text{otherwise} \qquad [108]$$

where:

$GPRTN_d$	=	protein added/lost on Julian day *d* (kg)
$REQSUMPRT_d$	=	energy required for protein deposition in summer on Julian day *d* (kJ)
23.85	=	energy content of dry protein ($kJ \cdot g^{-1}$)
1000	=	conversion coefficient ($g \cdot kg^{-1}$)
d	=	Julian day of the model run
STPRT	=	user-specified start date for summer protein gain (Julian day)
ENDPRT	=	user-specified end date for summer protein gain (Julian day)
PCTPRT	=	user-specified proportion of energy change from protein (unitless)
$REQPRO_d$	=	energy available for growth and fattening on Julian day *d* (kJ)

Similarly, the number of grams of fat added to or subtracted from body reserves is calculated as:

$$GFAT_d = \frac{REQPRO_d - REQSUMPRT}{39.75 \times 1000} \qquad \text{if } STPRT \le d \le ENDPRT \tag{109}$$

$$GFAT_d = \frac{PCTFAT \times REQPRO_d}{39.75 \times 1000} \qquad \text{otherwise} \tag{110}$$

where:

$GFAT_d$	=	fat added/lost on Julian day *d* (kg)
$REQPRO_d$	=	energy available for growth and fattening on Julian day *d* (kJ)
$REQSUMPRT_d$	=	energy required for protein deposition in summer on Julian day *d* (kJ)
39.75	=	amount of energy contained in fat ($kJ \cdot g^{-1}$)
1000	=	conversion coefficient ($g \cdot kg^{-1}$)
d	=	Julian day of the model run
STPRT	=	user-specified start date for summer protein gain (Julian day)
ENDPRT	=	user-specified end date for summer protein gain (Julian day)
PCTFAT	=	user-specified proportion of energy change from fat (unitless); note that *PCTFAT* + *PCTPRT* should sum to 1

While the magnitude of changes in protein reserves is not limited, the model restricts the maximum amount of fat loss as follows:

$$GFAT_d = \frac{-FATMOB}{1000} \qquad \text{if } GFAT < \frac{-FATMOB}{1000} \tag{111}$$

where:

$GFAT_d$	=	fat added/lost on Julian day *d* (kg)
FATMOB	=	user-specified maximum rate at which fat can be mobilized ($g \cdot day^{-1}$)
1000	=	conversion coefficient ($g \cdot kg^{-1}$)

The main site of protein deposition is muscle, which contains 27% protein (Pace and Rathbun 1945); this was increased to 29% for caribou (Fancy 1986), leaving water at approximately 71%. The weight of catabolized lean tissue can therefore be calculated as:

$$GMUSCLE_d = \frac{GPRTN_d}{0.29} \tag{112}$$

where:

$GMUSCLE_d$	=	amount of muscle added or removed on Julian day *d* (g)
$GPRTN_d$	=	protein added/lost on Julian day *d* (kg)
0.29	=	proportion of protein in muscle tissue (unitless)

The weight of fat and muscle reserves are updated each day:

$$FATWT_d = FATWT_{d-1} + GFAT_d \qquad [113]$$

$$MUSCLEWT_d = MUSCLEWT_{d-1} + GMUSCLE_d \qquad [114]$$

where:

$FATWT_d$	=	fat weight of the cow on Julian day *d* (kg)
$GFAT_d$	=	fat added/lost on Julian day *d* (kg)
$MUSCLEWT_d$	=	amount of muscle on the cow on Julian day *d* (kg)
$GMUSCLE_d$	=	amount of muscle added or removed on Julian day *d* (g)

Calculating water weight

The variable *WATRWT* (kg) monitors seasonal changes in the weight of the body water pool. If the cow is not pregnant, then the water weight of the cow is calculated as:

$$WATRWT_d = WATRWT_{d-1} \qquad \textit{if } ADJNETNRG_d \leq 0 \textit{ and } PREG_d = 0 \qquad [115]$$

$$WATRWT_d = 0 \qquad \textit{if } ADJNETNRG_d > 0 \textit{ and } PREG_d = 0 \qquad [116]$$

where:

$WATRWT_d$	=	cow water weight on Julian day *d* (kg)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day *d* (1 = pregnant, 0 = barren)

If the cow is pregnant the water conversion mechanism of Cameron *et al.* (1975) (see Fancy 1986) is used, where water replaces catabolized body fat and protein. When fat is catabolized, the water pool is augmented as follows:

$$WATRFAT_d = Maximum\,of\ \{-(GFAT_d \times CFAT),\ 0\} \qquad \text{if } PREG_d = 1 \qquad [117]$$

where:

$WATRFAT_d$	=	fat contribution to cow water weight on Julian day *d* (kg)
$GFAT_d$	=	fat added/lost on Julian day *d* (kg)
$CFAT$	=	user-specified proportion of fat replaced by water (unitless)
$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day *d* (1 = pregnant, 0 = barren)

Similarly, when muscle is catabolized, the amount of water added to the body water pool is computed as:

$$WATRMUS_d = Maximum\ of\ \left\{-\left(GMUSCLE_d \times CMUSCLE\right),\ 0\right\} \qquad \text{if } PREG_d = 1 \qquad [118]$$

where:

$WATRMUS_d$	=	muscle contribution to cow water weight on Julian day *d* (kg)
$GMUSCLE_d$	=	amount of muscle added or removed on Julian day *d* (g)
CMUSCLE	=	user-specified proportion of muscle replaced by water (unitless)
$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day *d* (1 = pregnant, 0 = barren)

The new daily water weight for pregnant cows is then calculated as:

$$WATRWT_d = WATRWT_{d-1} + WATRFAT_d + WATRMUS_d \qquad if\ PREG_d = 1 \qquad [119]$$

where:

$WATRWT_d$	=	cow water weight on Julian day *d* (kg)
$WATRFAT_d$	=	fat contribution to cow water weight on Julian day *d* (kg)
$WATRMUS_d$	=	muscle contribution to cow water weight on Julian day *d* (kg)
$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day *d* (1 = pregnant, 0 = barren)

Note that when the cow is pregnant, the water weight of the cow is limited as follows:

$$WATRWT_d = 0.15 \times COWWT_d \qquad \text{if } WATRWT_d > \left(0.15 \times COWWT_d\right) \text{ and } PREG_d = 1 \qquad [120]$$

$$WATRWT_d = 0 \qquad \text{if } WATRWT_d < 0 \text{ and } PREG_d = 1 \qquad [121]$$

where:

$WATRWT_d$	=	cow water weight on Julian day *d* (kg)
$COWWT_d$	=	weight of the cow on Julian day *d* (kg)
$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day *d* (1 = pregnant, 0 = barren)

Calculating caribou weight

In order to calculate the weight of the caribou, the first step is to calculate the amount of wet forage in the rumen (Staaland *et al.* 1984; White *et al.* 1984):

$$RFILLWET_d = \frac{RFILL_h}{0.166 \times 1000} \quad [122]$$

where:

$RFILLWET_d$	=	weight of wet forage in the rumen on Julian day *d* (kg)
$RFILL_h$	=	amount of forage in the rumen in last hour *h* of Julian day *d* (g)
0.166	=	proportion of dry to total wet rumen forage (unitless)
1000	=	conversion coefficient ($g \cdot kg^{-1}$)

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

$$GUTCONT_d = \frac{RFILLWET_d}{0.75} \quad [123]$$

where:

$GUTCONT_d$	=	weight of the contents of the gut on Julian day *d* (kg)
$RFILLWET_d$	=	weight of wet forage in the rumen on Julian day *d* (kg)
0.75	=	proportion of wet rumen forage to total gut contents (unitless)

The weight of dry protein is:

$$DRYPTN_d = MUSCLEWT_d \times 0.29 \quad [124]$$

where:

$DRYPTN_d$	=	dry protein weight of the cow on Julian day *d* (kg)
$MUSCLEWT_d$	=	amount of muscle on the cow on Julian day *d* (kg)
0.29	=	proportion of protein in muscle tissue (unitless)

Finally, the fat-free, ingesta-free body weight is calculated by rearranging the equation in Figure 5 of Reimers *et al.* (1981):

$$FFIFBW_d = \left(4.184 \times DRYPTN_d\right) + 0.343 \quad [125]$$

where:

$FFIFBW_d$	=	fat-free, ingesta-free body weight on Julian day *d* (kg)
$DRYPTN_d$	=	dry protein weight of the cow on Julian day *d* (kg)

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

$$COWWT_d = FFIFBW_d + FATWT_d + GUTCONT_d + WATRWT_d + CONCWT_d \quad [126]$$

$$EBW_d = FFIFBW_d + FATWT_d + WATRWT_d \quad [127]$$

$$MATERNALWT_d = COWWT_d - WATRWT_d - CONCWT_d \quad [128]$$

where:

$COWWT_d$	=	weight of the cow on Julian day *d* (kg)
$FFIFBW_d$	=	fat-free, ingesta-free body weight on Julian day *d* (kg)
$FATWT_d$	=	fat weight of the cow on Julian day *d* (kg)
$GUTCONT_d$	=	weight of the contents of the gut on Julian day *d* (kg)
$WATRWT_d$	=	cow water weight on Julian day *d* (kg)
$CONCWT_d$	=	weight of the conceptus on Julian day *d* (kg)
EBW_d	=	empty body weight on Julian day *d* (kg)
$MATERNALWT_d$	=	maternal weight of the cow on Julian day *d* (kg)

Finally, the rumen capacity of the cow is calculated each day as:

$$RCAP_d = \left(EBW_d - WATRWT_d\right) \times \frac{RCAPPCT}{100} \times 1000 \quad [129]$$

where:

$RCAP_d$	=	capacity of the rumen on Julian day *d* (g)
EBW_d	=	empty body weight on Julian day *d* (kg)
$WATRWT_d$	=	cow water weight on Julian day *d* (kg)
$RCAPPCT$	=	user-specified rumen dry matter capacity as a percentage of empty body weight (%)
100	=	a coefficient ($\%^{-1}$)
1000	=	conversion coefficient ($g \cdot kg^{-1}$)

3.0 FUTURE MODEL DEVELOPMENT

This report summarizes the structure and functioning of the energetics model of the Porcupine Caribou Herd, as of the date of publication. We see the modelling process as dynamic, and thus we will ensure that improvements are continuously made to the model to reflect the latest understanding of caribou energetics. However we felt that there was a need to document the current version of the model, as it is already being applied in a number of research projects that address current issues for the Porcupine Caribou Herd (Murphy *et al.* 2000; Russell *et al.* 1996) and for other herds where impacts of human activities require an assessment (Griffith *et al.* 2001b).

4.0 LITERATURE CITED

[ARC] Agricultural Research Council. 1980. The Nutrient Requirements of Ruminant Livestock. Commonwealth Agricultural Bureau, Slough, England. 351 pp.

Allaye-Chan, A.C. 1991. Physiological and ecological determinants of nutrient partitioning in caribou and reindeer. PhD Thesis, University of Alaska, Fairbanks. 135 pp.

Allaye-Chan, A.C., R.G. White, D.F. Holleman, and D.E. Russell. 1990. Seasonal concentrations of cesium-137 in rumen content, skeletal muscles and feces of caribou from the Porcupine herd: Lichen ingestion rates and implications for human consumption. Rangifer Special Issue No. 3:17-24.

Cameron R.D. 1994. Reproductive pauses by female caribou. J. Mammal. 75:10-13.

Cameron R.D. and J.M. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. J. Wildl Manage. 58:674-679.

Cameron, R.D., R.G. White, and J.R. Luick. 1975. The accumulation of water in reindeer during winter. In: J.R. Luick, P.C. Lent, D.R. Klein, and R.G. White, editors. Proc. First Int'l. Reindeer and Caribou Symp. Biol. Papers, Univ. of Alaska, Spec. Report No. 1. pp. 374-378.

Cameron, R. D., W. T. Smith, R. G. White, and B. Griffith. 2002. The Central Arctic caribou herd. In: D. C. Douglas, P. E. Reynolds, and E. B. Rhode, editors. Arctic Refuge coastal plain terrestrial wildlife research summaries. U.S. Geological Survey, Biological Resources Division, Biological Science Report USGS/BRD/BSR-2002-0001. pp. 38-45.

Cameron, R. D., W. T. Smith, R. G. White, and B. Griffith. 2005. Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. Arctic 58(1). (In press)

Chan-McLeod, A.C. Allaye, R.G. White, and D.E. Russell. 1995. Body mass and composition indices for female barren-ground caribou. J. Wildl. Manage. 59:278-291.

Chan-McLeod, A. C. Allaye, R. G. White, and D. E. Russell. 1999. Comparative body composition strategies of breeding and non-breeding female caribou. Can. J. Zool. 77: 1901-1907.

Chan-McLeod, A.C. Allaye, R.G. White, and D.F. Holleman. 1994. Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. Can. J. Zool. 72:938-947.

Duquette, L.S. 1984. Patterns of activity and their implications to the energy budget of migrating caribou. MSc Thesis. University of Alaska, Fairbanks. 95 pp.

Fancy, S.G. 1986. Daily energy budgets of caribou: a simulation approach. PhD Thesis. University of Alaska, Fairbanks, Alaska. 226 pp.

Fancy, S.G. and R.G. White. 1985a. Energy expenditures by caribou while cratering in snow. J. Wildl. Manage. 49:987-993.

Fancy, S.G. and R.G. White. 1985b. The incremental cost of activity. Chapter 7. In: R.J. Hudson and R.G. White, editors. Bioenergetics of Wild Herbivores. Boca Raton, Florida: CRC Press. pp. 143-159.

Fancy, S.G. and R.G. White. 1987. Energy expenditures for locomotion by barren-ground caribou. Can. J. Zool. 65:122-128.

Fancy, S.G., K. R. Whitten, and D. E. Russell. 1994. Demography of the Porcupine Caribou Herd, 1983-1992. Can. J. Zool. (72): 840-846.

Gerhart, K.L., D.E. Russell, D. van de Wetering, R.G. White, and R.D. Cameron. 1997. Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactational infertility. J. Zool., Lond. 242:17-30.

Gerhart, K.L., R.G. White, R.D. Cameron, and D.E. Russell. 1996a. Body composition and nutrient reserves of arctic caribou. Can. J. Zool. 74:136-146.

Gerhart, K.L., R.G. White, R.D. Cameron, and D.E. Russell. 1996b. Estimating fat content of caribou from body condition scores. J. Wildl. Manage. 60:713-718.

Griffith, B., A. Gunn, D. Russell, J. Johnstone, K. Kielland, S. A. Wolfe, and D. Douglas. 2001b. Bathurst Calving Ground Studies: influence of nutrition and human activity on calving ground location. Final Report to West Kitikmeot Slave Study Society, Yellowknife, NT. 85 pp.

Griffith, B., D. C. Douglas, D. E. Russell, R. G. White, T. R. McCabe, and K. R. Whitten. 2001a. Effects of Recent Climate Warming on Caribou Habitat and Calf Survival. In: R.E. Green, M. Harley, M. Spalding, and C. Zockler, editors. Impacts of climate change on wildlife. pp. 17-19.

Griffith, B., D. C. Douglas, N. E. Walsh, D. D. Young, T. R. McCabe, D. E. Russell, R. G. White, R. D. Cameron, and K. R. Whitten. 2002. The Porcupine caribou herd. In: D. C. Douglas, P. E. Reynolds, and E. B. Rhode, editors. Arctic Refuge coastal plain terrestrial wildlife research summaries. U. S. Geological Survey, Biological Resources Division, Biological Science Report USGS/BRD BSR-2002-0001. pp. 8-37.

Hobbs, N. T., J. E. Gross, L. A. Shipley, D. E. Spalinger, and B. A. Wunder. 2003. Herbivore functional response in heterogeneous environments: a contest among models. Ecology 84:666-681.

Hovey, F.W., D.E. Russell, F.L. Bunnell, R. Farnell, and K.R. Whitten. 1989b. Computer simulation models of the Porcupine caribou herd: III. Harvest. Tech. Rept. Ser. No. 55. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia. 10 pp.

Hovey, F.W., L.L. Kremsater, R.G. White, D.E. Russell, and F.L. Bunnell. 1989a. Computer simulation models of the Porcupine caribou herd: II. Growth. Tech. Rept. Ser. No. 54. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia. 16 pp.

Hudson, R.J. and R.G. White. 1985. Computer simulation of energy budgets. In: R.J. Hudson and R. G. White, editors. Bioenergetics of Wild Herbivores. Boca Raton, Florida: CRC Press. pp. 216-286.

Hudson, R.J. and R.J. Christopherson. 1985. Maintenance metabolism. In: R. J. Hudson and R. G. White, editors. Bioenergetics of Wild Herbivores. Boca Raton, Florida: CRC Press. pp. 121-142.

Kleiber, M. 1961. The Fire of Life. New York: Wiley. 453 pp.

Kofinas, G. P., D. E. Russell, and R. G. White. 2002. Monitoring Caribou Body Condition: Workshop Proceedings. Tech. Rept. Ser. No. 396. Canadian Wildlife Service, Ottawa, Ontario, 31 pp.

Kremsater, L.L., F.W. Hovey, D.E. Russell, R.G. White, F.L. Bunnell, and A.M. Martell. 1989. Computer simulation models of the Porcupine caribou herd: I. Energy. Tech. Rept. Ser. No. 53. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia. 14 pp.

Luick, B.R. and R.G. White. 1983. Indirect calorimetric measurements of the caribou calf. Acta Zool. Fenn. 175:89-90.

Luick, B.R. and R.G. White. 1985. Oxygen consumption for locomotion by caribou calves. J. Wildl. Manage. 50:148-152.

McEwan, E.H. 1970. Energy metabolism of barren ground caribou (*Rangifer tarandus*). Can. J. Zool. 48:391-392.

Murphy, S.M., D. E. Russell, and R.G. White. 2000. Modeling energetic and demographic consequences of caribou interactions with oil development in the Arctic. Rangifer Special Issue No. 12: 107-109 (Brief Communication).

Pace N. and E.N. Rathbun. 1945. Studies on body composition. III. The body water and chemically combined nitrogen content in relation to fat content. J. Biol. Chem. 158:685-692.

Parker, K.L., R.G. White, M.P. Gillingham, and D.F. Holleman. 1990. Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. Can. J. Zool. 68:106-114.

Reimers, E., T. Ringburg, and R. Sørumgård. 1981. Body composition of Svalbard reindeer. Can. J. Zool. 60: 1812-1819.

Robbins, C.T. 1983. Wildlife Feeding and Nutrition. New York: Academic Press. 343 pp.

Robbins, C.T. 1993. Wildlife Feeding and Nutrition. 2nd Edition. Academic Press, Inc. 352 pp.

Roine , K., M. Nieminen, and J. Timisjarvi. 1982. Foetal growth in the reindeer. Acta. Vet. Scand. 23:107-117.

Russell, **D. E. and R.G. White**. 2000. Surviving in the north- a conceptual model of reproductive strategies in arctic caribou. Proc. 8th North American Caribou Workshop. 23-25 April 1998. Whitehorse, YT, Canada. Rangifer Special Issue No. 12: 67.

Russell, D. E., A. M. Martell, and W. A. C. Nixon. 1993**.** The range ecology of the Porcupine Caribou Herd in Canada. Rangifer Special Issue No. 8. 168 pp.

Russell, D. E., D. van de Wetering, R. G. White, and K. L. Gerhart. 1996. Oil and the Porcupine Caribou Herd--Can we quantify the impacts? Rangifer Special Issue 9:255-257 (Brief Communication).

Russell, D. E., G. Kofinas, and B. Griffith. 2002. Barren-Ground caribou Calving Ground Workshop: Report of Proceedings. Tech. Rept. Ser. No. 390. Canadian Wildlife Service, Ottawa, Ontario. 39 pp.

Russell, D. E., K.L. Gerhart, R.G. White, and D. Van De Wetering. 1998. Detection of early pregnancy in caribou: evidence for embryonic mortality. J. Wildl. Manage.62: 1066-1075.

Russell, **D. E., K. R. Whitten, R. Farnell, and D. van de Wetering**. 1992b. Movements and distribution of the Porcupine caribou Herd, 1970-1990. Tech. Rept. Ser. No. 138. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.139 pp.

Russell, D.E., R.D. Cameron, R.G. White, and K.L. Gerhart. 2000. Mechanisms of summer weight gain in northern caribou herds. Proc. 8th North American Caribou Workshop. Rangifer Special Issue No. 12: 148.

Russell, D.E., S.G. Fancy, K.R. Whitten and R.G. White. 1991. Overwinter survival of orphan caribou, *Rangifer tarandus*, calves. Can. Field-Naturalist 105:103-105.

Russell, **D. E., W.A.C. Nixon, and A.M. Martell**. 1992a. Vegetation communities within the range of the Porcupine Caribou Herd in Canada. Tech. Rept. Ser. No. 139. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia. 51 pp.

Shipley, L. A., A. W. Illius, K. Danell, N. T. Hobbs, and D. E. Spalinger. 1999. Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. Oikos 84: 55-68.

Spalinger, D.E. and N.T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. Amer. Natur. 140:325-348.

Spalinger, D.E., T.A. Hanley, and C.T. Robbins. 1988. Analysis of the functional response in foraging in the sitka black-tailed deer. Ecology. 69:1166-1175.

Staaland, H., E. Jacobsen, and R.G. White. 1984. The effect of mineral supplements on nutrient concentrations and pool sizes in the alimentary tract of reindeer fed lichens or concentrates during winter. Can. J. Zool. 62:1232-1241.

Torbit, S.C., L. H. Carpenter, D. M. Swift, and A. W. Alldredge. 1985. Differential loss of fat and protein by mule deer during winter. J. Wildl. Manage. 49:80-85.

Trudell, J. and R.G. White. 1981. The effect of forage structure and availability on food intake, biting rate, bite size and daily eating time of reindeer. J. App. Ecology. 18:63-81.

Walsh, N.E., B. Griffith, and T. R. McCabe. 1995. Evaluating growth of the Porcupine Caribou Herd using a stochastic model. J. Wildl. Manage. 59 (2):262-272.

White, R.G. 1992. Nutrition in relation to season, lactation and growth of north temperate deer. In: R.D. Brown, editor. The Biology of Deer. New York: Springer-Verlag. pp. 407-417.

White, R.G. and J.R. Luick. 1984. Plasticity and constraints in the lactational strategy of reindeer and caribou. In: M. Peaker, R.G. Vernon, and C.H. Knight, editors. Physiological Strategies in Lactation. Symp. Zool. Soc. London No. 51, Academic Press. pp. 215-232.

White, R.G. and J. Trudell. 1980. Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. Arctic and Alpine Res. 12:511-529.

White, R.G. and M.K. Yousef. 1978. Energy expenditure of reindeer walking on roads and on tundra. Can. J. Zool. 56:215-223.

White, R.G., B.R. Thomson, T. Skogland, S.J. Person, D.E. Russell, D.F. Holleman, and J.R. Luick. 1975. Ecology of caribou at Prudhoe Bay, Alaska. In: J. Brown, editor. Ecological Investigations of the Tundra Biome in the Prudhoe Bay Region, Alaska. Biol. Papers, Univ. Alaska, Spec. Report No. 2. pp. 151-201.

White, R.G., E. Jacobsen, and H. Staaland. 1984. Secretion and absorption of nutrients in the alimentary tract of reindeer fed lichens or concentrates during the winter. Can. J. Zool. 62: 2364-2376.

White, R.G., K.L. Gerhart, D. E. Russell, and D. Van de Wetering. 2000. Composition of milk during lactation. . Proc. 8th North American Caribou Workshop. Rangifer Special Issue No. 12: 148.

White, R. G., K.L. Gerhart, D. van de Wetering, and D.E. Russell. 1995. Milk composition during late lactation: a tool for the diagnosis of lactational infertility in caribou. 2nd International Arctic Ungulate Conf., Fairbanks, AK Aug.13-17. Unpublished abstract.

Wickstrom, M.L., C.T. Robbins, T.A. Hanley, D.E. Spalinger, and S.M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. J. Wildl. Manage. 48:1285-1301.

APPENDIX – LIST OF VARIABLES AND THEIR DEFINITIONS

Variable Name		Variable Definition
$ACTCST_d$	=	metabolizable energy requirement for all activities on Julian day *d* (kJ · day^{-1})
$ACTIVEFOR_d$	=	user-specified proportion of Julian day *d* spent foraging (proportion)
$ACTIVELIE_d$	=	user-specified proportion of Julian day *d* spent lying (proportion)
$ACTIVERUN_d$	=	user-specified proportion of Julian day *d* spent running (proportion)
$ACTIVESTD_d$	=	user-specified proportion of Julian day *d* spent standing (proportion)
$ACTIVEWLK_d$	=	user-specified proportion of Julian day *d* spent walking (proportion)
$ACTSUMPRTGN_y$	=	average daily protein gain of the cow during the summer in year *y* (g)
$ACTPCALFWTGN_y$	=	annual average daily post-natal weight gain of the calf in year *y* (g)
$ADJNETNRG_d$	=	net energy remaining after accounting for activity, maintenance, and target summer protein gain (kJ)
$AMLKNRG_d$	=	amount of actual milk energy on Julian day *d* (kJ · ml^{-1})
AR_p	=	user-specified effective rate of search for plant group *p*, taking into account the area searched per unit time and the probability of caribou recognizing and successfully ingesting forage in that area (ha · min^{-1})
BDATE	=	Julian birth date (Julian day); calculated as: *CDATE* + *GESLEN* - 365
BFA_d	=	body fat available on Julian day *d* for lactation (g)
BFR_d	=	amount of body fat required on Julian day *d* to meet gestation costs (kJ)
BIRWT	=	user-specified target birth weight (kg)
$CALFAGE_d$	=	age of the calf on Julian day *d* (days)
$CALFWT_d$	=	calf body weight on Julian day *d* (kg)
CCDPNRG	=	user-specified digestible energy associated with cell contents (kJ · g^{-1})
$CCI_{p,h}$	=	cell content intake for plant group *p* in hour *h* (g · h^{-1})
CCK	=	user-specified digestion rate of cell contents (proportion · h^{-1})
CCMEC	=	user-specified proportion of digestible energy of cell contents that can be metabolized (proportion)
$CCNRG_h$	=	energy obtained in hour *h* from cell contents (kJ · h^{-1})
CDATE	=	user-specified Julian date of conception (Julian days)
$CELCON_h$	=	rumen cell content pool in hour *h* (g)
$CELWAL_h$	=	rumen cell wall pool in hour *h* (g)

CFAT	=	user-specified proportion of fat replaced by water (unitless)
$CHECKFAT_d$	=	critical amount of fat on Julian day *d* (kg)
CHKWT	=	user-specified proportion of the cow's weight that cannot be catabolized (unitless)
CMUSCLE	=	user-specified proportion of muscle replaced by water (unitless)
$CONCCOST_d$	=	cost of maintaining the conceptus on Julian day *d* ($kJ \cdot kg^{-1}$ fetus weight $\cdot day^{-1}$)
$CONCWT_d$	=	weight of the conceptus on Julian day *d* (kg)
$CONSTR1_h$	=	metabolic constraint - forage ingested in hour *h*, as constrained by energetic requirements (g)
$CONSTR2_h$	=	logistic constraint - forage ingested in hour *h*, as constrained by forage availability (g)
$CONSTR3_h$	=	rumen constraint - forage ingested in hour *h*, as constrained by rumen capacity (g)
COSTEAT	=	user-specified energy cost of feeding, includes cost of both eating plus standing while eating ($kJ \cdot kg^{-1} \cdot hour^{-1}$)
COSTLIE	=	user-specified energy cost of lying ($kJ \cdot kg^{-1} \cdot hour^{-1}$)
COSTPAW	=	user-specified energy cost of pawing ($kJ \cdot kg^{-1} \cdot hour^{-1}$)
COSTRUN	=	user-specified energy cost of running ($kJ \cdot kg^{-1} \cdot hour^{-1}$)
COSTSTD	=	user-specified energy cost of standing ($kJ \cdot kg^{-1} \cdot hour^{-1}$)
COSTWLK	=	user-specified energy cost of walking ($kJ \cdot kg^{-1} \cdot hour^{-1}$)
$COWWT_d$	=	weight of the cow on Julian day *d* (kg)
$CSTNRGEAT_d$	=	energy cost of eating on Julian day *d* ($kJ \cdot day^{-1}$)
$CSTNRGLIE_d$	=	energy cost of lying on Julian day *d* ($kJ \cdot day^{-1}$)
$CSTNRGPAW_d$	=	energy cost of pawing on Julian day *d* ($kJ \cdot day^{-1}$)
$CSTNRGRUN_d$	=	energy cost of running on Julian day *d* ($kJ \cdot day^{-1}$)
$CSTNRGSTD_d$	=	energy cost of standing on Julian day *d* ($kJ \cdot day^{-1}$)
$CSTNRGWLK_d$	=	energy cost of walking on Julian day *d* ($kJ \cdot day^{-1}$)
CWDPNRG	=	user-specified digestible energy associated with the cell wall ($kJ \cdot g^{-1}$)
$CWI_{p,h}$	=	digestible cell wall intake for plant group *p* in hour *h* ($g \cdot h^{-1}$)
CWK	=	user-specified digestion rate of cell wall (proportion $\cdot h^{-1}$)
CWMEC	=	user-specified proportion of digestible energy of cell wall that can be metabolized (proportion)
$CWNRG_h$	=	energy obtained from cell wall in hour *h* ($kJ \cdot h^{-1}$)

CWT	=	user-specified factor that relates weight of fetus to weight of conceptus (unitless)
d	=	Julian day of the model run
$DFI_{p,h}$	=	digestible forage intake for plant group *p* in hour *h* ($g \cdot h^{-1}$)
$DPCWAL_{p,d}$	=	user-specified proportion of cell wall for plant group *p* on Julian day *d*, as calculated from neutral detergent fibre analysis (unitless)
$DPDIG_{p,d}$	=	user-specified dry matter digestibility for plant group *p* on Julian day *d* (proportion)
$DPDP_{p,d}$	=	user-specified fraction of time spent eating plant group *p* on Julian day *d* (proportion) – note that this generally approximates the diet
$DPNIT_{p,d}$	=	user-specified percent nitrogen content for plant group *p* on Julian day *d* ($g \cdot 100g$ dry $matter^{-1}$)
$DPREG_d$	=	number of days, on Julian day *d*, the cow has been pregnant (days)
$DRYPTN_d$	=	dry protein weight of the cow on Julian day *d* (kg)
$EACTIVE_d$	=	total activity cost on Julian day *d* ($kJ \cdot day^{-1}$)
$EATINT_d$	=	user-specified proportion of foraging period spent eating on Julian day *d* (proportion)
EAWEAND	=	user-specified early wean date, expressed as days after birth (days)
EB_d	=	partial net energy balance on Julian day *d* ($kJ \cdot day^{-1}$)
EBW_d	=	empty body weight on Julian day *d* (kg)
$EFLACT_d$	=	efficiency of using metabolizable energy for lactation on Julian day *d* (unitless)
$EFMAIN_d$	=	efficiency at which metabolizable energy can be used for energy maintenance on Julian day *d* (unitless)
$EFPROD_d$	=	efficiency of using metabolizable energy for growth and fattening on Julian day *d* (unitless)
$EGEST_d$	=	actual energy cost of gestation on Julian day *d* ($kJ \cdot day^{-1}$)
$ELACT_d$	=	energy contained in actual milk production on Julian day *d* ($kJ \cdot day^{-1}$)
ENDPRT	=	user-specified end date for summer protein gain (Julian day)
ENEDIET	=	gross energy content of diet ($kJ \cdot g^{-1}$
EXNPWEAND	=	user-specified extended wean date for cows that are not pregnant, expressed as days after conception in the following year (days)
EXPRCHK	=	pregnancy check date for extended weaners (Julian day); calculated as: BDATE + EXPRWEAND – 1

$EXPRWEAND$	=	user-specified extended wean date for pregnant cows, expressed as days after birth in the following year (days)
$FALLD$	=	user-specified fall weaning check date, expressed as days after birth (days)
$FATMOB$	=	user-specified maximum rate at which fat can be mobilized ($g \cdot day^{-1}$)
$FATWT_d$	=	fat weight of the cow on Julian day d (kg)
$FB_{p,d}$	=	user-specified available forage biomass for plant group p on Julian day d ($kg \cdot ha$ dry weight^{-1})
$FECES_d$	=	output of non-digestible material from the rumen on Julian day d ($g \cdot day^{-1}$)
$FETUSWT_d$	=	weight of the fetus on Julian day d (kg)
$FFIFBW_d$	=	fat-free, ingesta-free body weight on Julian day d (kg)
$FIP_{p,d}$	=	actual forage intake rate for plant group p on Julian day d ($g \cdot h^{-1}$)
$FIPHR_{p,h}$	=	actual forage intake rate for plant group p in hour h ($g \cdot h^{-1}$)
$FIPHRCON_{p,h}$	=	actual constrainted forage intake rate for plant group p in hour h ($g \cdot h^{-1}$)
$FOOD_d$	=	forage intake on Julian day d (g)
$FOODIN_h$	=	actual forage intake in hour h (g)
$GESLEN$	=	user-specified gestation period (days)
$GESTCST_d$	=	metabolizable energy required for gestation on Julian day d ($kJ \cdot day^{-1}$)
$GFAT_d$	=	fat added/lost on Julian day d (kg)
$GMUSCLE_d$	=	amount of muscle added or removed on Julian day d (g)
$GPRTN_d$	=	protein added/lost on Julian day d (kg)
GR_d	=	calf growth rate on Julian day d ($kg \cdot day^{-1}$)
$GUTCONT_d$	=	weight of the contents of the gut on Julian day d (kg)
h	=	hour of the model run
$HACOST_h$	=	energy requirement of all activities in hour h ($kJ \cdot h^{-1}$)
HI_d	=	heat increment on Julian day d ($kJ \cdot day^{-1}$)
HP_d	=	heat production on Julian day d ($kJ \cdot day^{-1}$)
$KJPG_h$	=	energy yielded per gram of ingested forage in hour h ($kJ \cdot g^{-1}$)
$KNDIG_{p,d}$	=	rate of passage of non-digestible material from the rumen for plant group p on Julian day d (proportion $\cdot h^{-1}$)
$LACT_d$	=	state variable indicating lactation status of cow on Julian day d (1 = lactating, 0 = not lactating)
$LACTCST_d$	=	metabolizable energy required for lactation on Julian day d ($kJ \cdot day^{-1}$)

$MAINCST_d$	=	cost of maintenance on Julian day *d* (kJ $\cdot$ day^{-1})
$MATERNALWT_d$	=	maternal weight of the cow on Julian day *d* (kg)
$MAXGROW$	=	maximum growth rate (g $\cdot$ day^{-1})
MEI_d	=	metabolizable energy intake on Julian day *d* (kJ)
$MEIHR_h$	=	total metabolizable energy intake in hour *h* (kJ $\cdot$ h^{-1})
$MEIHRCON_h$	=	total constrained metabolizable energy intake in hour *h* (kJ $\cdot$ h^{-1})
MP_d	=	actual milk production on Julian day *d* (l $\cdot$ day^{-1})
$MUSCLEWT_d$	=	amount of muscle on the cow on Julian day *d* (kg)
$NETNRG_d$	=	net energy available for growth and reproduction on Julian day *d* (kJ)
$NEWNET_d$	=	actual energy available from both fat and energy intake for gestation on Julian day *d* (kJ)
$NIT_{p,h}$	=	digestible nitrogen intake for plant group *p* in hour *h* (g $\cdot$ h^{-1})
$NITRO_h$	=	rumen nitrogen pool in hour *h* (g)
$NONDIGFI_{p,h}$	=	non-digestible forage intake for plant group *p* in hour *h* (g $\cdot$ h^{-1})
$NOWEAND$	=	user-specified normal wean date, expressed as days after birth (days)
$NRFP_{p,h}$	=	non-digestible material in the rumen for plant group *p* in hour *h* (g)
$PAWINT_d$	=	user-specified proportion of foraging period spent pawing on Julian day *d* (proportion)
$PCMAX_{p,d}$	=	user-specified maximum consumption rate for plant group *p* on Julian day *d* (g $\cdot$ min^{-1})
$PCTFAT$	=	user-specified proportion of energy change from fat (unitless)
$PCTPRT$	=	user-specified proportion of energy change from protein (unitless)
$PEND$	=	user-specified end averaging date for post-natal mortality calf weight gain, expressed as days after birth (days)
$PFIP_{p,d}$	=	potential forage intake rate of plant group *p* on Julian day *d* (g $\cdot$ min^{-1})
$POWEAND$	=	user-specified post-natal mortality wean date, expressed as days after birth (days)
$PREG_d$	=	a state variable indicating pregnancy status of cow on Julian day *d* (1 = pregnant, 0 = barren)
$PREGEND$	=	user-specified end of window for conception (days); expressed as the number of days after CDATE that conception can last occur
$PREGFATWT$	=	user-specified threshold fat weight at conception above which the cow will become pregnant (kg)

PREGST	=	user-specified start of window for conception (days); expressed as the number of days after CDATE that conception can first occur
PSTD	=	user-specified start averaging date for post-natal mortality calf weight gain, expressed as days after birth (days)
QM_d	=	metabolizability coefficient of the gross energy of diet on Julian day *d* (unitless)
$RCAP_d$	=	capacity of the rumen on Julian day *d* (g)
RCAPPCT	=	user-specified rumen dry matter capacity as a percentage of empty body weight (%)
$REQPRO_d$	=	energy available for growth and fattening on Julian day *d* (kJ)
$REQSUMPRT_d$	=	energy required for protein deposition in summer on Julian day *d* (kJ)
$RFILL_h$	=	amount of forage in the rumen in last hour *h* of Julian day *d* (g)
$RFILLWET_d$	=	weight of wet forage in the rumen on Julian day *d* (kg)
SDPROP	=	user-specified proportion of the snow depth to which the cow sinks (proportion)
$SINKDEP_d$	=	cow's sinking depth in the snow on Julian day *d* (cm)
$SNODEP_d$	=	user-specified snow depth on Julian day *d* (cm)
$SNOWX_d$	=	change in cost associated with locomotion in snow on Julian day *d* (proportion)
STPRT	=	user-specified start date for summer protein gain (Julian day)
SUEND	=	user-specified end averaging date for summer weaning, expressed as days after birth (days)
$SUMPRTCST_d$	=	energy required to deposit target summer protein on Julian day *d* (kJ)
$SUMTRGPRT_d$	=	user-specified target for summer protein deposition on Julian day *d* ($g \cdot day^{-1}$)
SUSTD	=	user-specified start averaging date for summer weaning, expressed as days after birth (days)
SUWEAND	=	user-specified summer wean date, expressed as days after birth (days)
$TARMP_d$	=	target milk production on Julian day *d* ($l \cdot day^{-1}$)
$TEGEST_d$	=	target energy cost of gestation on Julian day *d* ($kJ \cdot day^{-1}$)
$TELACT_d$	=	target energy contained in target milk production on Julian day *d* (kJ)
TER_h	=	total energy obtained from the rumen pool before adding forage ingested in hour *h* ($kJ \cdot h^{-1}$)
$TFETWT_d$	=	target fetus weight in kg on Julian day *d* (kg)
$TFETWTR_d$	=	target fetus weight for reindeer in grams on Julian day *d* (g)

TGR_d	=	target daily growth rate on Julian day *d* (unitless)
THMAXCALFWT	=	user-specified threshold maximum extended weaner fall calf weight (kg)
THMINCALFWT	=	user-specified threshold minimum extended weaner fall calf weight (kg)
THPCALFWTGN	=	user-specified threshold post-natal average daily weight gain of the calf (g)
THSUMPRTGN	=	user-specified threshold protein gain of the cow (g)
$TMLKNRG_d$	=	amount of target milk energy on Julian day *d* ($kJ \cdot ml^{-1}$)
$TNRF_h$	=	total non-digestible pool in hour *h* (g)
$USERPREG_y$	=	user-specified annual pregnancy status for year *y* (0 = barren, 1 = pregnant)
$WATRFAT_d$	=	fat contribution to cow water weight on Julian day *d* (kg)
$WATRMUS_d$	=	muscle contribution to cow water weight on Julian day *d* (kg)
$WATRWT_d$	=	cow water weight on Julian day *d* (kg)
$WEANDAY_y$	=	user-specified annual number of days after birth when weaning occurs in year *y* (days)
y	=	year of the model run