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*Brief Communication*

# CARMA's integrative modeling: historical background of modeling caribou and reindeer biology relevant to development of an energy/protein model

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## Introduction

The objective of this brief communication is to review how development of spreadsheet and computer simulation models of *Rangifer* biology/ecology has influenced construction of the CircumArctic *Rangifer* Monitoring and Assessment (CARMA) energy/protein model, which simulates body weight and condition and reproduction characteristics of a female caribou (*Rangifer tarandus*) in response to environmental inputs and reproductive history. A full description of input variables, driving algorithms and output variables of the CARMA energy/protein model is being written for a peer-reviewed publication. This publication also will be the basis of a manual to assist users as they exercise the model. In this publication we give rationale for algorithms and we justify the hierarchy used to allocate energy and protein resources throughout the model. Also in preparation is a publication that addresses verification of key algorithms and performs a sensitivity analysis of key components of the model. This review is restricted to models specific to *Rangifer* and published since the early 1970s. It covers the scope of input that influenced our modeling process and has import to understanding modeling of caribou biology and ecology in the last 40 years.

## Initial models

Two simulation models presented at the first and second International Reindeer/Caribou Symposia were important to opening our appreciation for the potential modeling can play in understanding *Rangifer* ecology by quantifying biologically important relationships. At the first symposium a population-centric model specific to caribou (Bunnell *et al.,* 1975) was presented by Eoin McEwan who discussed how the model simulated caribou population responses to a suite of environmental variables. The objective was to use population trends in decision-making relative to caribou management. Input data were based on driving variables recommended by caribou biologists and managers who attended model development workshops. The workshop approach, led by Fred Bunnell of the University of British Columbia, initially used these experts to provide algorithms that constituted internal "mechanisms" of caribou responses to environmental drivers. To reflect the collaborative nature of its development, the model was fondly termed the "Buda Himimi McPapescaw Model", a title reflecting initials of participating experts. The primary impetus for the modeling approach was a need to better understand drivers of the "bottom-up" components of caribou ecology in order to assess the role of natural predation and hunter harvests on the population. The modeling exercise pointed to a need to better understand physiological responses of an animal to forage availability and digestion of dietary constituents relative to intake, and the energetic costs of migration, foraging, and harassment by flies and mosquitoes. Further, realistic assessments of maintenance and production costs were needed to add systematic responses imposed by environmental variables. These requirements were identified generally for modeling most cervid management systems. A contribution to advance our thinking on some of these identified physiological responses was addressed in a model presented at the second reindeer/caribou symposium in Norway by Swift et al. (1980), which focused on current aspects of rumen function from the cervid perspective and laid out a useful mechanism for modeling *Rangifer* rumen function.

## Energy balance models

A significant step forward toward current models was provided by the intensive studies in the tundra biome program, within the International Biological Program (IBP) (Brown, 1975; Brown *et al.,* 1980; Bliss *et al.,* 1981). This program focused on quantifying controls over primary and secondary production in the Arctic and resulted in publications of a range of models. Within the biome programs, energy was an important currency for comparing ecological transactions. Based on their biome work, White et al. (1975) used an energy balance sheet (*i.e.*, a spreadsheet model that balances energy intake with expenditure) to test the hypothesis that coastal Arctic tundra in the vicinity of Prudhoe Bay, Alaska, was sufficiently low in biomass of forage species to limit individual productivity of female caribou. They concluded that to be reproductively successful, caribou were likely dependent on access to upland tundra south of the coastal plain, an area of greater species richness and higher biomass. A spreadsheet model approach was subsequently used to address energy relations in a number of herds. Using a spreadsheet model of energy balance, Boertje (1985) suggested there was no nutritional limitation on caribou of the Denali herd in interior Alaska. Also this form of model analysis was used by L. Camps (in Bergerud *et al.,* 2008) to estimate nutritional influence over forage intake to evaluate calving and early summer range of the George River herd (GRH) for which degradation of the range had likely nutritional consequences (Manseau, 1996).

## Energy simulation model

A limitation of spreadsheet energy balance models is that they limit the user's ability to incorporate a larger number of variables and to project outcomes over long time frames using short time steps. Simulation modeling can fill these requirements. Thus, concurrently with development of the energy spreadsheet model for caribou at Prudhoe Bay, Russell (1976) formulated a simulation model that converted behavioral activity through decision-based modeling of caribou feeding cycles to determine energetic consequences of insect harassment superimposed on foraging strategies, again simulating an individual female caribou.

Following IBP funded research through the early 1970s, an evaluation of the modeling approach was made by a team of caribou biologists/ecologists/managers to determine if it could provide a linkage between habitat quality, body condition, and reproductive effort (Klein & White, 1978). To better understand these linkages, more research was recommended, as was the development of a comprehensive model. To that end and based on new energy expenditure estimates of reindeer and caribou, Fancy (1986) developed a Fortran based model for energy balance of female caribou in the Porcupine caribou herd (PCH) and concluded that an animal's control over energy input had a greater impact on balance than controls over energy expenditure. Subsequently, based on the potential for scenario building of the Bunnell et al. (1975) model and expanded algorithms in the Fancy (1986) model, a new model was developed to examine consequences for caribou of possible industrial development associated with drilling for oil in the Arctic National Wildlife Refuge, Alaska. Financial support from US and Canadian governments enabled this caribou modeling effort under the leadership of Fred Bunnell (Hovey *et al.,* 1989; Kremseter *et al.,* 1989). This energy-based model used the most advanced understanding of forage intake (White & Trudell, 1980; Trudell & White, 1981), ruminant physiology, biochemistry, and nutrition to simulate a female caribou driven by environmental variables measured in the range of the PCH (Russell *et al.,* 1993). The resultant PCH energy model was driven by an intake sub-model that produced metabolizable energy input to drive an energy allocation sub-model that accounted for expenditures associated with maintenance and deposition in body reserves, gestation, and lactation (Russell *et al.,* 2005). Protein-N inputs and transactions associated with changes in body composition were tracked as a bookkeeping component linked to energy through known stoichiometry (ARC, 1980; Torbit *et al.,* 1985). Components of the model have been verified through applications that emphasize energy expenditure such as energy consequences of low flying fighter jet aircraft (Delta caribou herd: Luick *et al.,* 1996), road and pipeline effects at Prudhoe Bay [Central Arctic herd (CAH): Murphy *et al.,* 2000], integration of nutritional components to determine responses to climate change (PCH: Griffith *et al.,* 2002; Kruse *et al.,* 2004), effects of climate change (PCH: Russell *et al.,* 1996; CAH: Murphy *et al.,* 2000), summer range assessment (GRH: Manseau, 1995), and full integration of components for application to development (*e.g.*, Bathurst caribou herd: environmental assessment of Diavik mine, cumulative effects pilot project, Gunn *et al.,* 2011).

**Energy/protein simulation model**

A limitation of the PCH energy model was that it did not mechanistically simulate protein and nitrogen dynamics and their interactions with energy when inputs are uncoupled. In particular the ability to explore more flexible use of energy and protein through seasonal changes in nutrition and to produce microbial protein from recycled nitrogen using metabolizable energy derived from highly digestible forages (ARC, 1980; NRC, 2007), like lichens in winter, was lacking. Questions addressing the ability of mushrooms to provide a flush to body reserves in late summer-autumn required a more mechanistic linkage between energy and protein-N dynamics. As in many studies, the energy and protein drain of parasites to the individual caribou needed to be simulated (Gunn & Irvine, 2003).

With the support of the CARMA network the original energy model was modified and expanded to integrate protein transactions. Thus, we now simulate separate but coordinated partitioning of energy and protein-N. The model consists of three sub-models: 1) forage intake (diet selection, logistic controls over eating rate, time allocation); 2) metabolic transactions (rumen/post-ruminal digestion and absorption to predict daily intake of metabolizable protein-N in parallel with metabolizable energy); and 3) energy and protein allocation (partition metabolic nitrogen and energy to meet the animal's protein-N and energy requirements for maintenance, growth, and reproduction). Partitioning of metabolic protein and energy is a complex hierarchical process as shown diagrammatically in Fig. 1. The model simulates maternal protein and fat reserves at the beginning of winter and tracks them through seasonal changes in intake and environmental effects such as snow and icing conditions in winter and forage availability on the calving grounds and post-calving ranges. Although not formally tracked by the model, the simulations take into account use of protein reserves required for intermediary metabolism that could become limiting to fetal growth and milk production (White *et al.,* 2013).

In previous versions of the model, we have not simulated seasonal requirements for growth of antlers and coat. Based on simulations of antler growth by Moen & Pastor (1998) we have now included the energy and protein transactions for growth of both antlers and coat. For the first time nutrient requirements of deer (*Odocoileus* spp.), elk (*Cervus elaphus*), and reindeer/caribou as well as New World camelids are now available (NRC, 2007) and the calculations provide data for validating model outputs. Another validation source is provided by Barboza et al. (2007) in their book on integrative wildlife nutrition. The authors have used a spreadsheet approach to assist the reader gain a quantitative understanding of nutrient interactions in a wide array of animals. This book and reviews by Parker (2003) and Parker et al. (2009) provide further in-depth understanding of nutritional underpinnings of ruminant wildlife ecology independent of the algorithms driving the CARMA energy/protein model.

One of our priorities is to simulate energy and protein-N dynamics of infestation by parasites. Although energy costs of exposure to biting insects is well simulated by the model, metabolic costs of hosting larval stages of them is not well known. Analysis to date suggests the over-winter cost by warble fly larvae to Greenland caribou could be significant (Cuyler *et al.,* 2012). Likewise, we plan to simulate metabolic costs of hosting intestinal parasites that are almost ubiquitous in *Rangifer* (Gunn & Irvine, 2003; Kutz *et al.,* 2004).

**Integrating remotely accessed data and scenario building**

An added objective of the restructuring of the CARMA energy/protein model is to better support "what-if" scenario analyses applicable to assessment of cumulative effects of climate change and industrial development (Gunn *et al.,* 2013). To more easily enter extant data sets, we use abiotic data from regionally downscaled sites such as NASA's Modern Era Retrospective Analysis (MERRA) website (Russell *et al.,* 2013). MERRA-derived data sets drive seasonal and year-specific abiotic variables such as temperature, wind, and precipitation. From these data users can infer biologically important variables such as snow depth, rain-on-snow and icing events in winter, and incidence of mosquito and warble/nasal bot flies in summer. By calculating growing degree days (GDD) above 0$^{o}$C from MERRA data users can now derive plant biomass, protein concentration, and fiber levels of dietary important species (Finstad, 2008) throughout summer. A new "dashboard" was added to the model that will allow users to view the entered MERRA data appropriate to the region or the herd of interest. Also, the user can enter new data in order to exercise or "game" with the model. Thus, by driving the model through this dashboard we anticipate it will be easier to determine how climate might induce changes in abundance and quality of *Rangifer* forage plants and how this will affect body weight and body composition. The objective is to provide basic drivers in sufficient detail that

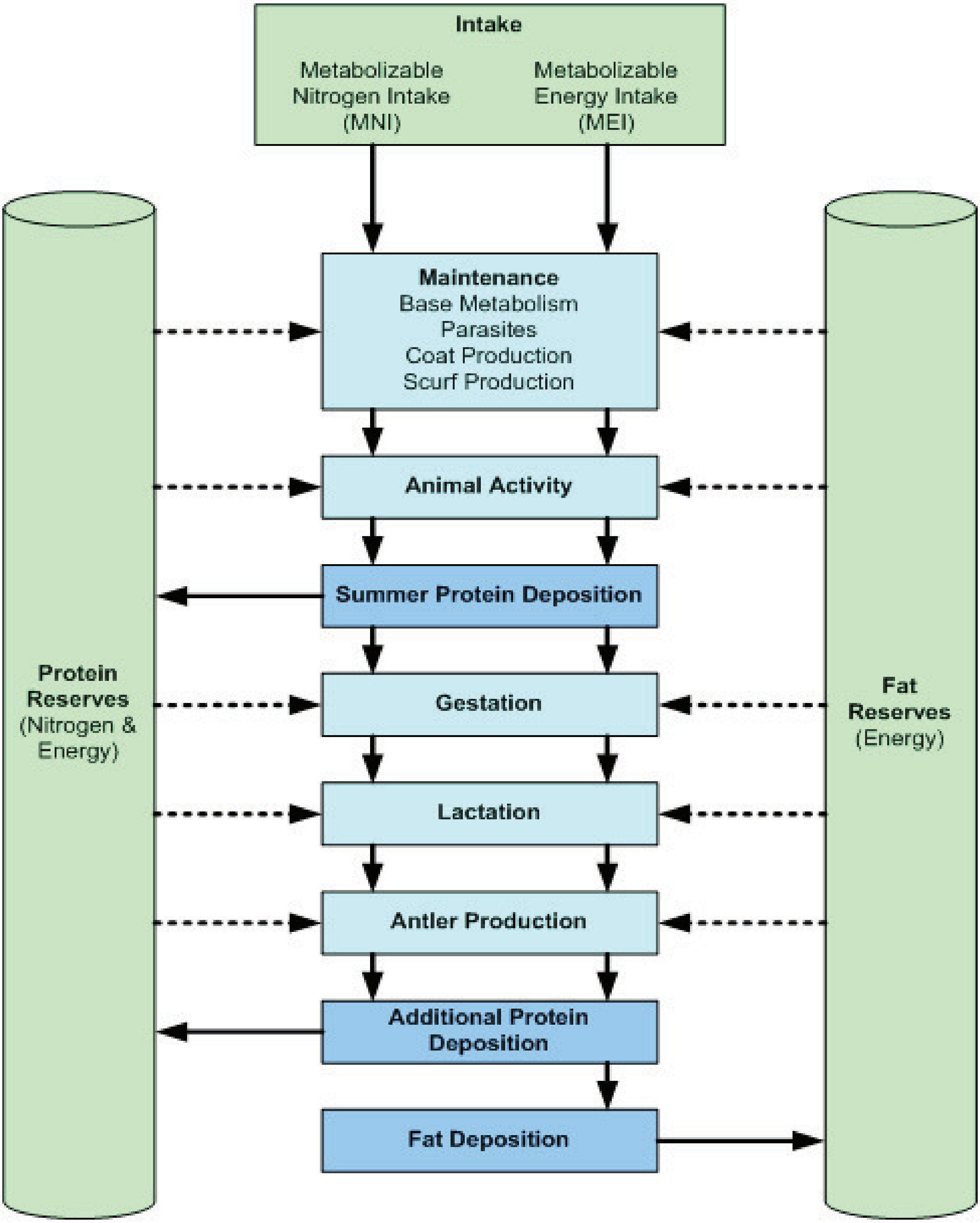


Fig. 1 Daily allocation of protein-N and energy showing the order of priority of each allocation stage.

biologists and managers of most circum-Arctic *Rangifer* populations will be able to drive the model either independently or with CARMA modeling staff. Regionally specific inputs with a 32 year historical record are currently available (Russell *et al.,* 2013).

We have operated under the assumption that the centerpiece of the model is a female caribou or reindeer whose reproductive performance and survival drives population dynamics. Thus, the female must be simulated in sufficient detail so as to provide insight into her responses to environmental variables as well as to emulate measures of body mass, body composition, and reproduction obtained from the field. By making multiple runs of the model with cohorts of varying reproductive history, the user can gain insight into population responses that may not be detectable in the field. From a CARMA perspective, the model will allow biologists and managers to compare caribou productivity in separate populations, it should allow the analysis of changes in female productivity in response to year-to-year variability in environmental drivers, and users of the model will be able to analyze the relative importance of drivers on classes of females in populations undergoing variable abundance.

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