

Simulating antler growth and energy, nitrogen, calcium and phosphorus metabolism in caribou

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Abstract: We added antler growth and mineral metabolism modules to a previously developed energetics model for ruminants to simulate energy and mineral balance of male and female caribou throughout an annual cycle. Body water, fat, protein, and ash are monitored on a daily time step, and energy costs associated with reproduction and body mass changes are simulated. In order to simulate antler growth, we had to predict calcium and phosphorus metabolism as it is affected by antler growth, gestation, and lactation. We used data on dietary digestibility, protein, calcium and phosphorus content, and seasonal patterns in body mass to predict the energy, nitrogen, calcium, and phosphorus balances of a "generic" male and female caribou. Antler growth in males increased energy requirements during antler growth by 8 to 16%, depending on the efficiency with which energy was used for antler growth. Female energy requirements for antler growth were proportionately much smaller because of the smaller size of female antlers. Protein requirements for antler growth in both males and females were met by forage intake. Calcium and phosphorus must be resorbed from bone during peak antler growth in males, when > 25 g/day of calcium and > 12 g/day of phosphorus are being deposited in antlers. Females are capable of meeting calcium needs during antler growth without bone resorption, but phosphorus was resorbed from bone during the final stages of antler mineralization. After energy, phosphorus was most likely to limit growth of antlers for both males and females in our simulations. Input parameters can be easily changed to represent caribou from specific geographic regions in which dietary nutrient content or body mass patterns differ from those in our "generic" caribou. The model can be used to quantitatively analyze the evolutionary basis for development of antlers in female caribou, and the relationship between body mass and antler size in the Cervidae.

Key words: Cervidae, energetics, mineral nutrition, model, nutrient requirements, seasonal rhythm.

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Introduction

Antlers are among the most striking features of the Cervidae. Despite the importance of antlers to behavior and evolution of cervids, very little work has been done on the nutritional physiology of antler growth (Goss, 1995). In part, the lack of experimental work is caused by difficulties in separating metabolism for antler growth from metabolism necessary for growth and tissue anabolism in live animals (Brown, 1990). A further complication is that it would be desirable to use an experimental protocol which could monitor the status of energy, protein, and mineral metabolism simultaneously on

several individuals. Such experiments quickly become technologically challenging and prohibitively expensive.

Simulation models are an alternative method to increase our understanding of the nutritional physiology of cervids. Most previous simulation models for wild ruminants have been limited to the winter months and dealt primarily with energy nutrition (Hobbs, 1989; Miquelle *et al.*, 1992). Some have been extended to other seasons (Hudson & White, 1985; Fancy, 1986) and nitrogen metabolism has been simulated (Swift, 1983). With the exception of the model developed by Swift, these models have

been developed to address specific questions about the metabolism of a single species. Swift's model could simulate many ruminant species with adequate parameterization, but did not implement costs of productive functions such as lactation or antler growth. We have developed and validated a model which is similarly adaptable with respect to ruminant species, and which can simulate the energetic costs of gestation and lactation (Moen *et al.*, 1997).

Caribou are unique among cervids in that both males and females can grow antlers (Kelsall, 1968). In addition, males have among the heaviest antlers of extant cervids in relation to body mass (Geist, 1987). These features are of interest from an evolutionary perspective, both between male and female caribou and among cervids in general. Our model can be used to investigate previously unaddressable questions on mineral metabolism (Brown, 1990; Goss, 1995), and can be used to develop research hypotheses to be tested on live animals. In this paper we formally describe the equations required to simulate antler growth and composition, and present initial validation of the model with respect to calcium and phosphorus metabolism during antler growth. We then use the model to demonstrate the energy, nitrogen, calcium, and phosphorus needs of adult male and female caribou throughout an annual cycle. We would like to emphasize that the input values for parameters such as antler mass, body mass or seasonal changes in calcium and phosphorus content of forage can be easily changed to represent the characteristics of caribou in a specific area.

Methods

The foundation for our modeling work is the Energetics and Activity Simulation Environment (EASE), which simulates the energetics and metabolism of a free-ranging ruminant (Moen *et al.*, 1997). Unlike previous energetics models, the EASE model was designed to accept "plug-in" modules which simulate processes other than energy metabolism, such as a spatially-explicit foraging model (Moen *et al.*, 1997; 1998), nitrogen metabolism (Moen & DelGiudice, 1997), and the antler growth model described in this manuscript. The stochastic nature of many model parameters in the EASE model is another unique feature that simulates variability in real animals. Examples of such parameters include browse digestibility, efficiency of energy use for gestation, lactation, and mainte-

nance, and the fat:protein catabolism ratio (Moen *et al.*, 1997). For parameters that are stochastic, parameter values are drawn from a normal distribution with variation such that the coefficient of variation is 5% of the mean value for the parameter each day.

The EASE model operates on a daily time-step. Each day the energy balance is determined from forage intake and the energetic needs of maintenance, activity costs, gestation, lactation, and antler growth. If the simulated animal is in negative energy balance, body fat and protein are catabolized to meet the energy deficit. If the simulated animal is in positive energy balance, fat and protein are deposited. Nitrogen metabolism was added to the EASE model and it was then used to predict urinary urea nitrogen:creatinine ratios (Moen & DelGiudice, 1997).

To simulate antler growth, we were required to add functionality in the following areas: (1) calcium and phosphorus metabolism, (2) antler mass changes and (3) energetic requirements for antler growth. Model parameters are defined in equations 1-22 with parameter values we used in the validation and model experiment simulations. Most of these parameter values have been derived directly from the published literature on wild or domestic ruminants. In a few cases, where experimental results were not available, we estimated parameter values based on related physiological processes. These model parameters can be easily changed if new data should become available in the future.

Simulation of calcium and phosphorus metabolism

The EASE model simulates the calcium and phosphorus stored in and flowing through the body (Fig. 1). The major storage depot for both calcium and phosphorus is the skeleton, which contains about 99% of calcium and more than 75% of the phosphorus in the body (Agricultural Research Council, 1980). Both calcium and phosphorus can be resorbed from bone when metabolic needs can not be met by forage intake (Braithwaite, 1983; Muir *et al.*, 1987a). Less than 20% of the bone mass can be resorbed from a replete skeleton (Hillman *et al.*, 1973). Ash is 5.5% of the fat and ingesta-free body mass in an animal with a replete skeleton in the EASE model, and 4.5% in an animal which has completely depleted the available minerals in its skeleton. Calcium and phosphorus comprise 60% and 30% of the available skeleton mass which can be resorbed, respectively (*MaxBoneCa* and *MaxBonePhos*, g). *CaStatus* and *PhosStatus* (unitless

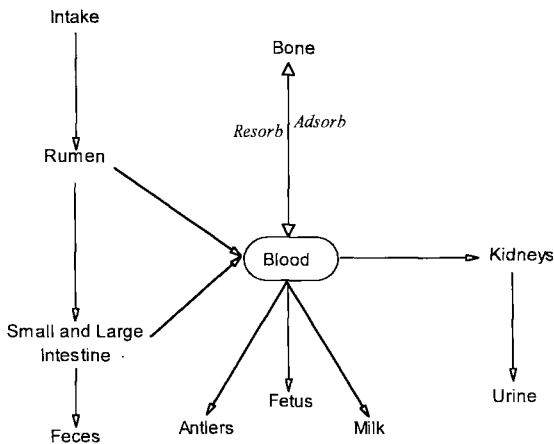


Fig. 1. Pathways calcium and phosphorus follow from ingestion to excretion as implemented in the simulation model.

fractions) range from 0.0 to 1.0 and indicate the fractional skeleton repletion for calcium and phosphorus, respectively.

Calcium and phosphorus intake is determined by the content of each of these elements in the diet. $IntakeCa_d$ (g Ca/day) is calculated from calcium content in the diet, and $IntakePhos_d$ (g P/day) is calculated from phosphorus content in the diet. Availability of ingested calcium and phosphorus depends on type of forage, mineral needs, and mineral status of the animal (Braithwaite, 1983; National Research Council, 1989). Availability increases as skeleton is resorbed, we use a base value of 35% availability when the skeleton is replete, which increases to 65% maximum availability when mineral stores in the skeleton are completely resorbed:

$$AvailFrcCa_d = 0.35 + (1.00 - CaStatus_d) \quad (1)$$

$$AvailFrcPhos_d = 0.35 + (1.00 - PhosStatus_d) \quad (2)$$

where $AvailFrcCa_d$ and $AvailFrcPhos_d$ are the available fraction of calcium and phosphorus in forage on day d .

Available calcium ($AvailIntakeCa_d$, g Ca / day) and phosphorus ($AvailIntakePhos_d$, g P/day) are used to meet daily requirements:

$$AvailIntakeCa_d = AvailFrcCa_d \cdot IntakeCa_d \quad (3)$$

$$AvailIntakePhos_d = AvailFrcPhos_d \cdot IntakePhos_d \quad (4)$$

The predicted daily requirements for endogenous urinary calcium ($EUCa_d$, g Ca/day) and endogenous urinary phosphorus ($EUPhos_d$, g P/day) are:

$$EUCa_d = 0.0025 \cdot weightKG_d \quad (5)$$

$$EUPhos_d = 0.0003 \cdot weightKG_d \quad (6)$$

where $weightKG_d$ is body mass in kg (Braithwaite, 1986; Muir *et al.*, 1987a).

The calcium and phosphorus leaving the rumen via the intestinal tract is excreted in the feces. We partition calcium and phosphorus in feces into metabolic fecal, unavailable, and dietary surplus fractions. The predicted daily requirements for metabolic fecal calcium ($MFCa_d$, g Ca/day) and metabolic fecal phosphorus ($MFPPhos_d$, g P/day) are:

$$MFCa_d = 0.0065 \cdot WeightKG_d \quad (7)$$

$$MFPPhos_d = 0.025 \cdot WeightKG_d \quad (8)$$

The requirements for calcium are lower than has been shown for domestic ruminants (Agricultural Research Council, 1980), but similar requirements have been measured in wild ruminants (Muir *et al.*, 1987a; Grasman & Hellgren, 1993). Unavailable calcium ($UnAvailIntakeCa_d$, g Ca/day) and phosphorus ($UnAvailIntakePhos_d$, g P/day) are calculated from dietary intake of calcium and phosphorus and availability:

$$UnAvailIntakeCa_d = IntakeCa_d - AvailIntakeCa_d \quad (9)$$

$$UnAvailIntakePhos_d = IntakePhos_d - AvailIntakePhos_d \quad (10)$$

The dietary surplus is calculated by difference between intake and the utilization of calcium and phosphorus for metabolic needs described below.

Calcium and phosphorus are required for gestation, lactation, and antler growth. If the animal is pregnant, gestation requirements for calcium and phosphorus ($GestCa_d$, g Ca/day, $GestPhos_d$, g P/day) are predicted from the number of fetuses, weight of fetus at birth (Table 1), and the day of gestation (Robbins & Moen, 1975), assuming a calcium content in the fetus of 13 g/kg and a phosphorus content of 7 g/kg (Agricultural Research Council, 1980). Calcium and phosphorus are also required for milk production if the animal is lactating ($LactCa_d$, g Ca/day, $LactPhos_d$, g P/day). $LactCa_d$ and $LactPhos_d$ are predicted from the day of lactation, the number of young suckled, a milk production curve (Moen *et al.*, 1997), initial and peak milk production per day, and the content of calcium and phosphorus in caribou milk (Robbins *et al.*, 1987; Parker *et al.*, 1990). Calcium and phosphorus are incorporated into antlers ($AntlCa_d$, g Ca/day,

$AntlPhos_d$, g Ca/day) with calcium content of 36% of ash and a phosphorus content of 18% (Brown, 1990). The ratio of Ca:P does not vary during antler growth (Muir *et al*, 1987b). Prediction of antler mass and ash content is described below (Eqs. 17-22).

The net calcium and phosphorus balances ($NetCa_d$, g Ca/day, $NetPhos_d$, g P/day) on a daily basis are calculated by summation of each factor:

$$NetCa_d = AvailIntakeCa_d - (EUCa_d + MFCa_d + LactCa_d + AntlCa_d) \quad (11)$$

$$NetPhos_d = AvailIntakePhos_d - (EUPhos_d + MFPhos_d + LactPhos_d + AntlPhos_d) \quad (12)$$

Gestation, lactation, and antler growth parameters are 0 when the animal is not pregnant, not lactating, or not growing antlers, respectively. A very important implication of Eqs. 11 and 12 is that calcium and phosphorus are conserved; all sources, sinks, and storage pools of calcium and phosphorus are updated each day on the same time step to ensure conservation.

If $NetCa_d$ is < 0.0 and $CaStatus_d$ is > 0.0 , or if $NetPhos_d$ is < 0.0 and $PhosStatus_d$ is > 0.0 , then resorption of mineral stores to meet mineral needs occurs ($ResorbCa_d$, g Ca/day, $ResorbPhos_d$, g P/day). We currently do not limit the mineral stores available for resorption each day, i.e., $MaxBoneCa \cdot CaStatus_d$ could be resorbed in the model. Although it is unlikely that the animal could resorb its entire calcium or phosphorus reserves in a single day, it is also unlikely, in a biologically accountable model, that an excessive amount of mineral would be resorbed on a given day.

If $NetCa_d$ is > 0.0 and $CaStatus_d$ is < 1.0 , or $NetPhos_d$ is > 0.0 and $PhosStatus_d$ is < 1.0 , then repletion of the mineral stores occurs ($AdsorbCa_d$, g Ca/day, $AdsorbPhos_d$, g P/day). We allow up to 5% of $MaxBoneCa$ and $MaxBonePhos$ to be resorbed each day. We do not currently consider the negligible amounts of calcium and phosphorus in fat and protein during anabolism and catabolism of body tissues in the model. If there is still calcium or phosphorus remaining after adsorption to the bone, it is excreted:

$$SurplusCa_d = NetCa_d - AbsorbCa_d \quad (13)$$

$$SurplusPhos_d = NetPhos_d - AbsorbPhos_d \quad (14)$$

where $SurplusCa_d$ and $SurplusPhos_d$ are the surplus of each element (g/day). Fecal calcium and phospho-

rus ($FecalCa_d$, g Ca/day, $FecalPhos_d$, g P/day) are calculated as:

$$FecalCa_d = UnAvailIntakeCa_d + MFCa_d + SurplusCa_d \quad (15)$$

$$FecalPhos_d = UnAvailIntakePhos_d + MFPhos_d + SurplusPhos_d \quad (16)$$

Simulation of antler mass and composition

Unlike changes in length, changes in antler mass during antler growth are extremely difficult to measure experimentally. We are aware of only 1 experiment in which antler mass was determined throughout the antler growth period (Muir *et al*, 1987b). We used data from this experiment, corroborated by data on phenology and changes in length of antlers of caribou, moose, and red deer (Bergerud, 1976; Van Ballenberghe, 1982; Fennessy *et al*, 1992), to predict changes in mass and composition of caribou antlers.

Antlers are metabolically active until velvet is shed. For about 75% of the period when velvet is on the antler, antler length and mass is increasing. Rapid mineralization and drying of the antler occurs during the last 25% of the period. Antler mass is predicted with a logistic equation during the increasing antler mass phase in the first 75% of the antler growth period (Eq. 17), and with a linear decline in mass during the period of rapid mineralization in the last 25% of the antler growth period (Eq. 18):

$$AntKG_d = 1.25 \cdot AntKg_{AntlGrowPeriod} \div (1.0 + 30.0 \cdot e^{-10.0 \cdot 0.95 \cdot AntlGrowPeriod}) \quad (17)$$

$$AntKG_d = MaxAntlerKG + FrcMin_d \cdot AntMassDecline \quad (18)$$

where $AntKG_d$ is antler mass in kg on day d , $AntlGrowPeriod$ is the length of the antler growth period in days, and $MaxAntKG$ is antler mass at the end of velvet shedding. In Eq. 18, $FrcMin_d$ is the fraction of the mineralization period completed, and $AntMassDecline_d$ is the difference between antler mass at the start of the mineralization period and $MaxAntKG$, assuming antlers are 85% dry matter at the end of velvet shedding (Muir *et al*, 1987b). Parameters in Eq. 17 result in a peak antler mass about 20% higher than antler mass at the end of velvet shedding (Muir *et al*, 1987b).

Antler tissue is composed primarily of water, protein, and ash. Antler ash is also predicted with a logistic equation for the entire antler growth period from data of Muir *et al*.

$$AntFrc_d = 1.07 \cdot AntFrc_{AntlGrowPeriod} \div (1.0 + 125.0 \cdot e^{-10.0 \cdot 0.95 \div AntlGrowPeriod}) \quad (19)$$

where $AsbFrc_d$ is the ash fraction of the antler, and $AntlGrowPeriod$ is the length of the antler growth period in days. Antler organic matter, which is essentially all protein (Brown, 1990) is predicted from data in Muir *et al.*:

$$AsbToOMratio_d = 0.17 + 1.46 \cdot FrcGrowPeriod_d \quad (20)$$

where $AsbToOMratio_d$ (unitless) is the ratio of ash to organic matter in the growing antler, and $FrcGrowPeriod_d$ is the fraction of the antler growth period on day d . The organic matter fraction of the growing antler ($OMFrc_d$, unitless), can then be calculated from the previously derived ash fraction in the growing antler:

$$OMFrc_d = \frac{AsbToOMratio_d}{AsbFrc_d} \quad (21)$$

Finally, water content of the growing antler is calculated by subtraction:

$$Waterfrc_d = 1.0 - (OMFrc_d + AsbFrc_d) \quad (22)$$

where $WaterFrc_d$ (unitless) is fraction of water in the antler on day d .

Simulation of energy and protein requirements

Daily energy and protein requirements have been previously described for our model (Moen & DelGiudice, 1997; Moen *et al.*, 1997). Briefly, energy needs are estimated in a factorial fashion, considering costs of basal metabolism, activity, gestation, and lactation. With the addition of antler growth, we needed to estimate the efficiency of energy use to produce antlers, a parameter which is difficult or impossible to obtain experimentally (Brown, 1990; Goss, 1995). Because most of the organic matter in antler tissue is protein, we used $OMFrc_d$ to predict the amount of protein deposition in antlers each day, and then estimated the efficiency of use of energy to be 25%, which is between the 13% efficiency of energy use for gestation and the 40% efficiency of energy use for lean tissue growth (ARC, 1980). Antler mass was considered to be a portion of body mass when antler tissue was metabolically active. Energy requirements are assumed to decline linearly to 0 during the period after the antler has stopped increasing in length until the end of velvet shed-

ding. This may underestimate the energy requirements for mineralization of antler tissue which occurs after the antler has stopped growing and before velvet shedding.

Protein metabolism is also calculated factorially, although urea nitrogen recycling must also be accounted for in a simulation model. The recycling rate of urea nitrogen is determined by the diet nitrogen content and the animal's energy balance (Moen & DelGiudice, 1997). In order to simulate antler growth, we modified the daily nitrogen requirements by adding an additional nitrogen sink, the antler, and assuming that antler protein was 6.25% nitrogen.

Energy balance and body mass changes are primarily determined by forage intake and digestibility input parameters. Activity budgets and energetic costs of different activities were set as in (Moen *et al.*, 1997). In year-long simulations, we set energy intake to approximately reproduce the observed annual patterns of body mass changes in free-ranging caribou (Kelsall, 1968; Adamczewski *et al.*, 1987; 1993; Huot, 1989). When simulating male caribou, we reduced intake during a rutting season of 10 days in early October to 40 kcal digestible energy/kg^{0.75} body mass. We did not increase activity costs during the rut (Miquelle, 1990). All of these input parameters could be easily modified if one wished to change energy costs of the rut or body mass parameters in the future. Phenological patterns in antler growth and reproduction were from Bergerud (1976). We set annual patterns in forage mineral content and digestibility according to the published literature (Hyvarinen *et al.*, 1977; Chapin *et al.*, 1980; Staaland *et al.*, 1983; Staaland & Sæbø, 1993; Chase *et al.*, 1994). Diet digestibility was highest in summer at 64%, and declined in winter to 40%. Crude protein in the diet was 13.5% in summer, and declined to 6% in winter. Calcium concentrations ranged from 0.50% in winter to 0.75% in summer, and phosphorus concentrations ranged from 0.30% in summer to 0.60% in winter. Diet digestibility, crude protein, calcium, and phosphorus all followed seasonal patterns with smooth transitions between minimum and maximum values (Moen *et al.*, 1997).

Model validation and simulation protocol.

We validated the calcium and phosphorus components of this model by simulating independent published experiments on mineral balances and antler mass during antlerogenesis and comparing mea-

sured calcium and phosphorus mineral balances to calcium and phosphorus balances predicted by the model (Stephenson & Brown, 1984; Muir *et al.*, 1987a; Grasman & Hellgren, 1993). We also compared predicted and measured fractional and absolute contents of calcium in the antler. We have previously validated the energetics and nitrogen components (Moen & DelGiudice, 1997; Moen *et al.*, 1997). The experiments used to validate the model were not used in model development. We changed input parameters which were specific to each experiment (e.g., time of year, length of experiment, initial body mass, start of antler growth period, food intake and digestibility, dietary nitrogen, calcium, and phosphorus) for each validation simulation. The same compiled executable was used in validation simulations for both red deer and white-tailed deer, and for the initial model experiments with male and female caribou.

We also set up a model experiment to determine the effect of increased energetic costs for growing antlers. In the first experiment, we changed the efficiency of use of energy for antler growth from 0.25 to 0.133, the efficiency with which energy is used for gestation by pregnant females (Agricultural Research Council, 1980). In the second experiment, in addition to decreasing efficiency of energy use to 0.133, we increased the energy requirements of the entire antler by 10 kcal/kg^{0.75} of antler mass.

We began model experiments on the first day of antler growth for male caribou, and the first day of lactation for female caribou. Male caribou began simulations weighing 150 kg with 5% body fat on Julian day 120, the first day of antler growth. Male and female antlers weighed 10 and 1 kg at the end of velvet shedding, respectively. The antler growth period (*AntlGrowPeriod*, eq. 17) was 125 days for both males and females. Female caribou carried a single fetus through gestation, nursed the calf for 120 days, and grew antlers weighing 1 kg at the end of velvet shedding. Females began simulations weighing 80 kg with 5% body fat on Julian day 143, the day a single 5 kg calf was born after a 220 day gestation. The first day of antler growth for females was Julian day 166. Rumen weight varied seasonally (Adamczewski *et al.*, 1987) from 10% of body mass in summer to 14% of body mass in winter. Milk production increased from 1.25 l/day at birth to 1.75 l/day at peak lactation 1 week after birth, then declined exponentially until lactation ended when the calf was 125 days old. Milk was

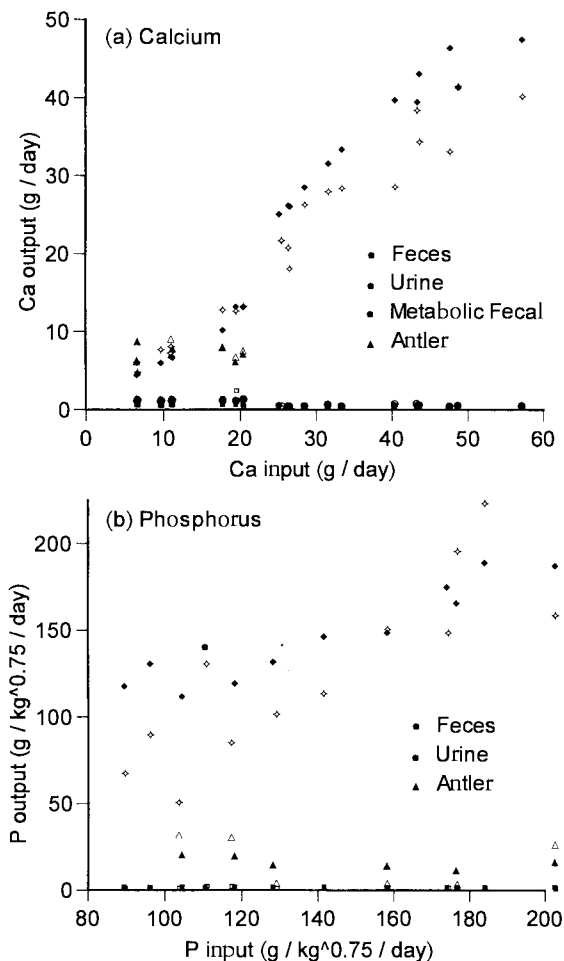


Fig. 2. Simulation of (a) calcium partitioning in adult red deer during antler growth and (b) phosphorus partitioning in adult male white-tailed deer throughout the year. Intake of each element in the model was equal to intake by experimental animals, and partitioning between urine, feces, and antlers was predicted. Solid symbols represent model output, hollow symbols of the same type are experimental results.

11% fat, 7% protein, 0.3% calcium, and 0.25% phosphorus (Robbins *et al.*, 1987; Parker *et al.*, 1990). *CaStatus* and *PhosStatus* were both set to 0.50 at the start of the simulations.

Energy costs of different activities, and activity budgets for each day are provided in Moen *et al.* (1997). The simulated activity budgets approximate activity budgets of free-ranging non-migratory ruminants and resulted in activity costs of about 20% of basal metabolic rate each day (Boettje, 1985; Fancy, 1986). Each experiment was replica-

ted 30 times. Conditions among replications in each experiment were identical except for stochastic variation in the EASE model.

Results

Validation

Independent validation simulations were done by simulating experiments that were not used in model development. Predicted calcium partitioning of red deer and white-tailed deer and phosphorus partitioning of white-tailed deer throughout the year to urine, feces, and antlers corresponded with measured values across a wide range of calcium and phosphorus intakes (Fig. 2). Fecal production of calcium corresponded well with measured values (Fig. 2a), but the model slightly over-predicted fecal phosphorus at low dietary phosphorus intakes (Fig. 2b). We also compared measured absolute and fractional contents of calcium in growing antlers of red deer (Muir *et al.*, 1987a) to those predicted by Eqs. 17 - 22. Predicted and observed calcium fractions in the antler were not different (paired *t*-test, $t_5 = 0.24$, $P > 0.81$), nor was the absolute amount of calcium present in antlers (paired *t*-test, $t_5 = 0.47$, $P > 0.65$).

Model Experiments

Antler composition

Most of antler ash was deposited in the latter half of the antler growth period (Fig. 3). Water content peaked about midway through the antler growth period, then declined to 15% at the end of velvet shedding (Eq. 18). Antler ash, including calcium and phosphorus, increased throughout the antler growth period, and antler protein declined slightly (about 100 g in the 10 kg male antlers) during the last week of the velvet shedding period. Water comprised > 60% of antler mass until about the 80th day of growth, shortly before maximum antler mass was reached and mineralization rate increased. The high water content of developing antler is corroborated by the only published report on composition of developing antlers we are aware of (Ullrey, 1982) and follows that measured in the study used to derive eqs. 17 - 22 (Muir *et al.*, 1987b).

Energy Partitioning

Peak energy requirements for antler growth were no more than 1200 kcal/day for the male using our initial estimate efficiency of energy use for antler growth, and fat lower for the female (Fig. 4a,b).

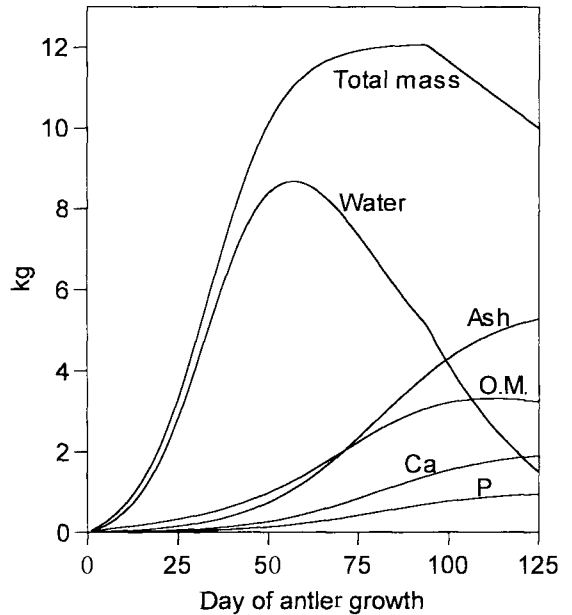


Fig. 3. Predicted antler mass and composition during the 125 day antler growth period for a pair of 10 kg antlers from a caribou bull.

During the period when antlers were growing, about 4.5 and 25 times more energy was expended on deposition of fat and protein than on antler growth in males and females, respectively. Antler growth increased energy requirements by 8.5% and 1.5% during the antler growth period for males and females, respectively. Energy required for antler growth by females was much less than energy required for lactation or gestation.

The low energy requirements for antler growth are due to our estimate of 25% efficiency of energy use for protein deposition in growing antlers and maintenance metabolism for the remainder of the antler. When we decreased the efficiency of energy use to 13.3% in Experiment 1, the male had to increase energy intake by 9% to maintain the same body mass, and energy required for antler growth increased to 14% of total energy requirements during the antler growth period. When we decreased the efficiency of energy use and increased the cost of maintaining antler tissue in Experiment 2, the animal had to increase energy intake by 23% to maintain a similar body mass, and energy requirements for antler growth increased to 16% of total energy requirements. In Experiment 2, the peak energy required for antler growth was about 60% of the basal metabolic rate, and energy requirements

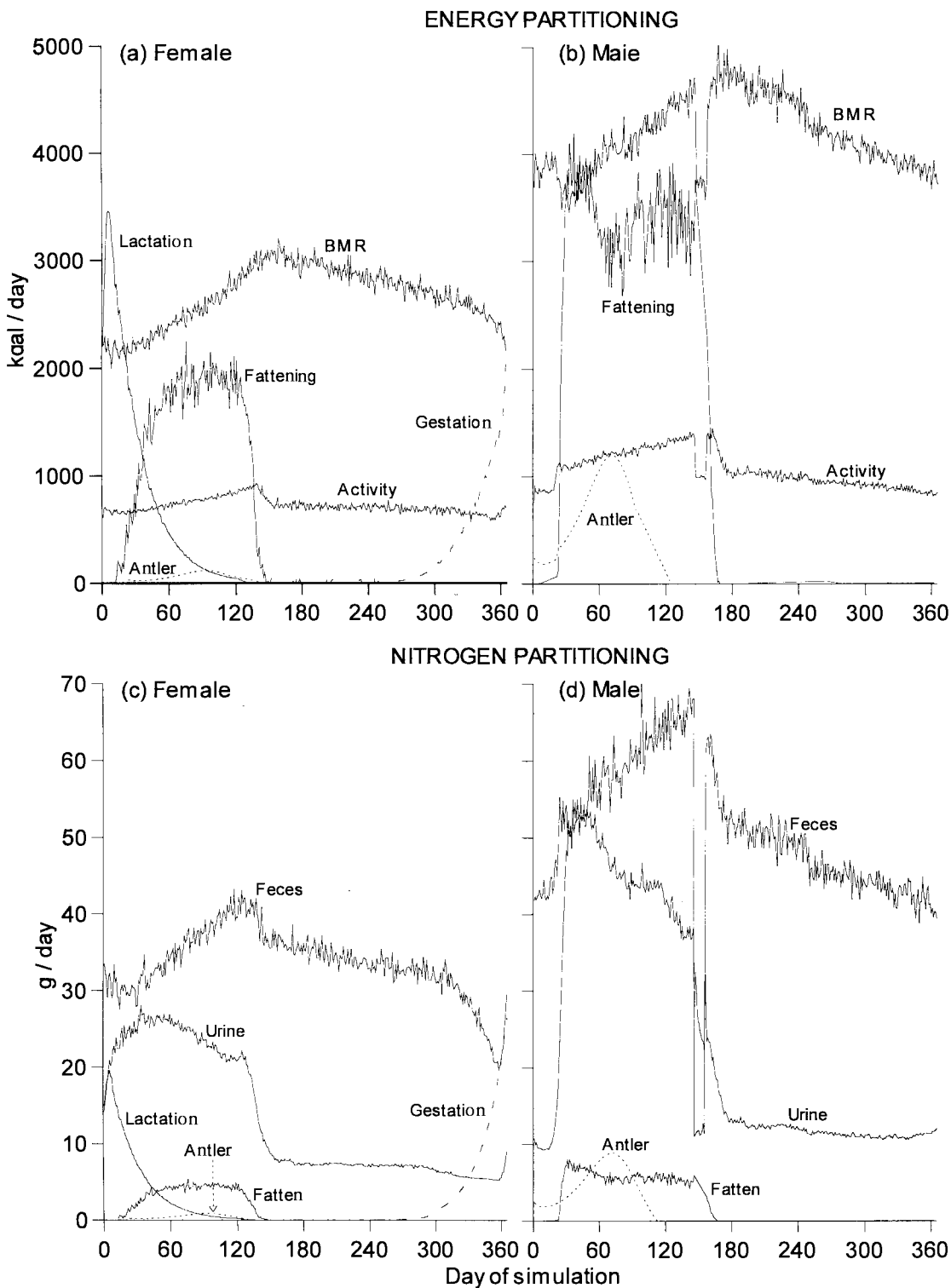


Fig. 4. Predicted annual energy partitioning for a caribou cow producing 1 calf (a) and a caribou bull (b) and predicted annual nitrogen partitioning for a caribou cow producing 1 calf (c) and a caribou bull (d).

for antler growth averaged 25% of basal metabolic rate during the period of antler growth.

Nitrogen Partitioning

Most of the ingested nitrogen from plant material is excreted in either feces or urine on a diet which is 13.5% protein in summer (Fig. 4c,d). Nitrogen is incorporated into antlers and muscle protein in the summer by males, but the total amount incorporated is < 20% of the amount of nitrogen excreted each day. Nitrogen requirements for females are higher because of requirements for gestation and lactation, but are still less than the amount excreted in summer. Nitrogen excretion declines in winter because dietary nitrogen content is low, forage intake decreases, and the nitrogen recycling rate increases.

Calcium Partitioning

Contrary to previous work with smaller antlered cervids, annual calcium requirements for male caribou are much larger than calcium requirements for gestation, lactation and antler growth in female caribou (Fig. 5a,b). For these simulations, annual calcium deposition in antlers was 1.9 kg in the male, compared to the 0.4 kg of calcium required for gestation, lactation, and antler growth in females. Calcium deposition in antlers by males was more than 25 g/day from day 66 to day 96 of antler growth. From days 55 to 96 of antler growth 0.1 kg of calcium was resorbed from the skeleton and deposited in the antler, maximum resorption was < 6 g/day. This represented about 5% of the total calcium in the antler, and > 25% of the calcium which could be resorbed from the skeleton before *CaStatus* became 0.0. These resorption rates are specific to the antler mass and calcium intake conditions of this simulation, but do demonstrate when calcium is likely to be in most demand under other conditions.

Phosphorus Partitioning

For these simulations, annual phosphorus requirements for antler growth in the male were 0.95 kg, compared to the 0.25 kg of phosphorus required for gestation, lactation, and antler growth in females (Fig. 5c,d). Phosphorus deposition in antlers by males was more than 12 g/day from day 65 to day 97 of antler growth. The male resorbed 0.1 kg of phosphorus from the skeleton and deposited it in the antler from days 47 to 101 of antler growth, with a maximum resorption rate of 4.5 g/day. This

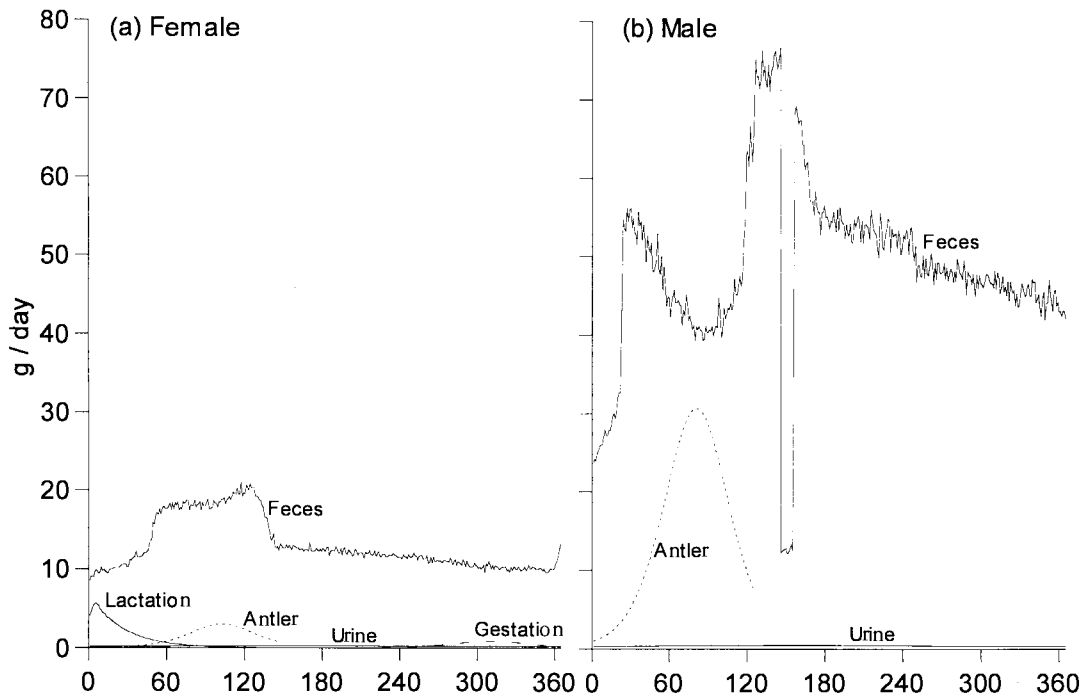
represented > 50% of the phosphorus which could be resorbed from the skeleton, and about 10% of the phosphorus in the male's antler. More resorption of phosphorus than calcium was required because of the lower concentration of phosphorus in the diet. As with calcium, these resorption rates are specific to the antler mass and phosphorus intake conditions of this simulation, but do demonstrate when phosphorus is likely to be in most demand under other conditions.

Discussion

Our results have important implications for understanding the partitioning of energy and nutrients to antler growth in caribou, and provide quantitative predictions of the daily requirements for energy, nitrogen, calcium, and phosphorus throughout the antler growth period. Energy required by males for growing antlers and increasing body mass required an intake rate up to 4.5 times the basal metabolic rate, depending on the efficiency with which energy was used for antler growth, a parameter that has not been determined experimentally. This approaches the maximum predicted energy requirements for female white-tailed deer nursing 2 fawns (Moen, 1978). Most of the energy intake of males in summer was used to meet maintenance requirements and for deposition of fat and protein. Energy requirements for antler growth in females were very low relative to other energy requirements. Strong selective pressures for growth of antlers in female caribou would exist if females can grow small antlers at a low energetic cost in summer, and then increase energy intake in winter through the behavioral dominance conferred by the presence of even small antlers.

The more negative balance for phosphorus than calcium was somewhat unexpected, given experimental work with white-tailed deer (Grasman & Hellgren, 1993). However, as those authors suggested, caribou would be the cervid species most likely to be phosphorus limited. The animal was in a more negative phosphorus balance because plant concentrations of phosphorus were lower than plant concentrations of calcium. During the period of antler growth in males, the bone Ca:P ratio increased from a normal value of about 2.0 to about 3.3 when calcium and phosphorus were uncoupled in bone resorption. This ratio may be higher than is physiologically acceptable, suggesting that some of the bone calcium should have been resorbed and excre-

CALCIUM PARTITIONING



PHOSPHORUS PARTITIONING

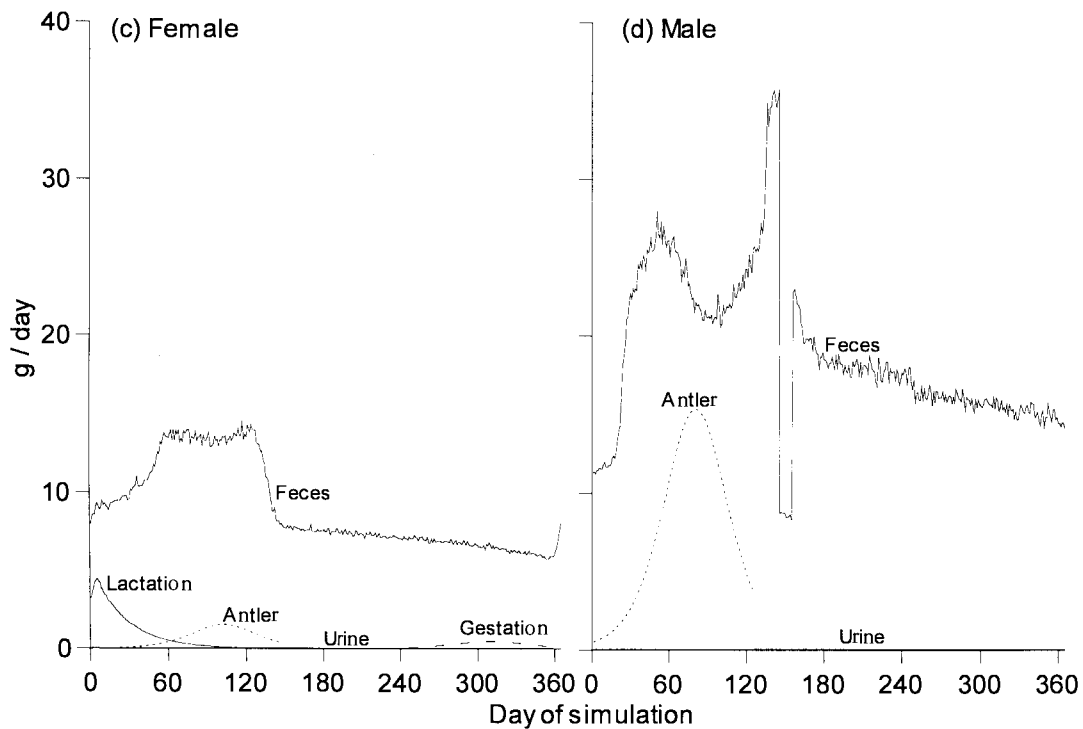


Fig. 5. Predicted annual calcium partitioning for a caribou cow producing 1 calf (a) and a caribou bull (b) and predicted annual phosphorus partitioning for a caribou cow producing 1 calf (c) and a caribou bull (d).

ted in our simulations with male caribou. An alternative mechanism to maintain a constant Ca:P ratio would be to increase the availability of phosphorus (Eq. 2, $AvailFrcPhos_2$) at a faster rate as bone phosphorus was depleted (Grasman & Hellgren, 1993). Demonstrating resorption of bone does not imply that phosphorus limitation has occurred, as resorption of bone for antler growth is a normal physiological process (Banks *et al.*, 1968a; b). Daily balance of phosphorus is less important than the seasonal balance, provided that resorption requirements on any single day of antler growth can be met.

There are some specific biological situations we do not consider in the model in its current state, and other areas where additional research would improve the model. For example, should an animal grow antlers when it is in negative energy balance in late winter and early spring, or should it just prepare antlers physiologically for growth, and begin growing as soon as spring flush of growth appears? The latter case would appear to be supported by the logistic increase in antler length observed in cervids. Antler composition during the first week of antler growth is predicted by extrapolation in the model. Experimental data from the first week of antler growth would be desirable, but given the relatively small antler mass during the first week of antler growth we feel that the extrapolation is acceptable, particularly since the alternative is to "do nothing". This is the type of data that could be collected opportunistically from caribou that are accidentally killed while antlers are growing.

The model does not currently adjust antler density. However, the model could be used to predict the effects that changes in antler density have on overall mineral requirements during antler growth. Another unresolved issue is how the animal should adjust antler growth or lactation if either phosphorus or calcium are completely depleted from bone. At the extremes of depletion, death would occur (Hyvarinen *et al.*, 1977). Prior to death, however, could the animal modify its foraging strategy so that it ate only those plants highest in available phosphorus? Results of the model suggest that peak requirements for antler growth in males would be shortly before the antler has stopped increasing in length. Selective foraging for high phosphorus plants could be tested by observation of food habits. A related issue is whether calcium and phosphorus status ($CaStatus$ and $PhosStatus$) should be coupled more tightly in the model, to prevent the high Ca:P ratios in bone that we observed in the model as it is

currently formulated. Coupling calcium and phosphorus status would have little effect on model results, only a small reduction in body and ash masses would occur.

Requirements for antler growth appear to be generalizable to the point that the same set of equations can be used to predict antler mass and composition for most if not all cervid species. Even though data on antler mass during growth are only available for red deer, patterns in changes of length of growing antlers are similar for red deer, moose, and caribou when scaled appropriately (R. Moen, unpubl. data). The set of 6 equations required to predict antler mass and composition (Eqs. 17-22) present the opportunity to develop many testable hypotheses on antler composition and growth for caribou, and also for cervids in general.

This simulation model represents a summary of current knowledge about cervid physiology, specifically energy, nitrogen, calcium, and phosphorus metabolism. We used it to predict the annual energy, nitrogen, calcium, and phosphorus metabolism in both male and female caribou on a daily time step. We believe that the integration of energy, nitrogen, calcium, and phosphorus metabolism within the same simulation is a strong test of the biological accountability of model predictions. The modeling effort identified several areas where research would result in an improved simulation model, and also would result in improved knowledge of caribou biology.

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References

- Adamczewski, J. Z., Gates, C. C., Hudson, R. J. & Price, M. A. 1987. Seasonal changes in body composition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an arctic island with limited winter resources. – *Can. J. Zool.* 65: 1149–1157.
- Adamczewski, J. Z., Hudson, R. J. & Gates, C. C. 1993. Winter energy balance and activity of female caribou on Coats Island, Northwest territories: The relative importance of foraging and body reserves. – *Can. J. Zool.* 71: 1221–1229.
- Agricultural Research Council. 1980. *The nutrient requirements of ruminant livestock*. Commonwealth Agricultural Bureau, Slough, England.

- Banks, W. J., Epling, G. P., Kainer, R. A. & Davis, R. W. 1968a. Antler growth and osteoporosis. I. Morphological and morphometric change in the costal compacta during the antler growth cycle. – *Anatomical Record* 162: 387–497.
- Banks, W. J., Epling, G. P., Kainer, R. A. & Davis, R. W. 1968b. Antler growth and osteoporosis. II. Gravimetric and chemical changes in the costal compacta during the antler growth cycle. – *Anatomical Record* 162: 399–405.
- Bergerud, A. T. 1976. The annual antler cycle in Newfoundland caribou. – *Can. Field-Nat.* 90: 449–463.
- Boertje, R. D. 1985. An energy model for adult female caribou of the Denali Herd, Alaska. – *J. Range Manage.* 38: 468–473.
- Braithwaite, G. D. 1983. Calcium and phosphorus requirements of the ewe during pregnancy and lactation. I. Calcium. – *Brit. J. Nutr.* 50: 711–722.
- Braithwaite, G. D. 1986. Phosphorus requirements of ewes in pregnancy and lactation. – *J. Agric. Sci. (Camb.)* 106: 271–278.
- Brown, R. D. 1990. Nutrition and antler development. – In: Bubenik, G. A. & Bubenik, A. B. (eds.). *Horns, pronghorns, and antlers*. Springer-Verlag, New York, pp. 426–441.
- Chapin, F. S., Ill, Johnson, D. A. & McKendrick, J. D. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. – *J. Ecol.* 68: 189–209.
- Chase, L. A., Studier, E. H. & Thorisson, S. 1994. Aspects of nitrogen and mineral nutrition in Icelandic reindeer, *Rangifer tarandus*. – *Comp. Biochem. Physiol.* 109B: 63–73.
- Fancy, S. G. 1986. *Daily energy budgets of caribou: a simulation approach*. Ph.D. Dissertation, Univ. Alaska, Fairbanks.
- Fennessy, P. F., Corson, I. D., Suttie, J. M. & Littlejohn, R. P. 1992. Antler growth patterns in young red deer stags. – In: Brown, R. D. (ed.). *The biology of deer*. Springer-Verlag, New York, pp. 487–492.
- Geist, V. 1987. On the evolution of optical signals in deer: a preliminary analysis. – In: Wemmer, C. M. (ed.). *Biology and management of the Cervidae*. Smithsonian Institution Press, Washington, D.C., pp. 235–255.
- Goss, R. J. 1995. Future Directions in Antler Research. – *Anatomical Record* 241: 291–302.
- Grasman, B. T. & Hellgren, E. C. 1993. Phosphorus nutrition in white-tailed deer: nutrient balance, physiological responses, and antler growth. – *Ecology* 74: 2279–2296.
- Hillman, J. R., Davis, R. W. & Abdelbaki, Y. Z. 1973. Cyclic bone remodeling in deer. – *Calcified Tiss. Res.* 12: 323–330.
- Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. – *Wildl. Monogr.* 101: 1–39.
- Hudson, R. J. & White, R. G. 1985. Computer simulation of energy budgets. – In: Hudson, R. J. & White, R. G. (eds.). *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida, pp. 261–290.
- Huot, J. 1989. Body composition of the George River caribou (*Rangifer tarandus caribou*) in fall and late winter. – *Can. J. Zool.* 67: 103–107.
- Hyvarinen, H., Helle, T., Nieminen, M., Vayrynen, P. & Vayrynen, R. 1977. The influence of nutrition and seasonal conditions on mineral status in the reindeer. – *Can. J. Zool.* 55: 648–655.
- Kelsall, J. P. 1968. *The caribou*. Queen's Printer, Ottawa, Canada.
- Miquelle, D. G. 1990. Why don't bull moose eat during the rut? – *Behav. Ecol. Sociobiol.* 27: 145–151.
- Miquelle, D. G., Peek, J. M. & Van Ballenberghe, V. 1992. Sexual segregation in Alaskan moose. – *Wildl. Monogr.* 122: 1–57.
- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. – *J. Wildl. Manage.* 42: 715–738.
- Moen, R. A. & DelGiudice, G. D. 1997. Simulating nitrogen metabolism and urinary urea nitrogen: creatinine ratios in ruminants. – *J. Wildl. Manage.* 61: 881–894.
- Moen, R. A., Pastor, J. & Cohen, Y. 1997. A spatially explicit model of moose foraging and energetics. – *Ecology* 78: 505–521.
- Moen, R. A., Cohen, Y. & Pastor, J. 1998. Evaluating foraging strategies with a moose energetics model. – *Ecosystems* 1: in press.
- Muir, P. D., Sykes, A. R. & Barrell, G. K. 1987a. Calcium metabolism in red deer (*Cervus elaphus*) offered herbages during antlerogenesis: kinetic and stable balance studies. – *J. Agric. Sci. (Camb.)* 109: 357–364.
- Muir, P. D., Sykes, A. R. & Barrell, G. K. 1987b. Growth and mineralization of antlers in red deer (*Cervus elaphus*). – *N. Z. J. Agric. Res.* 30: 305–315.
- National Research Council. 1989. *Nutrient Requirements of Dairy Cattle*. 6th ed. National Academy Press, Washington, D.C.
- Parker, K. L., White, R. G., Gillingham, M. P. & Holleman, D. F. 1990. Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. – *Can. J. Zool.* 68: 106–114.
- Robbins, C. T. & Moen, A. N. 1975. Uterine composition and growth in pregnant white-tailed deer. – *J. Wildl. Manage.* 39: 684–691.

- Robbins, C. T., Oftedal, O. T. & O'Rourke, K. I. 1987. Lactation, early nutrition, and hand-rearing of wild ungulates, with special reference to deer. – *In*: Wemmer, C. M. (ed.). *Biology and management of the Cervidae*. Smithsonian Institution Press, Washington, D.C., pp. 429–442.
- Staaland, H. & Sæbø, S. 1993. Forage diversity and nutrient supply of reindeer. – *Rangifer* 13: 169–177.
- Staaland, H., Brattbakk, I., Ekern, K. & Kildemo, K. 1983. Chemical composition of reindeer forage plants in Svalbard and Norway. – *Holarct. Ecol.* 6: 109–122.
- Stephenson, D. C. & Brown, R. D. 1984. Calcium kinetics in white-tailed deer. – *J. Nutr.* 114: 1014–1024.
- Swift, D. M. 1983. A simulation model of energy and nitrogen balance for free-ranging ruminants. – *J. Wildl. Manage.* 47: 620–645.
- Ullrey, D. E. 1982. Nutrition and antler development in white-tailed deer. – *In*: Brown, R. D. (ed.). *Antler development in Cervidae*. Caesar Kleberg Wildlife Research Institute, Kingsville, TX, pp. 49–59.
- Van Ballenberghe, V. 1982. Growth and development of moose antlers in Alaska. – *In*: Brown, R. D. (ed.). *Antler development in Cervidae*. Caesar Kleberg Wildlife Research Institute, Kingsville, TX, pp. 37–48.