

## A MODEL TO PREDICT NUTRITIONAL REQUIREMENTS FOR ANTLER GROWTH IN MOOSE

Ron Moen and John Pastor

Center for Water and Environment, Natural Resources Research Institute, 5013 Miller Trunk Highway, Duluth, MN 55811

**ABSTRACT:** We used a simulation model to predict energy, protein, and mineral requirements of moose. Body water, fat, protein, and ash are monitored on a daily time step, and energy requirements for reproduction and body mass changes are accounted for. We estimated energy requirements for antler growth because experimental data are not available. Antler growth increased energy requirements by 13% when energy requirements for antler growth were similar to energy requirements for tissue deposition, and by 20% when energy requirements for antler growth were midway between energy requirements for tissue deposition and gestation. Energy requirements for the latter part of gestation and milk production by females were greater than requirements for antler growth in mature males. Protein requirements for antler growth and lactation were met by forage intake. The model predicts that calcium and phosphorus must be resorbed from bone during peak antler growth. If antlers weigh 30 kg at the end of velvet shedding, > 60 g / day of calcium and > 30 g / day of phosphorus are deposited in the antlers for 40 days when mineralization rate is highest. Phosphorus was most likely to limit growth of antlers after energy. Input parameters can be changed to represent moose from other geographic regions and other cervid species. The model can be used to understand energy and mineral metabolism requirements for antler growth, and to understand the relationship between body mass and antler size in the Cervidae.

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**Key words:** *Alces alces*, antlers, Cervidae, energetics, mineral nutrition, moose, nutrient requirements, simulation model

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Surprisingly little work has been done on the nutritional and energetic requirements for antler growth despite the importance of antlers to behavior and evolution of cervids (Goss 1995). The lack of definitive experimental work is caused by difficulties in separating metabolism for antler growth from metabolism necessary for growth and tissue accretion in live animals (Brown 1990). Body mass, antler size, and antler density are reduced when feed intake is restricted (French *et al.* 1956, Hyvarinen *et al.* 1977, Ullrey 1982). Calcium and phosphorus are resorbed from bones during antler growth because dietary intake and absorption of these minerals is insufficient to meet mineralization requirements (Banks

*et al.* 1968a, Hillman *et al.* 1973, Muir *et al.* 1987a).

Simulation models can increase our understanding of the nutritional physiology of cervids when problems are experimentally intractable. 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 and White 1985, Fancy 1986) and nitrogen metabolism (Swift 1983, Hudson and White 1985). With the exception of the model developed by Swift these models have been applied to specific questions about the metabolism of a single species. Swift's model was not designed

for a specific ruminant species and did not implement costs of productive functions such as lactation or antler growth.

We have developed a model which is adaptable to many ruminant species, and which can be used to simulate the energetic costs of gestation and lactation (Moen and DelGiudice 1997, Moen *et al.* 1997). With the addition of antler growth to this model (Moen and Pastor 1998, Moen *et al.*, *in press*), we can predict energy and mineral metabolism during antler growth and compare these requirements to energy and mineral requirements of gestation and lactation in females.

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Seasonal patterns in energy requirements for maintenance and reproduction of female moose (*Alces alces*) were reviewed by Gasaway and Coady (1974). These generalizations were further refined with an annual energy budget for non-pregnant female moose by Schwartz *et al.* (1987b), using the Swift (1983) model. The energy and mineral requirements for antler growth of moose have not yet been quantified or compared to energy and mineral requirements for gestation and lactation in females.

In this paper we describe the equations required to simulate antler growth and composition in moose. The antler growth model has been modified slightly from the original presentation of the model for caribou (*Rangifer tarandus*) (Moen and Pastor

1998). We use the model to predict the energy, nitrogen, calcium, and phosphorus requirements of adult male and female moose in summer. The input values for parameters such as antler mass, body mass, growing season length, or seasonal changes in calcium and phosphorus content of forage can be changed to represent the characteristics of moose in a specific area.

## METHODS

The model of antler growth was integrated into the Energetics and Activity Simulation Environment (EASE) model, which simulates the energetics and metabolism of ruminants (Moen *et al.* 1997). The EASE model can simulate spatially-explicit foraging (Moen *et al.* 1997), nitrogen metabolism (Moen and DelGiudice 1997), and calcium and phosphorus metabolism (Moen and Pastor 1998, Moen *et al.*, *in press*).

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. To simulate antler growth, we added calcium and phosphorus metabolism, antler mass changes, and energetic requirements for antler growth to the model. These new processes are defined in Equations 1 - 22 (Table 1) with parameter values we used in the validation and model experiment simulations. Most of these parameter values have been derived 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 estimated model parameters are identified in the text.

### Simulating Ca and P Metabolism

The EASE model simulates the Ca and P stored in and flowing through the body (Fig. 1). Elemental Ca and P are monitored because Ca and P are incorporated into many different chemical compounds in the body. The major storage depot for both Ca and P is the skeleton, which contains about 99% of Ca and more than 75% of the P in the body (Agricultural Research Council 1980). Ca and P are resorbed from bone when metabolic needs are not 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. If the animal has completely depleted the available minerals in its skeleton the ash content of the fat and ingesta-free body is 4.5%. Ca and P comprise 38% and 18% of the available skeleton mass which can be resorbed (Chapman 1975). The repletion status of the skeleton is updated each day.

Ca and P intake are determined by the content of each of these elements in the diet. Availability of ingested Ca and P depends on type of forage, mineral needs,

and mineral status of the animal (Braithwaite 1983, National Research Council 1989). Availability increases as the skeleton is resorbed. We use a base value of 35% availability when the skeleton is replete and a 65% maximum availability when mineral stores in the skeleton are completely resorbed (Eqs. 1 and 2). Available Ca and P from the diet (Eqs. 3 and 4) are used to meet daily requirements. The predicted daily requirements for endogenous urinary Ca and endogenous urinary P (Eqs. 5 and 6) are based on body mass (Braithwaite 1986, Muir *et al.* 1987a). Ca and P leaving the rumen via the intestinal tract are excreted in the feces. The predicted daily requirements for metabolic fecal Ca and metabolic fecal P (Eqs. 7 and 8) are lower than for domestic ruminants (Agricultural Research Council 1980), but similar requirements have been measured in wild ruminants (Muir *et al.* 1987a, Grasman and Hellgren 1993). Unavailable Ca and P are calculated from dietary intake of Ca and P and availability (Eqs. 9 and 10). The dietary surplus is calculated by difference between intake and the utilization of Ca and P for metabolic needs.

Ca and P are required for gestation, lactation, and antler growth. If the animal is pregnant, gestation requirements for Ca and P are predicted from the number of fetuses, fetus mass at birth, and the day of gestation (Robbins and Moen 1975), assuming a Ca content in the fetus of 13 g/kg and a P content of 7 g/kg (Agricultural Research Council 1980). Ca and P requirements during lactation are predicted from the day of lactation, the number of young suckled, and a milk production curve (Reese and Robbins 1994) modified to produce 300 l of milk over a 140 day lactation. Milk was assumed to have 0.32% Ca and 0.25% P (Robbins *et al.* 1987). Ca and P content of antler ash is 36% and 18%, respectively (Brown 1990). The ratio of Ca:P in antlers

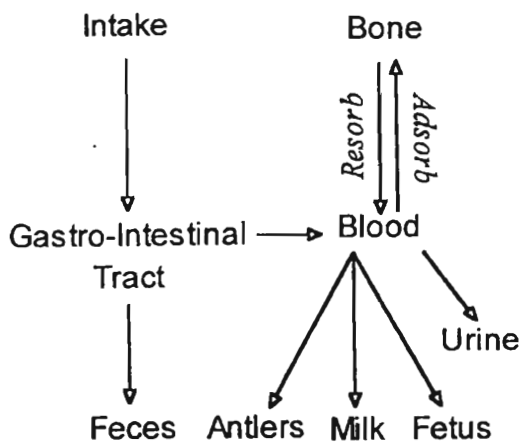


Fig. 1. Pathways calcium and phosphorus follow from ingestion to excretion as implemented in the simulation model.

Table 1. Equations and variables describing calcium metabolism, phosphorus metabolism, and antler growth. Numbers are referred to in the text.

$AvailFrcCa_d = 0.35 + (1.00 - CaStatus_d) \cdot 0.30$	(1)
$AvailFrcPhos_d = 0.35 + (1.00 - PhosStatus_d) \cdot 0.30$	(2)
$AvailIntakeCa_d = AvailFrcCa_d \cdot IntakeCa_d$	(3)
$AvailIntakePhos_d = AvailFrcPhos_d \cdot IntakePhos_d$	(4)
$EUCa_d = 0.0025 \cdot IntakePhos_d$	(5)
$EUPhos_d = 0.0003 \cdot weightKG_d$	(6)
$MFCa_d = 0.0065 \cdot weightKG_d$	(7)
$MFPhos_d = 0.025 \cdot weightKG_d$	(8)
$UnAvailIntakeCa_d = IntakeCa_d - AvailIntakeCa_d$	(9)
$UnAvailIntakePhos_d = IntakePhos_d - AvailIntakePhos_d$	(10)
$NetCa_d = AvailIntakeCa_d - (EUCa_d + MFCa_d + GestCa_d + LactCa_d + AntlCa_d)$	(11)
$NetPhos_d = AvailIntakePhos_d - (EUPhos_d + MFPhos_d + GestPhos_d + LactPhos_d + AntlPhos_d)$	(12)
$SurplusCa_d = NetCa_d - AbsorbCa_d$	(13)
$SurplusPhos_d = NetPhos_d - AbsorbPhos_d$	(14)
$FecalCa_d = UnAvailIntakeCa_d + MFCa_d + SurplusCa_d$	(15)
$FecalPhos_d = UnAvailIntakePhos_d + MFPhos_d + SurplusPhos_d$	(16)
$AntKG_d = AntKG_{AntlGrowPeriod} \div (1.0 + 30.0 \cdot e^{-10.0 \cdot 0.95 \cdot d + AntlGrowPeriod})$	(17)
$AntKG_d = MaxAntlerKG + FrcMinPeriod_d \cdot AntMassDecline$	(18)
$AshFrc_d = 1.0 \cdot AshFrc_{AntlGrowPeriod} \div (1.0 + 125.0 \cdot e^{-10.0 \cdot 0.75 \cdot d + AntlGrowPeriod})$	(19)
$AshToOMratio_d = 0.17 + 1.46 \cdot FrcGrowPeriod_d$	(20)
$OMfrc_d = AshToOMratio \div AshFrc_d$	(21)
$Waterfrc_d = 1.0 - (OMfrc_d + AshFrc_d)$	(22)

does not vary during antler growth (Muir *et al.* 1987b).

The net Ca and P balances on a daily basis are calculated by summation of each factor (Eqs. 11 and 12). Gestation, lactation, and antler growth parameters are 0 when the animal is not pregnant, not lactating, or not growing antlers, respectively. Eqs. 11 and 12 enforce conservation of Ca and P. All sources, sinks, and storage pools of Ca and P are updated each day on the same time step. If the net balance of either Ca or P is negative and there is sufficient

mineral in bones, the deficit is met by resorption. If there is insufficient Ca or P in the bones, then the simulation is ended. If the net balance of either Ca or P is positive and the bones are not fully replete, then the surplus is adsorbed to skeletal bones. Up to 5% of Ca and P that can be mobilized from bone may be resorbed or repleted each day. We do not simulate the negligible Ca and P in fat and protein during mobilization and accretion of body tissues in the model. Ca and P remaining after adsorption to the bone is excreted in feces (Eqs. 13-16).

Table 1 continued...

Variable	Units	Definition
<i>MaxBoneCa</i> , <i>MaxBoneP</i>	g	Maximum bone Ca and P content (when replete)
<i>CaStatus</i> , <i>PStatus</i>	unitless	Ca and P status of skeleton (1.0 = replete)
<i>d</i>	day	Day of simulation
<i>IntakeCa<sub>d</sub></i> , <i>IntakeP<sub>d</sub></i>	g /day	Ca and P intake
<i>AvailFrcCa<sub>d</sub></i> , <i>AvailFrcP<sub>d</sub></i>	unitless	Available Ca and P in forage
<i>AvailIntakeCa<sub>d</sub></i> , <i>AvailIntakeP<sub>d</sub></i>	g / day	Available Ca and P in forage
<i>EUCa<sub>d</sub></i> , <i>EUP<sub>d</sub></i>	g /day	Endogenous urinary Ca and P
<i>weightKG<sub>d</sub></i>	kg	Body mass in kg
<i>MFCa<sub>d</sub></i> , <i>MFP<sub>d</sub></i>	g /day	Metabolic fecal Ca and P
<i>UnAvailIntkCa<sub>d</sub></i> , <i>UnAvailIntkP<sub>d</sub></i>	g / day	Unavailable Ca and P in diet
<i>NetCa<sub>d</sub></i> , <i>NetPhos<sub>d</sub></i>	g / day	Net Ca and P balance
<i>GestCa<sub>d</sub></i> , <i>GestP<sub>d</sub></i>	g /day	Ca and P requirements for gestation
<i>LactCa<sub>d</sub></i> , <i>LactP<sub>d</sub></i>	g /day	Ca and P requirements for lactation
<i>AntlCa<sub>d</sub></i> , <i>AntlP<sub>d</sub></i>	g /day	Ca and P requirements for antler growth
<i>SurplusCa<sub>d</sub></i> , <i>SurplusP<sub>d</sub></i>	g /day	Surplus Ca and P in diet
<i>FecalCa<sub>d</sub></i> , <i>FecalP<sub>d</sub></i>	g /day	Ca and P in feces
<i>AntKG<sub>d</sub></i>	kg	Antler mass
<i>AntlGrowPeriod</i>	Days	Length of the antler growth period
<i>MaxAntKG</i>	kg	Antler mass at the end of velvet shedding
<i>FrcMinPeriod<sub>d</sub></i>	unitless	Fraction of mineralization period completed
<i>AntMassDecline<sub>d</sub></i>	kg	$MaxAntKG \cdot 0.20$
<i>AshFrc<sub>d</sub></i>	unitless	Ash fraction of the antler
<i>AshToOMratio<sub>d</sub></i>	unitless	Ash:organic matter ratio in antler
<i>FrcGrowPeriod<sub>d</sub></i>	unitless	Fraction of antler growth period
<i>OMFrc<sub>d</sub></i>	unitless	Organic matter fraction of growing antler
<i>WaterFrc<sub>d</sub></i>	unitless	Fraction of water in antler

### Simulating Antler Growth

We used data on red deer (*Cervus elaphus*) antler growth (Muir *et al.* 1987b) to predict changes in mass and composition of growing antlers. Antler length and mass increases for about 75% of the period when velvet is on the antler. Mineralization and drying of the antler occurs during the last 25% of the period. Antler mass is predicted with a logistic equation during the first 75%

of the antler growth period, and with a linear decline in the last 25% of the antler growth period (Eqs. 17 and 18). Peak antler mass is about 20% higher than antler mass at the end of velvet shedding, when antlers are 85% dry matter (Muir *et al.* 1987b). During the first 30% of antler growth we currently predict a constant antler composition of 86% water, 9% organic matter, and 5% ash. For the remaining 70% of antler growth

ash is predicted with a logistic equation (Eq. 19) from data of Muir *et al.* (1987b). The organic matter fraction of the growing antler is calculated from the previously derived ash fraction in the growing antler (Eqs. 20 and 21), and water content is calculated by subtraction (Eq. 22).

### Simulating Energy and Protein Needs

Daily energy and protein requirements have been previously described for the EASE model (Moen and 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 with which energy is used to produce antlers, a parameter which may be impossible to obtain experimentally (Brown 1990, Goss 1995).

We modified energy requirements used in the original formulation of the model (Moen and Pastor 1998) to account for energy requirements of mineral deposition in the antler. We used a caloric value of 5.5 kcal / g for deposition of new protein and minerals in the antler each day (Eqs. 19 and 21), and assumed an efficiency of energy use for deposition of 25%, which is midway between the efficiency of energy use for lean tissue deposition and the efficiency of energy use for gestation (Agricultural Research Council 1980). We tested the sensitivity of the model by using an estimated efficiency of 40% because the value of 25% efficiency has not been experimentally determined.

In addition to the cost of tissue deposition, we estimated a "maintenance" cost for antler tissues of  $35 \cdot \text{AntlerKG}_d^{0.75}$  kcals / day. The effect of the maintenance energy requirement was to increase energy requirements later in antler growth when new tissues are not being deposited as rapidly, yet the mass of living tissue in the antler is

still present. The specific value of  $35 \cdot \text{AntlerKG}_d^{0.75}$  kcals / day was necessarily arbitrary because no experimental data are available. Although a small fraction of the total energy costs, we believe the maintenance cost is biologically valid and should be included in the model.

We modified the daily nitrogen requirements in the EASE model (Moen and DelGiudice 1997) by adding an additional nitrogen sink, the antler. Nearly all of the organic matter in the antler is protein (Chapman 1975, Brown 1990). We assumed that antler protein was 6.25% nitrogen.

Energy balance and body mass changes are affected by forage intake and digestibility input parameters. We set energy intake to reproduce the observed patterns of body mass changes in moose (Schwartz *et al.* 1987a). Phenological patterns in antler growth were from Van Ballenberghe (1982). Peak diet digestibility was 64% in summer and declined to 40% in winter, and crude protein in the diet was 18% in summer and 6% in winter. Ca concentrations ranged from 1.00% in winter to 1.50% in summer, and P concentrations ranged from 0.50% in winter to 0.75% in summer. Diet digestibility, crude protein, Ca, and P followed seasonal patterns with smooth transitions between minimum and maximum values (Moen *et al.* 1997).

### Simulation Protocol

We began model experiments on 30 April, the first day of antler growth. Seasonal weight changes in the simulations were similar to seasonal weight changes in live moose (Schwartz *et al.* 1987a). Moose that began simulations weighing 367 kg grew 20 kg antlers and moose that began simulations weighing 437 kg grew 30 kg antlers. Females began simulations weighing 325 kg and raised either 1 or 2 calves. Single calves of 16 kg and twins weighing

13.5 kg each were born on 19 May after a 231 day gestation (Schwartz and Hundertmark 1993). Milk contained 7% protein and had an energy content of 1.29 kcal/g (Franzmann *et al.* 1975, Reese and Robbins 1994). Simulated cows raising single calves produced 300 kg of milk, more than measured by hand milking (Knorre 1961, Treus *et al.* 1992), but less than measured with other methods for larger cervids (Hudson and Adamczewski 1990, Reese and Robbins 1994). Milk production in females with twins was increased by 25% (Ofteidal 1985). Initial bone repletion was set at 100% for both Ca and P. Initial ingesta-free body fat content was set at 5%. Rumen weight varied seasonally from 10% of body mass in summer to 14% of body mass in winter.

We adjusted intake energy until the simulated moose gained 30% body mass by the end of velvet shedding on 12 September after a 135 day antler growth period. Energy costs of different activities and daily activity budgets are provided in Moen *et al.* (1997). The activity budgets approximate activity budgets of free-ranging non-migratory ruminants and resulted in activity costs of about 20% of basal metabolic rate (BMR) each day.

We compared Ca and P metabolism as predicted by the model to mineral balances and antler mass during antlerogenesis in published experiments (Moen and Pastor 1998). We also compared predicted and measured fractional and absolute contents of Ca and P in the antler throughout antler growth.

## RESULTS

### Antler Composition

Composition and mass of antlers throughout antler growth is predicted by Eqs. 17-22. Most of antler ash was deposited in the latter half of the antler growth period (Fig. 2). Water content of antlers

was predicted to be >80% until day 60 of antler growth, then declined to 15% at the end of velvet shedding (Eq. 18). Water comprised >60% of antler mass until shortly before maximum antler mass was reached and mineralization rate increased on about the 80th day of growth. The high water content of growing antler is corroborated by the few analyses of growing antlers that are

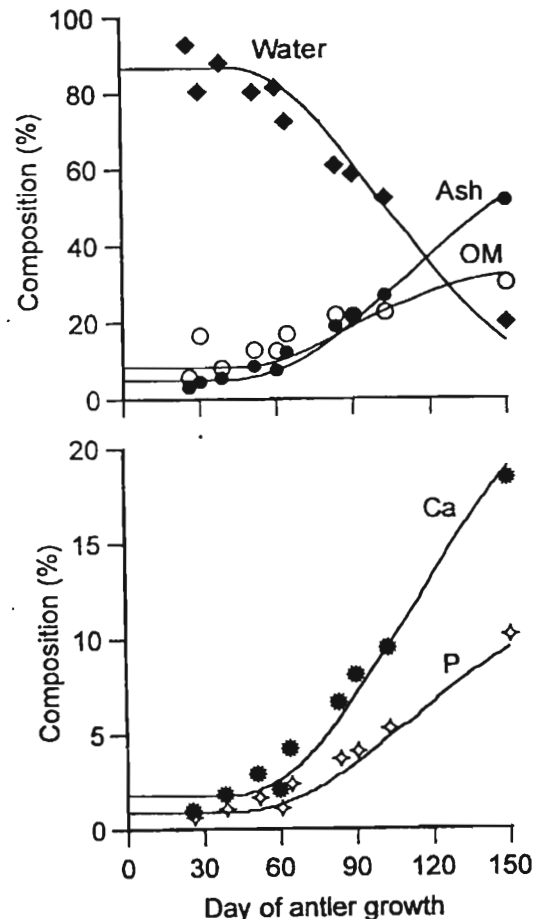


Fig. 2. Predicted changes in antler composition throughout an antler growing season standardized at 150 days. Water, ash, and organic matter sum to 100%, Ca and P are included in the ash fraction. Data points are for white-tailed deer on day 30 (Ullrey 1982), elk on day 60 (Sunwoo *et al.* 1995), moose on Day 90 (R. Moen, *unpubl. data*), and red deer on days 25, 38, 51, 64, 83, 102, and 150 (Muir *et al.* 1987b). Red deer data are circular because data were used in model development.

available (Fig. 2). Antler ash, including Ca and P, increased throughout the antler growth period, and antler protein declined slightly during the last week of the velvet shedding period (Fig. 3).

### Energy Metabolism

Energy intake required to meet the 30% gain in body mass and production requirements ranged from 340 - 365 kcal/kg body mass<sup>0.75</sup> (Table 2). The peak energy requirement for growing 30 kg antlers was

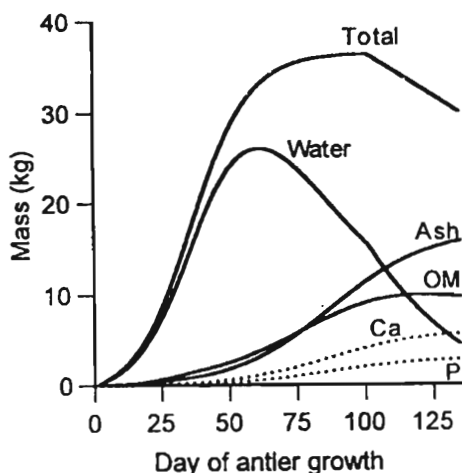


Fig. 3. Predicted antler mass over a 135 day antler growth period for antlers that weight 30 kg at the end of velvet shedding. Composition is predicted from Eqs. 17 - 22 (Table 1).

8800 kcal / day when efficiency of energy use for deposition in antlers was 25% (Fig. 4a). This was more than the energy required for the BMR each day. Antler growth increased overall energy requirements in summer by about 20%, and about 1.9 times more energy was expended on deposition of fat and protein than on antler growth. In contrast, requirements for gestation and lactation increased overall summer energy requirements by about 35% for cows (Fig. 4b), and about 10% more energy was expended on gestation and lactation than on tissue accretion over the summer. Forage intake peaked at about 2.75% of body mass except for females nursing twins, with peak intakes of 10-15 kg DM / day (Table 2).

The model predicts that female moose are more likely to deposit fat and protein throughout the summer after peak lactation. In contrast, males must use energy for antler growth in midsummer at the expense of tissue accretion (Fig. 5). If we increased the efficiency of energy deposition into antlers to 40% while maintaining a 30% body mass increase in summer, peak energy requirements for antler growth decreased to 5700 kcal / day, and 2.8 times more energy was expended on deposition of fat and protein than on antler growth.

Table 2. Required forage intakes to gain 30% body mass and meet energy requirements for gestation, lactation, and antler growth, the resulting body mass, and the pre-rut ingesta-free body fat content for male and female moose.

Sex	Calves	Milk (l)	Antler mass (kg)	Efficiency of energy use	Maximum intake (%)	Intake (kg DM / day)	Intake (kcal/kg MBW/day)	Pre-rut ingesta-free fat (%)
Male			30	25	2.7	15	361	14.0
				40	2.5	14	335	13.9
			20	25	2.7	13	348	14.5
				40	2.6	12	328	14.4
Female	1	300			2.7	10	343	12.3
	2	375			3.0	11	365	11.7



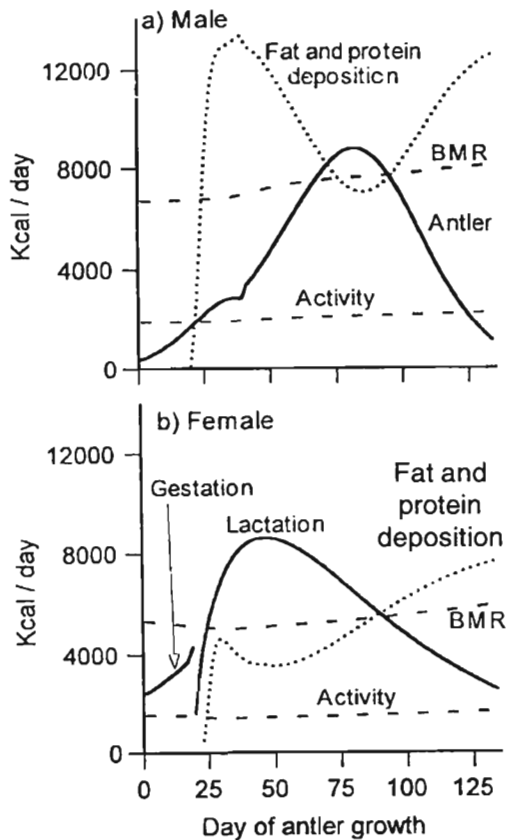


Fig. 4. Predicted energy partitioning for bull and cow moose gaining 30% body mass over the summer. The bull moose grew 30 kg antlers and the cow raised twin calves.

### Nitrogen Metabolism

Most ingested nitrogen is excreted in either feces or urine in summer (Fig. 6). Nitrogen is incorporated into antlers and muscle protein in the summer by males, but the total amount incorporated is <9% of the nitrogen intake over the summer. Nitrogen requirements for cows during late gestation, lactation, and for tissue accretion are about 20% of intake over the summer.

### Calcium Metabolism

Annual Ca requirements for moose with 30 kg antlers are about 2.5 times greater than annual Ca requirements for gestation and lactation in female moose (Fig. 7). Annual Ca deposition in 30 kg antlers was

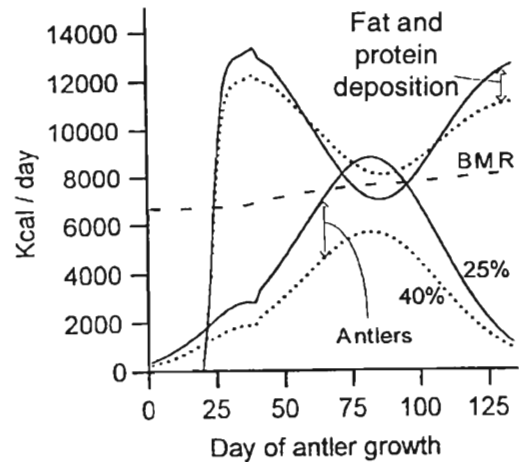


Fig. 5. Effect of different efficiencies of energy use on partitioning of energy in male moose antlers and fat and protein accretion. The default level in the model is currently 25% efficiency.

5.7 kg in the male, compared to 1.7 kg of Ca required for twin fetuses and lactation in females (Table 3). Ca deposition in antlers by males was more than 60 g / day from 5 July to 16 August. From 8 July to 1 August 144 g of Ca was resorbed from the skeleton and deposited in the antlers, with a maximum resorption of 9 g / day. The resorbed Ca represented about 2.5% of the total Ca in the antler, and about 20% of the Ca available from the skeleton. These resorption rates are specific to the antler mass and Ca intake conditions of this simulation, but do demonstrate when Ca is likely to be in most demand under other conditions. The effect of increased resorption on availability of Ca from the diet is reflected in the rise in the "Available" line in mid-summer (Fig. 7a). In contrast to males, female skeletal reserves of Ca did not need to be resorbed to meet requirements for gestation and lactation during summer.

### Phosphorus Metabolism

Females required proportionately more P than Ca because the ratio of Ca:P in milk

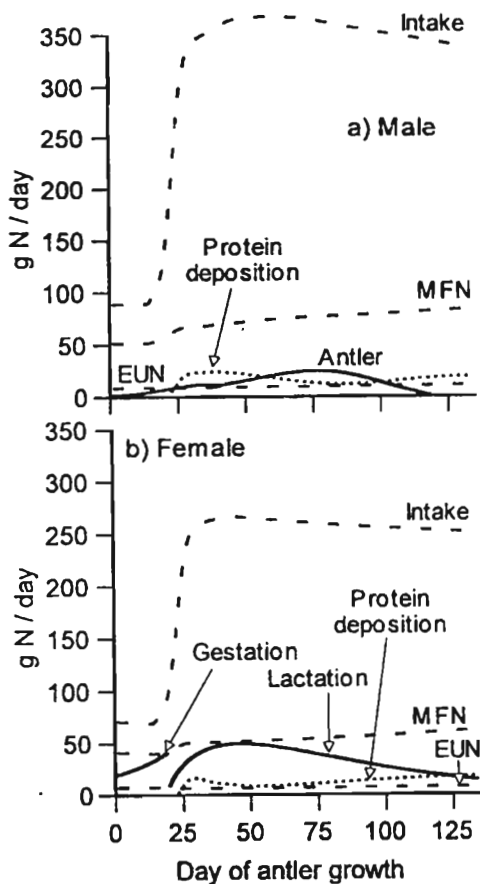


Fig. 6. Predicted nitrogen partitioning for bull and cow moose gaining 30% body mass over the summer. The bull moose grew 30 kg antlers and the cow raised twin calves.

is  $< 2.0$ . Phosphorus requirements for male moose with 30 kg antlers were still about 2.3 times greater than P requirements of cows (Fig. 8). The male moose deposited 2.8 kg of P in the antlers, compared to the 1.2 kg of P required for twin fetuses and lactation in a female (Table 3). P deposition in antlers was more than 30 g / day from 5 July to 17 August. The male resorbed 194 g of P from the skeleton and deposited it in the antler from 22 June to 3 August, with a maximum resorption rate of 7 g / day. The resorbed P represented about 60% of the P which could be resorbed from the skeleton, and about 7% of the P in the antler. More resorption of P than Ca was required be-

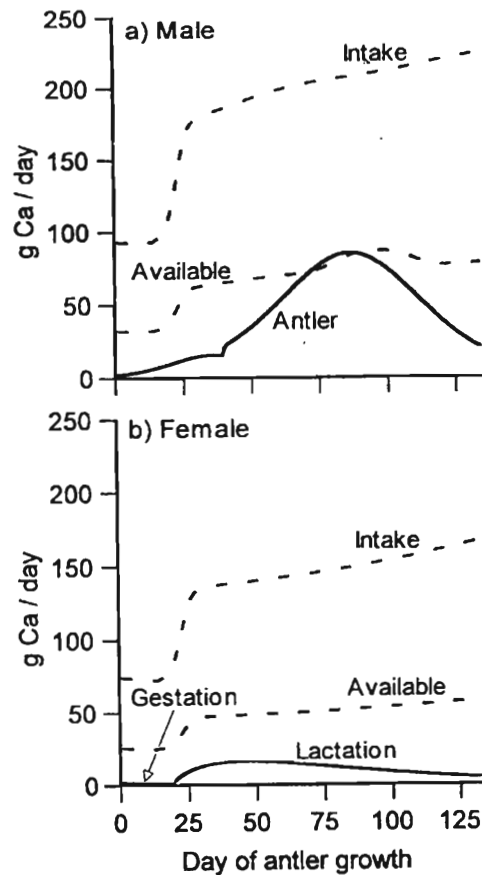


Fig. 7. Predicted calcium partitioning for bull and cow moose gaining 30% body mass over the summer. The bull moose grew 30 kg antlers and the cow raised twin calves. Endogenous urinary Ca and metabolic fecal Ca are small and not shown.

cause of the lower concentration of P in the diet, also indicated by the rise in the "Available" line in Fig. 8a. As with Ca, the model predicts that P resorption from the skeleton is not required to meet reproductive needs in cows during summer.

#### Antler mass: 20 and 30 kg

The effects of 20 kg antlers grown by 500 kg bulls and 30 kg antlers grown by 600 kg bulls on Ca and P metabolism were surprisingly different (Fig. 9). When 20 kg antlers were grown there was sufficient Ca in the diet so resorption was not required,

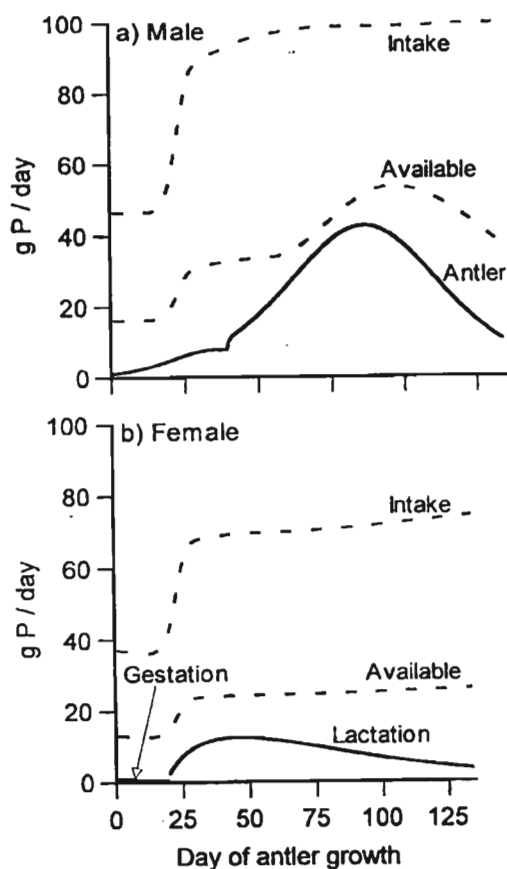


Fig. 8. Predicted phosphorus partitioning for bull and cow moose gaining 30% body mass over the summer. The bull moose grew 30 kg antlers and the cow raised twin calves. Endogenous urinary P and metabolic fecal P are small and not shown.

but 30% of available P in the skeleton was resorbed. In contrast, when 30 kg antlers were grown, about 30% of available Ca and 60% of available P in the skeleton was resorbed. The different effects of 20 and 30 kg antlers is caused in part because energy requirements do not increase as fast as mineral requirements, and also because of the narrow window of rapid mineral deposition in summer (Figs. 7 and 8). Intake per MBW increased from 350 to 365 kcal / kg body mass<sup>0.75</sup>, which was not sufficient to increase mineral intake to meet new antler demands from a diet that was already requiring resorption.

### DISCUSSION

Energy required by males for maintenance, activity, growing antlers, and increasing body mass could require energy intakes up to 5.0 times the basal metabolic rate when the least efficient energy requirements were used. This is similar to the maximum predicted energy requirements for female white-tailed deer nursing 2 fawns (Moen 1978). The actual increase will depend on the efficiency with which energy was used for antler growth. When efficiency of energy use for antler growth was increased, predicted forage intake de-

Table 3. Investment of Ca and P(g) by male and female moose into reproduction.

	Fetus(es)	Milk	Antlers	Total
<u>Calcium</u>				
Female, single calf	208	1075		1283
Female, twin calf	351	1344		1695
Male, 20 kg antlers			3793	3793
Male, 30 kg antlers			5689	5689
<u>Phosphorus</u>				
Female, single calf	112	830		942
Female, twin calf	189	1038		1227
Male, 20 kg antlers			1897	1897
Male, 30 kg antlers			2844	2844

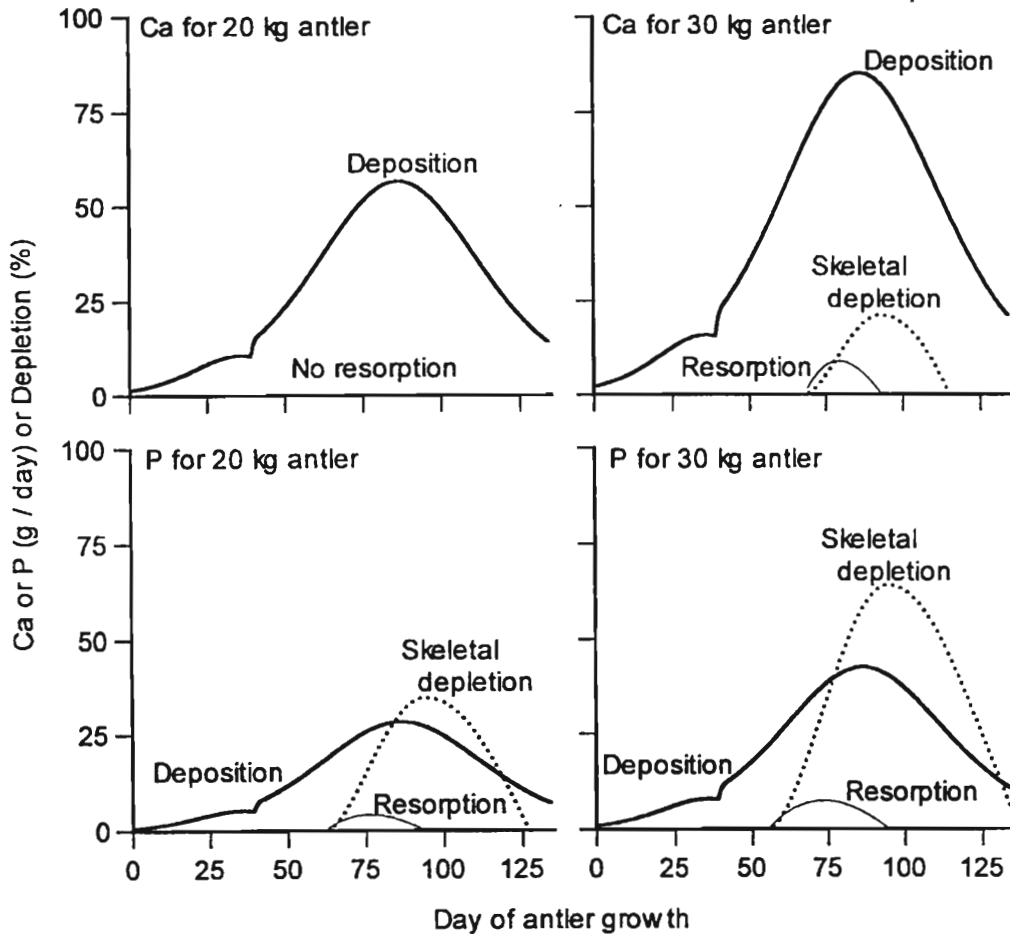


Fig. 9. Effect of 20 kg and 30 kg antler masses on calcium and phosphorus deposition into antlers, resorption, and cumulative resorption from the skeleton.

creased, and predicted resorption of Ca and P from the skeleton increased. We believe the efficiency of energy use for antler growth should be less than the efficiency of energy use for tissue accretion, but greater than the efficiency of energy use for gestation. Although it could be argued that the efficiency of energy use should be similar to tissue accretion because antlers are composed of bone and protein, it is known that bone formation is an energetically expensive process (Howell and Dean 1992, Buckwalter *et al.* 1995). Until direct experimental measurements of the energy required for bone formation are available, or feeding trial experiments are carried out in large antlered

cervids, the efficiency of energy use for antler growth must be estimated.

It has been observed that the largest antlers are correlated with longer growing seasons. This is supported by anecdotal evidence from work on caribou (Bergerud 1976). The longer growing seasons in the late Pleistocene have also been hypothesized to support the larger antlers and body masses in both extinct and extant cervids (Guthrie 1984a, b). Our simulated animals were able to grow large antlers in a growing season of 135 days without depleting skeletal mineral reserves while consuming vegetation weighing <3% of body mass each day in summer. The smooth changes in

energy and mineral requirements in our simulations occur because simulated moose were not faced with daily changes in temperature which would affect available foraging time in summer. The effects of reduced forage availability or reduced forage quality on antler mass could be predicted by varying the forage available to the simulated animal in the summer. Potential limits to antler mass in relation to body size could also be investigated by altering forage intake rates and the duration of antler growth each year.

Our model predicts that calcium and phosphorus requirements to grow 20 kg antlers are larger than requirements for gestation and lactation in females. For example, if females deposited as much P in milk as males deposit in 20 kg antlers, they would need to produce about 685 l of milk per lactation. Alternatively, if males were to deposit as much P into antlers as females put into milk, they would grow 10 kg antlers for cows with single calves, and 17 kg antlers for cows with twins. This contrasts with results of previous work on deer with smaller antlers (Hyvarinen *et al.* 1977, Grasman and Hellgren 1993). The temporal pattern in nutritional demands for reproduction is also different between males and females. Peak requirements occur shortly after birth when diet quality is very high for females, while peak nutritional requirements for antler growth occur in mid-summer after diet quality has started to decline. Requirements for nitrogen in lactation were higher than requirements for nitrogen deposition in antlers. The adequacy of nitrogen in the summer diet is supported by recent experimental work with white-tailed deer (*Odocoileus virginianus*) (Asleson *et al.* 1996)

The more negative balance for P than Ca may not hold for smaller cervids such as white-tailed deer (Grasman and Hellgren 1993). However, as those authors sug-

gested, moose would be more likely to be P limited than white-tailed deer. Simulated dietary Ca:P ratios were often  $> 2:1$ , while antler Ca:P ratios do not vary from  $2:1$ , therefore the simulated moose had to resorb more P than Ca from the skeleton. An alternative mechanism to maintain a constant Ca:P ratio would be to increase the availability of P (Eq. 2,  $AvailFrcPhos_d$ ) at a faster rate as bone P was depleted (Grasman and Hellgren 1993). Demonstrating resorption of bone does not imply that P limitation has occurred, as resorption of bone for antler growth is a normal physiological process (Banks *et al.* 1968a, b). Daily balance of P is less important than the seasonal balance, provided that resorption requirements on any single day of antler growth can be met.

That females or small antlered males did not need to resorb Ca or P from the skeleton does not mean that milk would have no Ca or P from the skeleton. Bone is being continuously remodeled, therefore Ca and P from the skeleton could appear in milk throughout lactation or antler growth. Some female moose from Isle Royale have a reduced bone density (Hindelang *et al.* 1992), indicating that some factor can negatively affect Ca and P metabolism in free-ranging female moose.

Predictions and questions arise from our model of antler growth that we would like to see tested with experimental data. Antler composition during the first 2 weeks of antler growth is predicted by extrapolation in the model because experimental data from the first weeks of antler growth are not currently available. Another unresolved issue is how the animal should adjust antler growth when energy, nitrogen, calcium, or phosphorus can all potentially limit antler growth. Predicted peak requirements for each antler component occur at the same time, in mid-summer. The extent to which tissue accretion in the body could be de-

creased, as implied by Fig. 4, is unknown. The model could be easily modified to account for observed differences in antler density on low and high mineral diets (Hyvarinen *et al.* 1977). The implications of model predictions to moose foraging behavior could also be tested. For example, selective foraging for high P plants when P requirements are highest could be tested by observation of food habits.

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 are only available for red deer, patterns in length of antlers are similar for all cervids when scaled appropriately (Moen *et al.*, *in press*). The set of 6 equations required to predict antler mass and composition (Eq. 17-22) present many testable hypotheses on antler composition and growth for moose. This simulation model is a summary of current knowledge about cervid physiology, specifically energy, nitrogen, Ca, and P metabolism. We believe that the integration of energy, nitrogen, Ca, and P metabolism within the same simulation is a strong test of the biological accountability of model predictions.

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