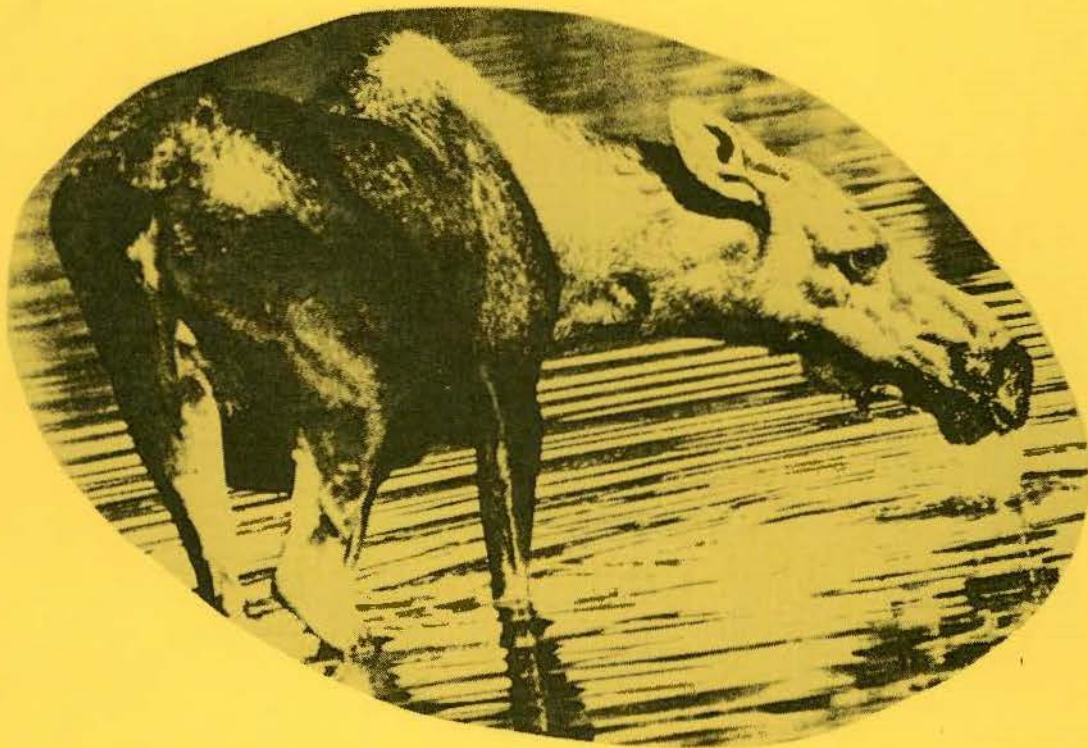


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Research Final Report

MOOSE RESEARCH CENTER REPORT



by
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STATE OF ALASKA
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SUMMARY

This report summarizes results of nutritional studies directed at development of a carrying capacity model for moose (Alces alces). Several different objectives were addressed and are summarized. A formulated ration was developed that meets maintenance and growth requirements of captive moose, and it was this ration that allowed nutritional studies to continue. The ration fiber source was an aspen byproduct (Fiberite), and it may be the major reason for its success. Seasonal estimates of energy metabolism were obtained for moose at monthly intervals. Mean heat production during summer exceeded that during winter by a factor of 1.4. Fasted heat production in moose averaged 94.1 kcal/kg BW^{0.75}/day during winter to 131.9 kcal/kg BW^{0.75}/day during summer. During winter, the cost of standing was estimated at 0.23 kcal/hr/kg or 1.0 kcal/kg BW^{0.75}/hr, an increase of 22% over the cost of lying. Measures of the effects of food intake on seasonal metabolism indicated that there was a linear effect related to the intake of metabolizable energy for the previous 28 days. We also estimated the efficiency of metabolizable-energy retention at 71%. Studies of food intake in moose indicated that consumption of dry matter cycled seasonally; peak intakes occurred in the summer and lows in the winter. Intake rates for males were different than that for females. Daily during summer and winter, moose generally consumed about 3% and 0.5-1%, respectively, of their body weight in dry matter. Males fasted during the rut. Studies of foods with varying caloric content indicated that moose ate to energy fill,

rather than dry-matter fill, as long as food quality was not limiting. Estimates of metabolizable-energy intake for maintenance of winter moose were 131 kcal/kg BW^{0.75}/day, based on controlled-feeding trials. Maintenance requirement for nitrogen was 0.627 g/kg BW^{0.75}/day, while metabolic fecal nitrogen was estimated to equal 0.457 g/100 g dry-matter intake. Effects of energy intake on body condition and fat composition demonstrated that moose on restricted intakes lost 57% of their body fat, while those receiving ad libitum amounts of food gained fat and body composition. Browse digestion studies demonstrated that moose on winter range are in negative-energy balance and the rate of fat depletion is determined by the quality and availability of winter food. Moose in our studies consumed between 25.4 and 38.6 g/kg BW^{0.75}/day of a mixed-browse diet. Rumen turnover studies were conducted to evaluate the ability of moose to process and pass fibrous diets. Rates of passage of solids and liquids were similar. Results of the nutrition studies were used to modify an existing ruminant simulation model. The modified model was tested to determine our ability to predict level of utilization of paper birch (*Betula papyrifera*) browse in four pens stocked with different levels of moose. Browsing by snowshoe hares confounded studies, but predicted vs. actual levels of utilization were similar in 3 of 4 pens. The fourth pen was dissimilar because of inaccurate estimates of food habits. Our studies indicate that the concept of predicting carrying capacity can be applied to those areas of management where quantified information is required. Applying the concept of nutritional carrying capacity is discussed in light of (1) our current information base, (2) economic considerations, and (3) the need for quantitative data. Recommendations for future studies are presented.

Key Words: Alces alces, body condition, browse digestion, carrying capacity, dry-matter intake, energy metabolism, formulated ration, maintenance energy, moose, protein requirements, simulation modeling, weight dynamics.

CONTENTS

Summary	i
Background.	1
Objectives.	4
Methods	4
Results	5
Job 1.	5
Job 2, 3, and 4.	6
Job 5.	18
Discussion and Recommendations.	19
Literature Cited	22
Appendix A. Raising, training, and maintaining moose (<u>Alces alces</u>) for nutritional studies.	31
Appendix B. A formulated ration for captive moose.	32
Appendix C. Stability of a formulated ration for moose	33
Appendix D. Respiration chamber for study of energy expenditure of moose	34
Appendix E. Seasonal energy metabolism of adult moose.	35
Appendix F. Energy cost of standing in adult moose	36
Appendix G. The effect of diet on energy partitioning in moose.	37
Appendix H. Seasonal dynamics of food intake in moose.	38
Appendix I. Nutritional energetics of moose.	39
Appendix J. Seasonal weight dynamics of moose.	40
Appendix K. Energy requirements of adult moose for winter maintenance.	41
Appendix L. Protein digestion in moose	42
Appendix M. Changes in body composition of moose during winter	43
Appendix N. Estimates of digestibility of birch, willow, and aspen mixtures in moose.	44
Appendix O. Food passage rate in moose	45
Appendix P. Field test of a moose carrying capacity model.	46
Appendix Q. Supplemental publications incidental to major research projects conducted under the nutrition and physiology studies	47

BACKGROUND

Long-term moose-nutrition studies with the ultimate objective of developing a carrying-capacity model were initiated in 1978 (Franzmann and Schwartz 1979). The studies were part of a cooperative endeavor between the Alaska Department of Fish and Game (ADF&G), Moose Research Center (MRC) and the U. S. Fish and Wildlife Service (USFWS), Denver Wildlife Research Center (DWRC). The overall objectives were to integrate information on the nutritional requirements of moose (Alces alces) with the nutrients supplied from the vegetation.

Land resource managers have strived for years to quantify the carrying capacity of native ranges. For range management purposes, carrying capacity is defined as the density of cattle providing maximum sustained production of beef. An index of this density is the species composition and growth stage of range plants (Stoddart et al. 1975). Among theoretical ecologists, there has been a unanimity of opinion that carrying capacity means K of the logistic equation (McCullough 1979). This concept of carrying capacity has been applied to wildlife populations, and the term has come to mean many different things to wildlife managers (Edwards and Fowle 1955), but rarely without confusion (McCullough 1979, Macnab 1985). Moen (1973), Robbins (1973), Wallmo et al. (1977), and Mautz (1978) have advanced the concept of predicting carrying capacity based upon an understanding of nutrition. This concept of biological carrying capacity is based on the nutrient requirements of the animal and the capacity of range forage to supply necessary nutrients. Mautz (1978) defined nutritional carrying capacity as the ratio of the nutrient supply of the range divided by the nutrient demand of individual animals or as the size of a healthy and productive population that the food resources of a unit of land would maintain. This approach is useful because, by expressing range supply in units of energy or nutrients, individual bioenergetic requirements can be considered in carrying-capacity estimates (Schwartz and Hobbs 1985). Estimation of nutritional carrying capacity based on range supply of forage energy, nitrogen, and dry matter have been derived for habitats of elk (Cervus elaphus) (Hobbs et al. 1982), white-tailed deer (Odocoileus virginianus) (Potvin and Huot 1983), mule deer (O. hemionus) (Wallmo et al. 1977), and African ungulates (Mentis and Duke 1976).

Many complex interactions between range nutrient availability and animal nutrient requirements must be considered before carrying capacity can be determined. The nutritional interfaces between animal and range include distribution, abundance, availability, and palatability of forage; plant defenses; and the selective pressures imposed by the feeding herbivore and its nutritional demands that interact with and are partially determined by the plant environment. The most essential nutrients that the range must supply are protein and energy (Moen 1973; Wallmo et al. 1977). Other nutritional entities are required for the health of animals but are seldom the primary limiting factor.

The integration of the nutritional requirements of the animal with that supplied by the vegetation requires a submodel of the animal performance that interfaces with a submodel of range nutrient supply. Swift (1983) provided the basis for a ruminant simulation submodel. The submodel is a synthesis of

information on ruminant digestion and physiology that estimates the effects of dietary energy and nitrogen levels and ambient environmental conditions upon ruminant nutritional status and performance. The submodel is a generalized version of energy and nitrogen balance for nonreproducing ruminants: it can be used to simulate the functioning of a variety of ruminant species by altering certain input parameters that characterize the species under study.

This submodel provided the foundation for our studies with moose. Input parameters specific to moose were obtained from the literature or determined from studies outlined in this report. As our research progressed, it became apparent that some of the underlying assumptions made by Swift (1983) were inappropriate for moose, and we modified his general ruminant model to suit moose.

The original objectives of the cooperative efforts (Regelin 1978) between the MRC and DWRC were to develop a carrying-capacity model for moose that could be used by both ADF&G and USFWS: (1) ADF&G was interested in evaluating moose habitat throughout the state where mitigation, enhancement, or other programs dictated quantitative information about nutritional carrying capacity and (2) the USFWS wanted to apply the concept of nutritional carrying capacity to moose populations on the Kenai National Wildlife Refuge (formally the Kenai National Moose Range). Initially, personnel from the DWRC were to measure nutrient quality and vegetation biomass on the refuge, and personnel from the MRC were to establish baseline measures of the nutrient requirements and digestive capabilities of moose. Cooperative research began in 1979 and continued through 1982. Research programs were directed at developing inputs for the carrying-capacity model.

Support for the DWRC's portion of the studies was terminated in 1982 when there was a change in emphasis away from resident-wildlife research within the USFWS as well as the proposed development of a new USFWS Alaska wildlife research center, which would remove Alaska from DWRC's geographic responsibility. Work on the moose submodel was continued by ADF&G, but much of the work on vegetation was stopped. In 1983 the USFWS agreed to provide limited financial support for 2 years of field studies to test the accuracy of the existing carrying-capacity model. In addition, the Alaska Power Authority expressed interest in the potential application of the concept for determining habitat loss and mitigation on the proposed Susitna Hydroelectric Project. Testing of the vegetation model, including forage-sampling procedures and a field test of the carrying-capacity concept, was undertaken in 1983 and 1984. Refinement of the ruminant-simulation submodel and its application were completed in 1986. This report

contains a summary of the studies dealing with the development and testing of the carrying-capacity concept.

OBJECTIVES

Study Objective

To measure relationships between browse quantity and quality and moose productivity in selected areas of Alaska.

Job Objectives

Job 1:

To develop a formulated diet meeting the essential nutrient requirements of captive moose.

Job 2:

To determine nutritional values and digestibilities of the common moose-forage species.

Job 3:

To compare and contrast the ability of captive moose to digest and assimilate a formulated diet versus four major food items consumed by wild moose either singly or in combination during winter.

Job 4:

To determine optimum crude protein and gross energy requirements for various sex and age classes of captive moose on a seasonal basis and to monitor the effects of various levels of nutrient quality on moose blood parameters.

Job 5:

In cooperation with the Denver Wildlife Research Center, to develop a basis for quantifying the capacity of the Kenai National Moose Range to support moose.

METHODS

The information presented in this report either has been published in proceedings or technical journals or is awaiting publication. Each of these manuscripts deals with one or several of the listed objectives. Rather than present methods for each one here, we refer the reader to the specific manuscript dealing with each Job (see Appendices).

RESULTS

Job 1

We began our nutrition studies in 1979 with the acquisition of several moose calves that were abandoned by their cows as a result of another study (Franzmann et al. 1980). These calves, which formed the nucleus of our "tame animal herd," were used for nutrition studies. Techniques used to rear these animals to weaning were reported by Regelin et al. (1979; Appendix A).

A review of the literature, as well as a survey of zoos and research facilities throughout North America, revealed that most institutions consider moose an extremely difficult species to maintain in captivity. The basis for this contention was founded on a lack of a suitable diet that was simple and readily available. In the few places that kept moose, the animals were maintained on harvested native browse, supplementing it with the same rations fed to many other less-specialized ungulates. The labor and logistics of such feeding programs were not realistic or practical for our intended studies at the MRC. To overcome these problems, our first task was to develop a formulated ration suitable for the maintenance and production requirements of moose. The basis for our ration, "the MRC Special," and the assumptions that led us to the ingredients used in its formulation have been presented in Schwartz et al. (1980; Appendix B) as well as in a paper on our long-term studies dealing with the suitability of the ration to maintain moose (Schwartz et al. 1985; Appendix C.). The ration has been so successful that it is now used by several zoos in North America to feed moose and other cervid species (Ellis 1987). Although the purpose of developing the ration was to assure success with the nutrition studies outlined at the MRC, it was gratifying to make it possible for the moose to be elevated to an immensely popular exhibit animal.

Anecdotal information subsequently collected during ongoing studies at the MRC also indicated the ration was readily accepted by wild moose. Thus it has the potential for use as a supplemental winter food. Although decisions dealing with any winter-feeding program must be dealt with on an individual basis, catastrophic winters and public concerns may dictate that such programs be implemented. This situation occurred in the Rocky Mountain states during the winter of 1983-84 (Baker and Hobbs 1985). The MRC Special can provide the basis for any emergency winter-feeding program.

Jobs 2, 3, and 4

The development of the carrying-capacity model required determination of certain inputs specific to moose for the ruminant submodel. The basis of this submodel (Swift 1983) was the flow of energy and nitrogen in the ruminant system. Consequently, it was necessary to determine the seasonal dynamics of energy and protein in moose and relate these to some of the more common browse species available during winter. We designed a series of experiments to measure (1) seasonal metabolic rates, (2) effects of intake on seasonal metabolism, (3) seasonal dynamics of food intake, (4) body weight as it relates to food intake, diet quality, and body condition, (5) protein digestion, (6) body composition, (7) digestion of browse, and (8) rate of passage of food.

Seasonal Metabolic Rates:

Numerous factors determine the nutritional carrying capacity of a given range, but the basic variables are the quantity and quality of forages and the species' nutrient requirements. Knowledge of seasonal energy requirements is essential for determining estimates of carrying capacity. Energy requirements for several ungulates have been estimated using measurements of metabolic rate or heat production or by correlating energy intake with changes in body weight. White-tailed deer clearly demonstrate an annual pattern of energy expenditure, with high metabolic rates in spring and summer and reduced rates in winter (Silver et al. 1969; Holter et al. 1977); this annual pattern appears to be typical for most North American cervids. The objectives of our studies were to (1) measure metabolic rates of moose, (2) determine if they followed a seasonal pattern, and (3) obtain baseline data for use in the carrying-capacity model. Results of these studies were reported by Regelin et al. (1981, 1985, 1986; Appendix D, E, and F). Results indicated that the seasonal energy metabolism of moose was higher than the interspecific mean of $70 \text{ kcal/kg BW}^{0.75}/\text{day}$, cycling seasonally with the peak in summer (May-Sep) and the low in winter (Nov-Mar). Initially, data from these studies provided inputs used for earlier runs made with the ruminant submodel (Swift 1983); subsequently, data provided a basis for comparison with additional studies addressing the effects of intake on seasonal metabolism.

Effects of Intake on Seasonal Metabolism:

Basal metabolic rate (BMR) represents the minimal energy expenditure necessary to support life (Kleiber 1975). Classically, it has been estimated as the heat production of the resting animal (postabsorptive state) in a thermoneutral

environment. This is frequently termed standard fasting metabolism (SFM), and empirical measurements indicate an allometric relationship with body weight raised to the 0.75 power (Kleiber 1975). For SFM in eutherian mammals, the empirical measure of BMR is 70 kcal/kg BW^{0.75}/day; however, within a species the allometry is often different from 0.75 (Robbins 1983). Thus the allometry of BMR is a broad generalization, and many species lie above and below the standard value of 0.75. Larger wildlife species are usually above this line, and much variation is attributed to seasonal differences in SFM: white-tailed deer (Silver et al. 1969), caribou (Rangifer tarandus) (McEwan and Whitehead 1970), roe deer, (Capreolus capreolus) (Weiner 1977), and moose (Regelin et al. 1985).

In species other than human, confusion surrounds both the BMR-SFM terminology and protocol. Empirically defined conditions are difficult to attain with wildlife species. Moose vary greatly in their tolerance to confinement and therefore may not lie quietly in the metabolism stall (Schwartz et al. 1987a). Furthermore, any requirement of fasting lends itself to error because different levels of intake, body size, and food passage rate can alter the time required to reach the postabsorptive state (Marston 1948; Blaxter 1962; Kleiber 1975).

Kleiber (1975) suggested measurements of SFM follow a prolonged period of feeding at maintenance. Energy intake and body condition in moose are in a constant flux; a component of the change is of endogenous origin (McEwan and Whitehead 1970), making it virtually impossible to maintain constant weight or intake. Heat-production measurements at other than the winter period are seldom done at maintenance. Most estimations of SFM with wild ruminants have been made when animals were fed ad libitum (Silvers et al. 1969; Pauls et al. 1981; Regelin et al. 1985). Seasonal estimates of SFM with moose fed ad libitum varied from 76 to 143 kcal/kg BW^{0.75}/day during winter and summer, respectively (Regelin et al. 1985). This seasonal difference in SFM is consistent with most reported results of other studies where wild ruminants were fed at ad libitum. Objectives of our study were to estimate BMR independently from seasonal weight and intake dynamics. Such an estimate would determine if seasonal variation in fasting metabolism was due to the plane of nutrition or to a seasonal endogenous change in BMR. A good understanding of the underlying cause-effect relationships between intake, seasonal plane of nutrition, and metabolic rate was necessary for refining energy flows within the ruminant submodel. Results of these studies (Hubbert 1987; Appendix G) illustrated that resting metabolism was linearly related to the intake of metabolizable energy for the previous 28 days. Our

best estimate of basal metabolism was $68.8 \text{ kcal/kg BW}^{0.75}/\text{day}$, which was slightly higher than cattle and sheep. We also were able to estimate the efficiency of metabolizable-energy retention (71%) for moose.

Swift's model adds the costs of various activities (energy expenditures) as a proportion of basal metabolic costs. This method is inherently prone to the uncertainty of the BMR estimate. The formulation of an energy model based solely on empirical knowledge of resting metabolism and metabolizable-energy intake would overcome the uncertainty of additive models. Based on this conclusion, as well as information from other studies that clearly demonstrate food intake rates are not entirely a function of digestibility and rate of passage and metabolic rates are linked to intake, we restructured the ruminant simulation to include these concepts.

Seasonal Dynamics of Food Intake:

The ability of moose to utilize energy resources within their environment is dependent upon food intake, forage digestibility, and rate of passage of materials through the digestive tract. Voluntary food intake is controlled by physiological mechanisms of the animal and physical capacity and function of the digestive system (Church 1971; Van Soest 1982; Robbins 1983). As summarized by Robbins (1983) and demonstrated for white-tailed deer by Ammann et al. (1973), regulation of intake changes from primarily physical (i.e., bulk limitation) to physiological (i.e., caloric or self limitation) as nutritive value of food increases. At very low nutritive values, limited gastrointestinal capacities and passage rates may prevent an animal from meeting its energy requirements. As nutritive value increases, the animal is ultimately able to ingest enough dry matter to meet its energy requirements. Once nutritive value is high enough to overcome physical limitations, physiological regulation maintains a constant energy intake at increasing nutritive values by decreasing dry-matter intake.

In the nonproductive animal (i.e., a moose in winter) a further increase in nutritive value of food may result in a decrease in food intake. Data presented by Spalinger (1980) demonstrated that when deer were fed diets of increasing digestible energy (DE) (1.5 to 2.2 kcal/g) voluntary food intake increased. Once DE content increased from 2.2 to 3.0 kcal/g, a decrease in voluntary intake occurred and metabolizable energy intake became constant. This suggested that intake of diets with a digestibility greater than 50% were regulated by physiological constraints (Robbins 1983).

Baumgardt (1970) and Conrad et al. (1964) have also demonstrated this principle with domestic sheep and cattle, respectively. Furthermore, this system of physical-physiological control of food intake can be responsive to energy demands (or a lack of demand) based on the animal's productive state. The relationship between the voluntary energy intake and the production level of an animal has been investigated by Baumgardt (1970) with domestic sheep, steers, dairy cattle, and rats. These studies indicated that as production requirements increased voluntary intake also increased when not limited by gut fill. Likewise, studies by Montgomery and Baumgardt (1965) demonstrated that intake decreased as production requirements decreased during the later stages of lactation.

Seasonal intake of food in moose has been associated with a reduction in diet quality and forage availability during winter (LeResche and Davis 1973; Gasaway and Coady 1975). However, an endogenous rhythm that preadapts northern-temperate cervids to the food resources can also be inferred from numerous studies (McEwan and Whitehead 1970; Ozoga and Verme 1970; Westra and Hudson 1981; Wheaton and Brown 1983).

The objectives of our studies were to measure intake rates and energy metabolism models on a seasonal basis and relate these results to those of other studies. Our studies with moose (Schwartz et al. 1984; Appendix H) demonstrate a seasonal voluntary reduction in food intake, accompanied by weight loss or stasis when animals were offered a high-quality diet ad libitum through the year. These results compare favorably with data recently presented by Renecker and Hudson (1985; Appendix I).

In the ruminant simulation model presented by Swift (1983), food intake is regulated by rumen fill and body composition is one of the outputs; Swift assumes that ruminants always eat to rumen fill, which is regulated by forage digestion and rate of passage. Based on our intake studies with moose, this assumption is incorrect. Our modified submodel corrects this error.

Body Weight, Diet Quality, and Body Condition:

Wild moose weight loss during winter (Franzmann et al. 1978) is presumably caused by declines in forage quality and abundance. However, our studies with captive moose that had been fed for several 1-year periods with constant-quality rations demonstrated these animals lost weight during winter, regardless of food availability (Schwartz et al. 1984, 1987b; Appendix J). Under natural conditions, moose lose weight in response to declines in forage quality and availability during winter. However, our studies show that weight loss is also

affected by certain physiological mechanisms that affect metabolic rate. Metabolic rate can vary seasonally (Regelin et al. 1985) with changes in food consumption (Hubbert 1987) and fat catabolism (Abbott et al. 1984).

The mechanisms controlling weight loss in moose are not simply driven by food quality and availability. Therefore, we designed a study to determine the responses of moose in winter to varying amounts of the same quality of food and the same amount of food with varying nutritional quality. By determining these responses, we were able to calculate energy requirements for maintenance during winter and document changes in weight associated with various levels of energy consumption (Schwartz et al. 1988a; Appendix K).

Our best estimate of digestible energy for maintenance (148.6 kcal/kg BW^{0.75}/day) was similar to that for white-tailed deer (158-160 kcal/kg BW^{0.75}/day; Ullrey et al. 1969, 1970) but slightly lower than an earlier estimate for moose (179 kcal/kg BW^{0.75}/day; Renecker and Hudson 1985). Our calculated estimate of metabolizable energy for maintenance (131.3 kcal/kg BW^{0.75}/day) was identical to that for white-tailed deer (Ullrey et al. 1969, 1970) but lower than a value for free-ranging moose (139.75 kcal/kg BW^{0.75}/day; Renecker and Hudson 1985).

During our studies, 2 males on restricted intakes lost too much weight to remain on trial and were returned to ad libitum intake in February. During March and April, both of these males consumed significantly ($P = 0.0005$) more dry matter (105.7 ± 16.3 g/kg BW^{0.75}/day [SD]) than the 3 animals that were fed ad libitum for the entire winter (53.7 ± 13.0 g/kg BW^{0.75}/day). We feel this increase in dry-matter intake indicated that physiological mechanisms regulating intake were influenced by body condition. The 3 moose in the ad libitum treatment group exhibited normal changes in dry-matter intake that we had observed in previous studies; they reduced levels of intake as winter progressed. The 2 males that had depleted their body reserves adjusted intake when food was made available.

Arnold (1985:82) reviewed mechanics of intake control and concluded that "long term stability of energy balance is thought to be controlled by the size of the fat reserves." He further stated that "many species in temperate and arctic areas appear not to have stability in energy balance even in a constant nutritional environment." Moose and probably other northern cervids may have evolved with body condition and photoperiod as mechanisms that control level of intake. These mechanisms operate regardless of availability of high-quality food. Moose (Schwartz et al. 1984), white-tailed deer (Ozoga

and Verme 1970), and caribou (McEwan and Whitehead 1970) voluntarily reduce intake in winter, even when offered high-quality food ad libitum. Changes in voluntary food intake coincide with changes in forage quality and availability (i.e., summer vs. winter). These mechanisms are not rigidly fixed and exhibit plasticity when the animal is stressed.

We agree with the synopsis provided by Arnold (1985:97-98) that "the regulation of forage intake by free-ranging wild herbivores is through both internal controls concerned with digestion, rate of passage of digesta through the digestive system, and set points probably including energy balance and body composition." We propose the following for the moose we studied. Body condition in fall peaked, and an activated mechanism (set point) depressed intake. Decreased intake resulted in a lower metabolic rate (Hubbert 1987) and a shift to a negative-energy balance. Body stores were depleted in spring, resulting in a low body condition (set point); the process was then reversed. Reversals in spring and fall corresponded with environmental changes in food quality and availability (Schwartz et al. 1984). Set points varied with individuals and level of intake. A similar mechanism was also demonstrated with captive moose calves that gained weight in winter when offered ad libitum feed while wild calves lost weight (Schwartz et al. 1987b); this implied body condition may drive intake in the winter. If the lower set point was reached prior to a change in food availability (i.e., green-up), animals in the wild starved to death. However, data from our study suggest that if food was available, moose that reached the lower set point increased intake, while moose in good condition (above the set point) did not.

Although biologists have no control over the length of winter, they can influence the physical condition of animals through habitat enhancement of summer and winter ranges. It has been assumed that winter range is the most critical habitat for moose, and most enhancement programs have been conducted on winter range. If body condition controls animal intake as we observed, it is likely that summer and transitional fall and spring ranges, which provide high-quality, abundant forage, play an important roll in the survival of individuals and, ultimately, populations. Similarly, if food intake, body condition, and seasonal metabolism work in concert, as we have demonstrated with our studies, then simulation modeling must include all of these components. We used this concept when modifying the basic ruminant submodel of Swift (1983).

Protein Digestion:

The literature concerning nutrient requirements, metabolic rates, and digestive capabilities of deer is extensive. The literature is also replete with information on food habits of moose (Peek 1974), but studies of their nutritional requirements are rare, according to a review of the literature by Gasaway and Coady (1975). By necessity, much of the data they presented was from studies with other cervid species or from literature on livestock. The information base on moose nutrition is scant. Many statements in the text attest to this; e.g., (1) "estimates of BMR of moose is difficult, particularly considering that metabolic data have not been reported for the species," (2) "while maintenance energy for moose is uncertain, maintenance requirements for wild and domestic species have been estimated," or (3) "food intake, passage rates, and digestibility in moose have received little consideration."

The objectives of our study were to better understand protein requirements in moose and to facilitate predicting carrying capacities of the ranges they occupy. Protein digestion and nitrogen dynamics in Schwartz et al. (1987c; Appendix L) demonstrated that the maintenance requirement for nitrogen was $0.627 \text{ g/kg BW}^{0.75}/\text{day}$. Each additional unit of ingested nitrogen resulted in increases of 0.346 units in retained body nitrogen and 0.561 units in urinary nitrogen loss. Metabolic fecal nitrogen was 0.457 g/100g dry matter consumed. For any food, regardless of its protein content, the first 3.29 g of nitrogen/100g of dry matter offsets metabolic fecal nitrogen; the remainder goes to maintenance and production. We demonstrated that as the protein content of forage decreased toward 3.29%, the amount of dry matter required to maintain nitrogen balance increases at an accelerating rate. This rapid increase in intake, which is required as crude protein declines in the diet, presents moose with a dilemma during winter: intake of poor-quality forage is limited by digestibility and rate of passage. Diets containing <3.29% crude protein cannot meet maintenance-nitrogen requirements because no matter how much food is eaten, the level of nitrogen intake is less than the losses associated with metabolic fecal nitrogen; moreover, there is no leftover nitrogen to meet urinary losses. Information from these studies was used in the ruminant simulation submodel (Hubbert 1987).

Body Composition:

Use of individuals to assess the nutritional status of populations has received increased attention from researchers in recent years. Franzmann (1985:240-259) outlined the steps required to apply the animal-indicator concept to assess

nutritional status of large herbivores: (1) identify boundary conditions, (2) establish baseline values, (3) determine parameter response to perturbation, and (4) determine the resilience of an animal to further perturbation.

Body composition and fat reserves have been used as indicators of animal condition (Ledger and Smith 1964; Robbins et al. 1974; Monro and Skinner 1979; Verme and Ozoga 1980; Torbit 1981; Torbit et al. 1985a). Fat metabolism in northern cervidae is a dynamic process with large gains and depletions associated with the summer flush of forage and winter declines in food availability and quality. Seasonal weight dynamics of northern cervidae have been associated with reduced diet quality and forage availability (Severinghaus 1955, 1979; Park and Day 1942). However, numerous studies (McEwan and Whitehead 1970; Ozoga and Verme 1970; Westra and Hudson 1981; Wheaton and Brown 1983; Schwartz et al. 1984) have demonstrated a seasonal reduction in intake of dry matter with subsequent weight loss for various deer species maintained on a high-quality feed offered ad libitum throughout the year. Intake, including its subsequent effect on body composition, is a complex physiological phenomenon that is regulated by the central nervous system (Forbes 1980). Arnold (1985:82) provided an excellent review of these mechanisms, suggesting that "long term stability in energy balance is thought to be controlled by the size of the fat reserves."

Torbit et al. (1985b) examined the relationships between body composition estimates of mule deer (Odocoileus hemionus) using two different procedures. They concluded that body composition could be reliably estimated by using dilution techniques to estimate the total body water pool with tritiated water (HTO). This technique provided estimates of body composition of individuals in a nondestructive manner.

Objectives of this study were to (1) determine if fat dynamics could be measured in moose using indirect estimates of total body water, as suggested by Torbit et al. (1985b), (2) evaluate the potential of using these estimates as indicators of animal condition using the criteria outlined by Franzmann (1985), and (3) relate changes in body composition and weight to food intake.

Estimates of body composition measured in this study (Appendix M) are the first presented for moose. Estimates of body composition for our moose were slightly higher than those reported for white-tailed deer but lower than those for cattle and sheep (Reid et al. 1955, 1968) and the Svalbard reindeer (Rangifer tarandus platyrhynchus) (Reimers 1983).

Changes in body constituents were consistent with our expectations; however, absolute measures of fat, protein, and ash may have been inaccurate. These problems could have been minimized if detailed knowledge of the relationships between body composition and the HTO technique had existed for moose. Data for white-tailed (Robbins et al. 1974) and mule deer (Torbit et al. 1985a, 1985b) appear inadequate for predicting body composition in moose. Similarly, we were unable to accurately predict the effect of variability of gut water on the total body-water estimate, and unlike Torbit (1981), we did not equilibrate food intake among treatments prior to HTO estimation.

Because the HTO technique is an estimation of dilution, the amount and concentration of the HTO injected into the animal must be accurately known. Errors in HTO estimation can occur if (1) an unknown amount of marker is lost during injection, (2) the concentration of the injected material is calculated incorrectly, or (3) there is great variation in water content of individuals. We attempted to minimize the first 2 sources of error. Each dosage was individually weighed prior to injection. Animals were injected while they stood on a scale, and the material was dispensed from the syringe only after the needle had penetrated the muscle. On those occasions where there was a question about complete injection, we noted it but those few instances did not account for all the variations. To minimize errors with the standard, we used material from the same dilution for animals in all treatments. We used different dilutions over time, but analysis of the data indicated that there was no relationship between material used and subsequent estimates in body water (i.e., obvious trends between batches did not exist).

The sources of energy lost or gained (Kcals) in the moose averaged 100% fat and 0% protein. The variation about these estimates was large, particularly as the energy change approached zero. This error appeared to be associated with the variation in our ability to accurately predict fat and protein levels in the moose. Torbit et al. (1985a) measured fat and protein catabolism in mule deer. Their studies showed that when total energy losses were considered, protein contributed 23-29%, depending on treatment. The variation about their estimates appeared to be quite small relative to ours (Torbit 1981: 62).

Body-composition estimates determined from this study can serve as crude estimates for the criteria outlined by Franzmann (1985). We used the HTO dilution technique because it provided an inexpensive and nondestructive measure of body composition dynamics in moose. Correction equations developed for deer may be useful for moose, but verification of the

technique must require whole-body measurements of body constituents using chemical analysis. We were unable to verify our data because (1) a whole-body grinder capable of processing a moose carcass was not available and (2) the study animals were too valuable for totally destructive sampling. Recently, Hout (1985) has developed a technique to determine body composition from a carcass using a bandsaw sample. The technique still requires partially destructive sampling, but before we can accurately determine body composition based on HTO or other techniques, these data suggest that validation is imperative.

Digestion of Browse:

In vivo digestion studies with moose are costly because of the extensive manpower required to collect sufficient quantities of browse for the duration of each trial. We were able to accomplish this task primarily because of the efforts of a group of youths working for the Young Adult Conservation Corporation.

Estimates of diet quality for moose have been based on chemical analysis of major constituents and estimates of digestion obtained in vitro (Oldemeyer 1974; Regelin et al. 1986). Except for the work of Hjeltjord et al. (1982) and Renecker and Hudson (1985), there were no in vivo determinations of diet quality for moose. Oldemeyer (1974) and Regelin et al. (1987a) provided estimates of apparent dry-matter digestion, and Hjeltjord et al. (1982) provided estimates of apparent energy digestion. No data were available for the energy loss associated with methane and urine.

Paper birch, willow, and aspen are 3 plant species constituting >95% of the hardwood browse consumed by moose on the Kenai Peninsula, Alaska, during winter (LeResche and Davis 1973; Regelin et al. 1987a). The proportion of these 3 browse species and lowbush cranberry (*Vaccinium vitis idaea*) in the winter diet of moose is apparently determined by species composition of the winter range, plant availability, and snow depth (LeResche and Davis 1973; Sigman 1977:78-85). Moose appear to prefer willow over aspen and aspen over paper birch. Lowbush cranberry is consumed when quantities of available browse are low and snow depths permit ground feeding and/or cratering by moose (Sigman 1977:78-85; Johnson et al. 1973). On heavily used winter range, the preferred species of willow and aspen are rare and the amounts of birch and cranberry in the diet of moose are high. Chemical analysis and in vitro digestion estimates indicate that aspen has the highest nutritive quality, followed by willow, cranberry, and birch (Oldemeyer 1974; Regelin et al. 1987a). Consequently, as moose winter range deteriorates, the availability and nutritional quality of willow and aspen declines. The objective of

our study was to examine dry-matter intake and digestion of paper birch, willow, and aspen as well as mixed diets of these 3 species so that we could better understand their nutritional importance to moose. Results of these digestion and balance trials were reported in Schwartz et al. (1988b; Appendix N) and are summarized below.

For moose the value of winter food depends upon nutritive quality and the quantity that an animal can process each day. In our studies, moose that were consuming equal portions of mixed browse ate between 25.4 and 38.6 g/kg BW^{0.75}/day. Renecker and Hudson (1985) estimated DMI for free-ranging moose on winter range varied from 38 to near 60 g/kg BW^{0.75}/day, depending on method of estimation and month of measurement (December-March). Maintenance-energy requirements for adult moose (Schwartz et al. 1987a) were estimated at 148 kcal/kg BW^{0.75}/day of digestible energy. Digestible-energy intake for moose in the first birch, willow, and aspen trial averaged 72.4 kcal/kg BW^{0.75}/day. Estimates based upon Renecker and Hudson's (1985) data ranged from 62 to 126 kcal/kg BW^{0.75}/day. With its maintenance requirement of 148 kcal/kg BW^{0.75}/day, an average moose (weight 400 kg) consuming only 72.4 kcal/kg BW^{0.75}/day would lose about 2 kg/day, assuming 70% of the energy to make up the deficit comes from fat and 30% from muscle tissue (Torbit et al. 1985b). Assuming a maximum over-winter weight loss of 30% (Franzmann et al. 1978), a moose can lose weight at this rate for 60 days. However, if the moose selected a diet higher in digestible energy and/or increased intake, the rate of weight loss would decline. If the moose consumed birch, willow, and aspen in different proportions (i.e., mostly aspen and willow) and with no change in dry-matter intake, then their digestible-energy intake might approach 100 kcal/kg BW^{0.75}/day. The moose would remain in negative-energy balance, but weight loss would decline to around 1.3 kg/day, and 92 days would be required to loose 30% body weight.

Our browse-digestion studies demonstrate that moose consuming ad libitum amounts of winter browse are in negative-energy balance. It is also apparent that the quality of winter browse influences how fast energy reserves are burned. The length of time that an animal can survive on winter range is a function of energy stores and rate of depletion. Energy stores are determined by the quality of the summer range, while depletion is a function of winter length and range. As winter range deteriorates on the Kenai Peninsula, the rate of utilization of energy stores increases. Management then becomes a balancing act because the interaction between quality and quantity of food on the summer and winter range for moose cannot be treated independently. Additional studies

are required to determine when summer- or winter-range enhancement is the most appropriate form of management.

Rumen Turnover Studies:

Utilization of energy by moose is dependent upon voluntary food intake and forage digestion, both of these factors may be directly controlled by rate of passage of digesta through the gastrointestinal tract. Different species of ruminants have evolved with markedly different adaptations and modifications of the forestomach that allow for optimal extraction of nutrients. Hoffman (1973) described the structure of the rumen complex of 28 East African ruminants. He categorized most of these ruminants; roughage eaters and concentrate selectors represent the two extremes of the categories.

Forage selection, digestibility, and rate of passage vary widely among species within Hoffman's classification. Comparatively speaking, concentrate selectors and some mixed feeders have a characteristically short forage-retention time irrespective of their diet (Kay et al. 1980). Also, findings for roughage eaters (e.g., domestic sheep and cattle) suggest that the flow of the fibrous and liquid components are widely separated and this separation is most obvious as the fiber content increases or the digestibility of the diet declines. To our knowledge, no comparative studies have been made of classical concentrate selectors. However, we would hypothesize a closer association of the passage of the fibrous and liquid phases because the rumen-omasal orifice is larger and permits outflow of particles having relatively large diameters (Renecker 1986).

Based on rumen structure and summer food habits (Hoffman 1985), the moose has tentatively been classified as a concentrate selector. Other than the recent work of Hjeltjord et al. (1982), Renecker and Hudson (1985), and Renecker (1986), there is no information available on food-passage rates in moose. Hjeltjord et al. (1982) used a liquid-phase marker, but no particulate marker was used. Their work demonstrated that rumen turnover time of the liquid phase depended on diet quality. This finding could be interpreted as evidence that the moose is a roughage eater because similar associations are well documented in sheep and cattle (Thornton and Minson 1972; Ellis and Lascano 1980). The most definitive evidence would be provided by comparing the parameters of studies involving liquid- and solid-phase turnovers and rates of passage for typical concentrate selectors consuming diets of similar fiber content to those related studies of sheep and cattle (i.e., roughage eaters). We compared two nonabsorbed radiolabeled markers to determine the liquid- and particulate-phase dynamics. In our initial studies (Appendix O), the fiber

content in the moose's feed was gradually increased (e.g., a pelleted ration, a mixture of pelleted ration and winter-clipped aspen, and a mixture of paper birch, willow, and aspen) to determine if the fiber levels changed the relative dynamics of the liquid and solid phases. If our hypothesis is correct, we should expect a minimal separation in rate of passage of the liquid and solid phases of the digesta. Results of this study were confounded because of the migration of the marker from the solid particle phase to the liquids, and definitive testing was not possible. We designed a 2nd series of experiments to test the retention time of liquid and particulate phases in the rumen and alimentary tract and to determine if there is a seasonal shift in alimentary fill and retention time in moose fed a low-quality, browse-based diet. Results from these studies were published as part of a Ph.D. Thesis (Hubbert 1987; Appendix G.). In general, rumen-turnover studies indicated that digestibility and intake of low-quality foods can be controlled by the retention time in the alimentary tract. Therefore, insight into the relationship between food intake and retention time in the digestive tract is important in understanding the winter-feeding strategy of moose. In addition, ruminal and alimentary capacity may vary seasonally. The later studies (Hubbert 1987) also confirmed that the liquid and solid phases of digesta in moose move at approximately the same rates. This also suggests that moose seasonally optimize forage nutrient intake by altering the digestive fill. Results of these studies, as well as studies of intake rates, (Schwartz et al. 1984) suggested that regulation of food intake was probably controlled by both physiological and physical limitations imposed by food quality. The model presented by Swift (1983) used rumen fill and turnover rate as the controlling variables dictating forage-intake rates. For this reason, we altered the ruminant model to include other variables to regulate intake. This will be discussed later in this report.

Job 5

The ultimate objective of the nutrition and physiology studies at the MRC was to develop a carrying-capacity model for moose based on nutritional requirements; two computer submodels were involved. The ruminant portion (moose submodel) was developed to predict forage intake based upon nutritional physiology, nutrient requirements, and quality of available forage. The second submodel was developed to determine the amount of available forage and nutrients with different diet mixes and levels of utilization for each forage species. The final output is an estimation of the potential carrying capacity of the range being evaluated. The term potential carrying capacity is used rather than the actual population level

because the two may be quite different. Any moose population has a number of decimation factors (e.g., predation, hunting, starvation, etc.) operating upon it at any time.

During the early phases of our research with the ruminant submodel presented by Swift (1983), it became apparent that certain assumptions (previously discussed) were incorrect. For that reason, we restructured this model to include energy flows that were regulated not only by bulk limitation of the diet (rate of passage and digestion as in Swift's model) but by physiological mechanisms that were driven by body condition on a seasonal basis. The new version of the model (Hubbert 1987; Appendix G) was tested using simulation modeling. This model and the original ruminant simulation model were used in a test of the carrying-capacity concept at the MRC (Regelin et al. 1987b; Appendix P). Results of these studies indicated that both models successfully predicted the level of utilization of paper birch in 3 of 4 pens. Excessive browsing by snowshoe hares and inaccurate knowledge of food habits reduced successful predictions in all pens. In addition to testing the practicality of the modeling approach, several new methods of data analysis relative to vegetation sampling were developed.

DISCUSSION AND RECOMMENDATIONS

Results from these studies have increased our basic understanding of moose nutrition and physiology. Prior to much of the work presented here, there were virtually no data available on this topic. Concurrent to our studies, other researchers have also provided useful information relative to moose nutrition (Schwartz et al. 1987a). Data collected under this project have allowed us to develop a fairly sophisticated computer submodel that simulates flows of energy and nitrogen within the animal's system. This "paper moose" accurately predicts energy consumption and changes in body composition on a seasonal basis. When our moose submodel is coupled with a vegetation submodel, accurate predictions of nutritional carrying capacity are possible.

Our initial attempts at developing the model were successful, but the current version represents a nonreproductive female. In the real world of moose, very few females are not pregnant. Additional flows should be included to incorporate the costs of fetal development. Much of these data can be obtained from existing literature and would require little additional effort (Ofstedal 1985).

Initially, we had hoped to develop a carrying-capacity model that would prove useful for a wide variety of management decisions. Our experience indicates that this is probably not the case. Since the carrying-capacity model is composed of 2 submodels (animal and vegetation), its application is dependent on the strength of both. Our work at the MRC has allowed us to refine the animal submodel, and the inputs for this segment are quite good. However, the strength of the output is also influenced by the vegetation submodel. Our experience during the testing phase of the carrying-capacity concept indicated that our ability to accurately measure the available amounts of "moose foods" within the MRC enclosures was limited by available techniques, labor, and money. It became apparent that accurate measurements within a complex vegetative community required intensive vegetation sampling. This sampling is costly and time consuming. Consequently, until we have accurate, inexpensive, and reliable techniques to measure vegetation, the usefulness of the carrying-capacity concept will be limited in its application.

The concept, however, is not without application. The technique will provide reliable estimates of carrying capacity on ranges where accurate measurements of vegetation are available. Application is appropriate when habitat loss is anticipated and mitigation estimations are needed. Such was the case on the Susitna Hydroelectric project where an accurate estimate was made (Becker 1987). The model may also prove useful where accurate estimates of habitat enhancement are necessary. Pre- and post-treatment measurements can be expressed in units of moose food and, hence, moose numbers; also cost-benefit ratios can be calculated. Additionally, the moose submodel can prove useful where estimates of seasonal dry-matter intake are required but no measurements are available. Estimates can be generated with information from the literature and some detailed knowledge of the specific range in question (i.e., species composition, food habits, nutrient quality). The degree of accuracy and reliability of the carrying-capacity estimates required will dictate which inputs need to be generated as well as the costs to obtain these inputs.

Although the 2 submodels form a carrying-capacity model, the output of the model is dependent upon the level of utilization of "available food" established by the researcher. For example, nutritional carrying capacity is the number of animals supported by a given number of units of food. Food is measured as unit/area (i.e., kg/ha). For woody browse, current annual growth (CAG) is a convenient unit of measure easily distinguished by field crews. Most woody biomass is thus estimated as amounts of CAG. This system of measurement provides unity to researchers, but it is largely ignored by

moose. Studies by Hubbert (1987), which were conducted as part of this project, showed that moose often ate 2-year-old wood. Hence, estimates of CAG may underestimate total available food. Second, plants are subject to increasing and decimating components within their population. Plants can produce additional biomass during the growing season in two ways: (1) by growing additional tissue on the same plant or (2) by producing offspring. On most moose ranges, growth of the same plant represents the major source of new food to moose.

Like plant growth, tissue loss occurs in many ways. Here we are concerned with tissue removal by moose; i.e., utilization. Levels of utilization of plant tissues by moose are equivalent to levels of predation or hunting on game populations. As long as production (plant growth) exceeds mortality (moose browsing), the population will be healthy and able to grow. Once mortality exceeds production, the population will be driven downward. If overharvest continues, extinction can occur. Levels of utilization represent harvest of plant tissues; hence, estimation of carrying capacity is not simply determined by dividing the animal's requirements by the amount of food available. Rather, one must determine for the plant community what level of utilization will produce the optimum, maximum, or other level of sustained yield of food desired. Plants must be managed similarly to animals to ensure efficient use of ranges. Levels of utilization must be determined by objectives that address both animals and vegetation. For example, levels of utilization to maximize total numbers of moose produced on a range would be substantially higher than utilization to maximize forest regeneration. Similarly, summer utilization of leaves affects production of winter twigs. Unfortunately, there is no information dealing with the effects of varied levels of utilization on common browse species eaten by moose. Long-term studies should be initiated to address this topic. Additionally, studies to efficiently estimate the biomass of available moose food are required if we wish to expand the application of the current carrying-capacity concept.

Several other important contributions were made during this study. The new moose submodel provides a new conceptual framework for assessing carrying capacity. Using body condition of moose as the unit of measurement, it will become a valuable tool for measuring habitat quality and carrying capacity. Results of our studies indicate that body condition is a major indicator of range condition and, hence, a reliable estimator of population quality. Moose condition on fall range is indicative of quality of the summer range, while body condition in spring reflects quality and conditions of the winter range. It is highly likely that animal condition can

be used to indirectly monitor ranges. In some uses, this can eliminate the need for expensive and time-consuming vegetation measurements. Studies should be directed at refining our ability to accurately measure total body fat in moose in a nondestructive fashion. The tritiated-water techniques tested under this study apparently are not applicable to moose under field conditions. New and different measurement methods should be investigated and related to this existing data base.

Finally, the tame moose herd has provided the Department with a reliable source of animals to test many techniques; however, it has also provided study animals for projects not related to the nutrition and physiology studies. In addition to the manuscripts that deal directly with data collected during this report period, a number of other publications were the direct result of this study. These publications are listed in Appendix Q.

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Appendix A.

RAISING, TRAINING, AND MAINTAINING MOOSE (Alces alces) FOR NUTRITIONAL STUDIES

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Abstract: Alaska Moose (Alces alces gigas) calves were successfully hand-reared and trained for nutritional studies. Calves were captured 2-5 days after birth and bottle-fed a commercial milk replacer. Calves were trained to accept handling, weighing, and confinement in an energy chamber. As yearlings, they continued to accept close human contact and experimental procedures. The moose are being used to gain knowledge of digestive and blood physiology and energy requirements. Data from these studies and others are being used to produce a mathematical model of moose carrying capacity on the Kenai National Moose Range.

Proc. Int. Congr. Game Biol. 14:425-429. 1979.

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Appendix B.

A FORMULATED RATION FOR CAPTIVE MOOSE

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Abstract: A formulated ration suitable for animal maintenance or experimental purposes has been developed for moose (Alces alces). It contains 11.8% crude protein and has an apparent dry-matter digestibility of 64%. Performance was measured over 1.5 years with data from six moose. Daily gain from weaning to 1 year of age was 0.62 ± 0.4 kg SD. Possible diet problems and improvements are presented. Aspen (Populus tremuloides) sawdust, the primary constituent, is believed to be the major reason for the diet's success. A discussion based on extensive literature review is presented concerning fiber types and their effects on animal welfare.

Proc. 16th N. Am. Moose Conf. Workshop. 16:82-105. 1980.

Appendix C.

SUITABILITY OF A FORMULATED RATION FOR MOOSE

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Abstract: A formulated ration for maintenance or experimental purposes has been developed for moose (Alces alces). It contains 12.7% crude protein and has an apparent dry-matter digestible-energy concentration of 2.4 kcal/g. Metabolizable-energy concentration is 2.1 kcal/g. Performance was measured over 5 years with data from 11 moose. Daily gain in calves from weaning in August through October and November through April was $0.9 \text{ kg} \pm 0.06 \text{ SE}$ and $0.4 \text{ kg} \pm 0.03 \text{ SE}$, respectively, exceeding those of wild moose. Mean body weights of adult males and females on the diet were greater than those of wild moose. Reproductive performance was also excellent, with 83.1% of the yearling females breeding and producing calves at age 2. The ration has been used as the only food for moose for up to 5 years with no apparent adverse effects. It lends itself to constituent alteration for experimental purposes.

J. Wildl. Manage. 49(1):137-141. 1985.

Appendix D.

RESPIRATION CHAMBER FOR STUDY OF ENERGY EXPENDITURE OF MOOSE

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Albert W. Franzmann, Alaska Department of Fish and Game, Kenai
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Abstract: The respiration chamber and associated equipment used at the Kenai Moose Research Center to measure energy expenditure of moose is described. Methods used to construct the chamber and to measure respired gas volume and composition are discussed.

Alces 17:126-135. 1981.

Appendix E.

SEASONAL ENERGY METABOLISM OF ADULT MOOSE

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Abstract: Energy expenditure of tame adult moose (Alces alces gigas) was measured at approximately monthly intervals for a period of 13 months using an indirect-respiration chamber. Mean heat production (HP) in summer (May-Sep) exceeded that in winter (Nov-Mar) by a factor of 1.4. Fasted HP in moose while lying down averaged $394 \text{ kJ/kg}^{0.75}/\text{day}$ in winter and $552 \text{ kJ/kg}^{0.75}/\text{day}$ in summer.

J. Wildl. Manage. 49(2):388-393. 1985.

Appendix F.

ENERGY COST OF STANDING IN ADULT MOOSE

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Abstract: The energy cost of standing in adult moose (Alces alces gigas) was 0.23 kcal/hr/kg or 1.0 kcal/hr/kg^{0.75}, an increase of 22% over the cost of lying during the winter season. Moose had a lower cost of standing than many other wild ruminants.

ALCES 22:83-90. 1986.

Appendix G.

THE EFFECT OF DIET ON ENERGY PARTITIONING IN MOOSE

Hubbert, M. E. 1987. Ph.D. Thesis, Univ. Alaska, Fairbanks. 158pp.

Abstract: Moose (Alces alces) have dynamic seasonal patterns of food intake and body-weight changes. Body weight may vary by 35% from winter lows to summer highs. Food intake levels during summer may exceed winter levels by up to a factor of five. Forage quality and availability are thought to drive the seasonal patterns of food intake and weight loss.

Changes in digestive strategy of moose in winter and spring were analyzed in this thesis. During December, the total mean retention time (TMRT) of food in the alimentary tract increased as dry-matter intake decreased, while alimentary fill remained constant. In contrast, during April TMRT did not increase with increased intake; rather, alimentary fill increased. There appeared to be a seasonal digestive strategy for optimizing nutrient intake.

True basal metabolic rate (TBM) was estimated using regression analysis of heat production on metabolizable energy intake. TBM was estimated at 68.8, close to the interspecies mean of 70 (kcal/kg/BW^{0.75}/d). However, differences in TBM noted during December, February, and April were not significant.

Paper birch (Betula papyrifera) twigs were collected during winter, cut from the tip to 8 specific diameters (2-9 mm), and analyzed for neutral detergent fiber, acid detergent fiber, crude protein, acid detergent lignin, ash, and in vitro dry-matter disappearance. Results indicated that dietary quality decreased with increasing diameter. Moose subjected to 4 different stocking rates (23%, 31%, 41%, and 66% utilization of paper birch) showed no difference in the diameter of paper birch (mean = 2.66 mm) harvested.

A simulation model was presented in which food intake by moose was controlled by both physiological demands and alimentary capacity. Seasonal estimates of food intake changed with energy demands. The model proved useful in estimating seasonal energy requirements of moose.

Appendix H.

SEASONAL DYNAMICS OF FOOD INTAKE IN MOOSE

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Abstract: The seasonal dynamics of dry-matter intake were measured by feeding 12 tame moose (Alces alces) a pelleted ration from 1979 to 1983. Composition and digestibility of the diet were constant, so changes in dry-matter intake reflected changes in physiological appetite of moose. Dry-matter intake (DMI) in adults (age >1 year) paralleled seasonal changes in metabolic rates, with peak consumption (104-142 g DMI/body weight ($BW^{0.75}$ /day) occurring during summer months (June-September) and the nadir occurring in late winter (50-59 g DMI $BW^{0.75}$ /day) (March-April). Complete fasting for as long as 18 days was observed in bulls during the rut. Cows reduced intake during part of the breeding season (54-58 g DMI/ $BW^{0.75}$ /day); the lowest intakes were similar to those observed during late winter. Information presented serves as a baseline for comparison to other studies where dry-matter digestibility and rate of passage vary seasonally with diet quality.

ALCES 20:223-242. 1984.

Appendix I.

NUTRITIONAL ENERGETICS OF MOOSE

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Abstract: Nutritional energetics of moose (Alces alces) are reviewed and discussed. Moose are classified as concentrate selectors, based on their digestive morphology, dietary selection, and rate of passage. Seasonal intake, which is a function of forage availability, digestibility and rate of passage, varies seasonally with a low occurring in late winter and a high in the summer. Bulls fast for a period of 14-18 days during peak rut, while cows reduce intake but do not fast. Rates of passage of food material through the gastrointestinal tract varies with diet and digestibility, ranging from 21-34 hours for browse and 9-28 hours for hay and pelleted diets. Energy partitioning of moose foods indicates that approximately 15-75% of the gross energy intake is digestible. Significant correlations are established between dry-matter digestion (DMD) and lignin content of the food and between DMD and ash content of the food: DMD is highly correlated with digestible energy (DE). Estimates of urine energy vary with diet, and protein content of the diet ranges from 1.7-6.1% of gross energy (GE) intake. Methane production in moose varies from 3.1-4.8% and is generally comparable to other ruminants. Estimates of metabolizable and net energy content of tested diets are presented and discussed. Basal metabolic rates of moose do not conform to the $70 \text{ BW}^{0.75}$, where BW is body weight, but vary seasonally with a high in summer and a nadir in late winter. Winter activity budgets for moose indicate that moose spend approximately 46% of their time feeding, with 5-6 feeding bouts per circadian cycle. Increments of energy expenditure for various activities above resting are 1.07, 1.08, 1.34, 1.29 and 1.66 for bedded-alert, bedded and ruminating, cratering, standing, and walking, respectively. No information on summer activity budgets is available. Energy partitioning for moose consuming a pelleted diet with known energetic loss is modeled to demonstrate the usefulness of nutritional energetics for moose management. Additional areas of needed research are presented and discussed.

Viltrevy (Swedish Wildlife Research Suppl):In press.

Appendix J.

SEASONAL WEIGHT DYNAMICS OF MOOSE

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Abstract: Total body-weight data for moose are presented and discussed. Information from 6 animals (3 males and 3 females) over a 5-year period was analyzed and fitted to standard growth equations. Changes in weight were seasonally dynamic; periods of weight loss and gain were different for males and females. Males obtained maximum weights just prior to the rut in late August. They lost between 11-19% of their body weight during the breeding season, representing the greatest weight loss at any season. Weight loss from pre-rut maximums to postwinter lows ranged from 7-23% and were dependent upon the combined weight loss during the rut and subsequent winter losses. Weight gains from winter lows to prerut maximums ranged from 33-41%. Females reached maximum weight in midwinter, much later than males, while minimum weights occurred shortly after parturition. Average weight loss ranged from 15-19%. Weight gains from lows to highs ranged from 25-43%. Females giving birth to single and twin calves lost an average of 34.8 and 63.0 kg, respectively. Using a Brody equation, mathematical fits of maximum weights for males and females are presented. Data would not fit sinusoidal equations, and reasons for the lack of fit are presented. Comparisons are made with other published weight data for moose.

Viltrevy (Swedish Wildlife Research Suppl):In press.

Appendix K.

ENERGY REQUIREMENTS OF ADULT MOOSE FOR WINTER MAINTENANCE

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Abstract: Nine adult moose (Alces alces) were randomly assigned to one of 3 diets in 2 separate feeding trials. Our objectives were to determine how moose respond in winter to varying amounts of the same quality and amount of food that possessed varying nutritional quality. During trial 1, moose were fed a pelleted diet ad libitum as well as 85.1% and 72.5% of the ad libitum diet. During trial 2, moose were fed ad libitum one of 3 pelleted diets containing digestible-energy concentrations of 2.4, 2.1, and 1.8 kcal/g dry matter. Linear-regression equations of digestible-energy intake (kcal/kg body weight $BW^{0.75}$ /day) with mean monthly body-weight gain or loss (kg/day) provided the basis for estimating maintenance energy requirements. Our best estimates of energy required for maintenance were 148 and 131 kcal/kg $BW^{0.75}$ /day of digestible and metabolizable energy, respectively. The relationship between heat production and metabolizable-energy intake provided an estimate for theoretical basal metabolism of 73 kcal/kg $BW^{0.75}$ /day.

J. Wildl. Manage. 52(1):26-33 1988.

Appendix L.

PROTEIN DIGESTION IN MOOSE

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Abstract: Protein digestion trials were conducted with 4 moose (Alces alces) fed isocaloric diets varying in crude protein from 8% to 16%. Maintenance requirement for nitrogen was 0.627 ± 0.073 g/kg BW^{0.75}/day. This represented a minimum dietary crude protein content of $6.8\% \pm 0.8\%$. Each additional unit of ingested nitrogen resulted in 0.346 ± 0.140 units increase in urinary nitrogen loss. Metabolic fecal nitrogen was 0.457 g/100 g dry matter consumed.

J. Wildl. Manage. 51(2):352-357. 1987.

Appendix M.

CHANGES IN BODY COMPOSITION OF MOOSE DURING WINTER

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Abstract: Nine adult moose (Alces alces) were assigned to one of 3 treatments in 2 separate trials. In trial 1, 3 treatment groups of 3 moose were fed a pelleted diet ad libitum or at 85% and 70% of ad libitum intake. During trial 2, 3 treatment groups of moose were fed ad libitum one of 3 pelleted diets containing a metabolizable energy (ME) content of 2.4, 2.1, and 1.8 kcal/g dry matter. Estimates of body composition were determined with tritiated water. In trial 1, moose fed restricted quantities (85% or 70% of ad libitum intake) of food lost weight and fat at faster rates than moose fed ad libitum. The percentage change in kg of fat from pretrial measurements in October until the end of the trial in April was 33.0%, 26.8%, and -57.2% for the high-to-low intake treatments, respectively. In trial 2, moose fed 1.8 and 2.1 kcals ME compensated for lower levels of available energy by increasing dry-matter intake. Fat dynamics were not different ($p > 0.05$) among the treatments but were different ($p < 0.05$) over time. Change in the energy pool indicated that fat catabolism/metabolism contributed about 94.7-108% of the calories, although the variation was high. Estimates of body composition based on the tritiated-water technique were variable, and reasons are discussed.

ALCES: Submitted for review in 1988.

Appendix N.

ESTIMATES OF DIGESTIBILITY OF BIRCH, WILLOW, AND ASPEN MIXTURES IN MOOSE

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Abstract: Four feeding trials were conducted during winter with captive moose (Alces alces) at the Moose Research Center, Soldotna, Alaska. Our objectives were to estimate intake and digestibility of (1) a mixed diet of 70% paper birch (Betula papyrifera), 20% aspen (Populus tremuloides), and 10% willow (Salix spp.); (2) a mixed diet of 30% aspen and a 70% pelleted ration; and (3) mixed diet containing equal portions of paper birch, willow, and aspen browse. Moose would not consume the mixed diet containing 70% birch, and the trial was terminated after 1 week. Dry-matter intake (DMI) of the aspen and pelleted ration was 52.4 ± 12.5 g/kg body weight (BW)^{0.75}/day. The estimate of dry-matter digestion (DMD) for aspen was $40.9 \pm 8.5\%$. Dry-matter intake and DMD for the mixed-browse diets ranged from 25.4 to 38.6 g/kg BW^{0.75}/day and 31.1% to 38.6%, respectively. Digestible and metabolizable energy represented 37.0% and 27.8% of gross energy intake, respectively. Energy intake was below levels required for winter maintenance.

J. Wildl. Manage. 52(1):33-37 1988.

Appendix O.

FOOD PASSAGE RATE IN MOOSE

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Abstract: Four tame moose (Alces alces) were used to measure dry-matter digestion and rates of passage of three diets: (1) a pelleted ration, (2) a mixture of pellets and winter-clipped aspen (Populus tremuloides), and (3) a mixture of winter-clipped aspen, willow (Salix spp.), and paper birch (Betula papyrifera). Dry-matter digestion was greatest for the pellets (64.3%), followed by the pellet-aspen mix (60.5%) and the mixed browse (42.0%). Time of first appearance, rumen turnover time, and total mean retention time for both the solid and liquid phases of digesta were longest for the mixed-browse diet. There was a significant correlation ($r=0.97$, $P<0.05$) between the movement of the solid and liquid components of digestion.

ALCES: Submitted for review 1988.

Appendix P.

FIELD TEST OF A MOOSE CARRYING CAPACITY MODEL

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Abstract: The amount of moose forage was estimated in each 1-mi² exclosure at the Moose Research Center (MRC) near Soldotna, Alaska, in July 1983 and 1984. The amount of forage consumed by the moose from 15 October to 1 May was calculated using 2 computer simulation models. These models predicted daily forage intake of moose based on nutrient requirements, physiological constraints, and forage quality. Each exclosure was stocked during winter with a number of moose to remove a different amount of the current annual growth (CAG) of paper birch. Tagged paper birch shrubs were measured before and after browsing to determine the utilization level of CAG.

Alces:23 Submitted for review 1987.

Appendix Q.

Supplemental publications incidental to major research projects conducted under the nutrition and physiology studies.

Franzmann, A. W., C. C. Schwartz, and D. C. Johnson. 1982. Chemical immobilization of moose at the Moose Research Center, Alaska (1968-1981). *Alces* 18:94-115.

Franzmann, A. W., C. C. Schwartz, and D. C. Johnson. 1984. Baseline body temperature, heart rates, and respiratory rates of moose in Alaska. *J. Wildl. Dis.* 20:333-337.

Franzmann, A. W., C. C. Schwartz, D. C. Johnson, J. B. Faro, and W. B. Ballard. 1984. Immobilization of moose with carfentanil. *Alces* 20:259-282.

Peterson, R. O., C. C. Schwartz, and W. B. Ballard. 1983. Eruption patterns of selected teeth in three North American moose populations. *J. Wildl. Manage.* 47:885-888.

Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, C. C. Schwartz, and W. W. Mautz. 1987. Tannins in difending plants against ruminants: reduction in protein avaliability. *Ecology* 68:98-107.

Schwartz, C. C., W. L. Regelin, and A. W. Franzmann. 1982. Male moose successfully breed as yearlings. *J. Mamm.* 63:334-335.

White, R. G., D. F. Holleman, C. C. Schwartz, W. L. Regelin, and A. W. Franzmann. Control of rumen turnover in northern ruminants. *Can J. Anim. Sch.* 64(suppl):349-350.

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