

# Predicting body fat and body mass in moose with ultrasonography

Thomas R. Stephenson, Kris J. Hundertmark, Charles C. Schwartz, and Victor Van Ballenberghe

**Abstract:** Lipids are the primary energy store of the body and estimation of these reserves provides an indication of nutritional status in moose (*Alces alces*). Estimates of total body fat enhance our understanding of reproductive potential, survival rate, energy balance, and nutritional carrying capacity. We developed predictive equations of total body fat and body mass from ultrasonographic fat measurements for application in live animals. We detected a strong linear relationship ( $r^2 = 0.96$ ) between ingesta-free body fat and rump fat thickness measured by ultrasonography. Rump fat thickness was measurable over a range of body fat levels (5.8–19.1%). Rump fat mass ( $r^2 = 0.92$ ) and kidney fat mass ( $r^2 = 0.95$ ) were curvilinearly related to ingesta-free body fat level. For adult females, total length and chest girth were not related to body mass. Ingesta-free body fat, however, explained 81% of the variability in body mass, and ultrasonically measured rump fat thickness predicted body mass ( $r^2 = 0.80$ ).

**Résumé :** Les lipides constituent la principale source d'énergie du corps et l'estimation de ces réserves permet d'évaluer le statut nutritionnel chez l'Original (*Alces alces*). L'estimation du contenu total de graisses aboutit à une meilleure compréhension du potentiel reproducteur, de la survie, de l'équilibre énergétique et de la capacité limite du corps en éléments nutritifs. Nous avons mis au point des équations applicables à des animaux vivants et permettant d'estimer le contenu total de graisses et la masse totale à partir de mesures des graisses de la croupe obtenues par ultrasons. Nous avons constaté une forte relation linéaire ( $r^2 = 0,96$ ) entre les graisses corporelles à l'exclusion de celles du bol alimentaire et l'épaisseur de graisse de la croupe mesurée par ultrasons. L'épaisseur des graisses de la croupe est mesurable lorsque le contenu total de graisses se situe entre 5,8 et 19,1%. La masse des graisses de la croupe ( $r^2 = 0,92$ ) et la masse des graisses du rein ( $r^2 = 0,95$ ) sont en relation curvilinéaire avec les graisses du corps sans compter celles du bol alimentaire. Chez les femelles adultes, la longueur totale et le tour de poitrine ne sont pas reliés à la masse du corps. Cependant, les graisses, à l'exclusion de celles du bol alimentaire, expliquent 81% de la variabilité de la masse du corps et l'épaisseur des graisses de la croupe déterminée par ultrasons permet de prédire la masse corporelle totale ( $r^2 = 0,80$ ).

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## Introduction

Determination of the lipid reserves of individuals within a population provides valuable information about nutritional status. Lipids are the primary energy store of the body (Price and White 1985) and are stored primarily in the form of triglycerides (Allen 1976). Furthermore, triglycerides, a dense, efficient form of stored energy, provide 9.45 kcal/g upon catabolism, whereas carbohydrates and proteins provide 3.75–4.23 and 3.11–5.92 kcal/g, respectively (Robbins 1993). Thus, the energy available per unit mass from lipid reserves may be more than twice that of muscle. In addition, fat stores can be depleted to a greater extent than body protein. Estimates

of total body fat enhance our understanding of reproductive potential (Thomas 1982), survival rates and energy balance (Hobbs 1989; Miquelle et al. 1992), and nutritional carrying capacity (Regelin et al. 1987).

Prediction of lipid reserves in ungulates has received considerable study. Advantages and disadvantages of different techniques for estimating body fat have been reviewed extensively elsewhere (Franzmann and Ballard 1993; Stephenson et al. 1993; Chan-McLeod et al. 1995; Harder and Kirkpatrick 1994). Although accurate, nonsubjective, rapid in vivo approaches, such as bioelectrical impedance analysis, have been successfully developed for monogastrics such as rats (Hall et al. 1989) and bears (*Ursus* spp.; Farley and Robbins 1994), none have been validated for ruminants.

Franzmann and Schwartz (1978) were unable to measure fat reserves in moose precisely using amplitude-mode (A mode) ultrasound technology. A-mode scanners produce a one-dimensional, imprecise display of echo amplitudes for various tissue depths (Ginther 1986). Brightness-mode (B mode) real-time ultrasound measurements of subcutaneous fat thickness indicated potential for repeatedly monitoring fat levels of free-ranging moose in vivo (Stephenson et al. 1993). B-mode generates gray-scale two-dimensional images. The brightness of pixels is proportional to the amplitude of returning echoes emitted from piezoelectric crystals located in the transducer. Tissue density determines the level of echogenicity and produces characteristic cross-sectional images on the

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**T.R. Stephenson.**<sup>1</sup> Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844, U.S.A.

**K.J. Hundertmark and C.C. Schwartz.** Alaska Department of Fish and Game, Moose Research Center, 34828 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669, U.S.A.

**Victor Van Ballenberghe.** U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, 3301 C Street, Suite 200, Anchorage, AK 99503-3954, U.S.A.

<sup>1</sup> Present address: Alaska Department of Fish and Game, Moose Research Center, 34828 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669, U.S.A. (e-mail: tomst@fishgame.state.ak.us).

B-mode monitor (Ginther 1986). Tissue layers such as skin, fat, and muscle are displayed clearly and their thickness can be measured accurately with electronic calipers.

Stephenson et al. (1993) determined that real-time ultrasound permitted accurate measurement ( $\pm 1$  mm) of subcutaneous fat thickness in moose but did not consistently permit scanning of visceral fat deposits because of large body size and limited signal penetration. Our primary objective was to develop predictive equations for total body fat from ultrasonic fat measurements for application in live animals. In addition, we wished to elucidate the relationships between total body fat, specific lipid deposits, and body mass.

## Materials and methods

We used captive moose, including 2 adult males (3.5 years old), 3 pregnant and 6 nonpregnant adult females (3.5–13.5 years old), and a male calf (6 months), to evaluate this technique. Animals were reared at the Kenai Moose Research Center on the Kenai Peninsula, Alaska (60°N, 150°W), and were fed a formulated, pelleted ration (Schwartz et al. 1985) ad libitum to supplement natural browse (aspen (*Populus tremuloides*), birch (*Betula balsamifera*), and willow (*Salix* spp.)) during the winter; they fed primarily on natural browse, with pelleted feed available, during the remainder of the year. Moose were immobilized during November–January in 1993–1995 with carfentanil citrate + xylazine hydrochloride (Schmitt and Dalton 1987) as part of a detailed study to assess body composition in moose (Hundertmark et al. 1994). Immobilized moose were maintained in sternal recumbency. Total length and chest girth were measured. The rump region was scanned using an Aloka Model 210 portable ultrasound device (Corometrics Medical Systems, Inc., Wallingford, Conn.) with a 5-MHz 8-cm linear-array transducer. Subcutaneous fat thickness was measured at 2 sites along a line between the spine, at its closest point to the coxal tuber (hip bone), and the ischial tuber (pin bone). Fat thickness was measured with electronic calipers to the nearest 0.1 cm at the midpoint and point of maximum thickness (immediately adjacent to the cranial process of the ischial tuber) along the line. We evaluated the maximum fat thickness along this line (MAXFAT) and the sum of the maximum thickness and the thickness at the midpoint (SUMFAT).

Animals were euthanized immediately following ultrasonographic measurements while still chemically immobilized. Whole body mass was determined and then each animal was eviscerated and skinned (subcutaneous fat remained on the carcass). The carcass was bisected longitudinally along the vertebral column, and one half was frozen for chemical analysis. For rump fat mass (RFM), subcutaneous rump fat caudal to the fifth lumbar vertebra and proximal to the knee was dissected from the carcass half not used for chemical analysis and weighed. The gastrointestinal tract was emptied of ingesta. The concepta and amniotic fluid of pregnant females were removed and their mass was determined to permit mass to be calculated without the concepta. For kidney fat mass (KFM), trimmed fat attached to the kidney was measured to the nearest 1 g (Riney 1955). The entire viscera and samples of shaved hide were frozen for analysis. The frozen half carcass and visceral mass were sliced at 51- and 25-mm intervals, respectively, on a commercial band saw. The homogenate at the base of the blade was collected for each component, mixed, and refrozen (Huot and Picard 1988). Hide samples were freeze-dried and ground in a Wiley Mill to create a homogenate. Chemical analysis of frozen samples was conducted at Washington State University's Wildlife Habitat Laboratory. Crude fat was determined in triplicate samples by ether extraction (Association of Official Analytical Chemists 1975).

We expressed the amount of fat in the carcass, viscera, and hide

components, determined chemically, as a percentage. Values for viscera exclude the ingesta and uterine contents. We calculated percent ingesta-free body fat (IFBFAT) by summing the products of each component's percent fat and its respective mass, dividing by ingesta-free body mass, and multiplying by 100.

## Statistical analyses

We examined plots of raw and transformed data to assess the validity of regression assumptions (Zar 1984), and, when appropriate, curvilinear data were log-transformed. Arcsine transformations of percentages were evaluated relative to regression assumptions. Scaling factors were applied to fat mass and fat thickness of adult males and calves to permit comparison with adult females, owing to differences in body size. Scaling factors were the ratio of maximum mean body mass of 3.5-year-old males or calves to adult female body mass ( $\bar{x} = 472.5$  kg). Thus, the scaling factors were 0.83 and 2.64 for adult males and calves, respectively. We assumed that although the extent of lipid deposition might vary among sex and age classes, the relative distribution of fat among deposits was similar.

We employed linear regression to develop predictive equations for body fat and body mass. We analyzed the relationship between carcass fat, visceral fat, and IFBFAT. We used stepwise multiple regression to generate additional predictive equations for body mass from several morphometric measurements. Equations were compared using coefficients of determination and standard errors of the estimates.

## Results

We found a strong linear relationship between IFBFAT and both percent carcass fat (CARCFAT,  $r^2 = 0.94$ ,  $n = 10$ ,  $p = 0.0001$ ) and percent visceral fat (VISC FAT,  $r^2 = 0.98$ ,  $n = 10$ ,  $p = 0.0001$ ).

Ultrasonically measured MAXFAT predicted IFBFAT (%; Fig. 1) better than CARCFAT (Fig. 1). In addition, MAXFAT was a strong predictor of total body fat mass (IFBFAT (kg); Fig. 1). Similarly, SUMFAT was more closely related to IFBFAT (Fig. 2) than to CARCFAT (Fig. 2).

Rump fat mass (RFM) was curvilinearly related to both IFBFAT (Fig. 3) and CARCFAT (Fig. 3). Kidney fat mass (KFM) was also curvilinearly related to IFBFAT (Fig. 4) and VISC FAT (Fig. 4).

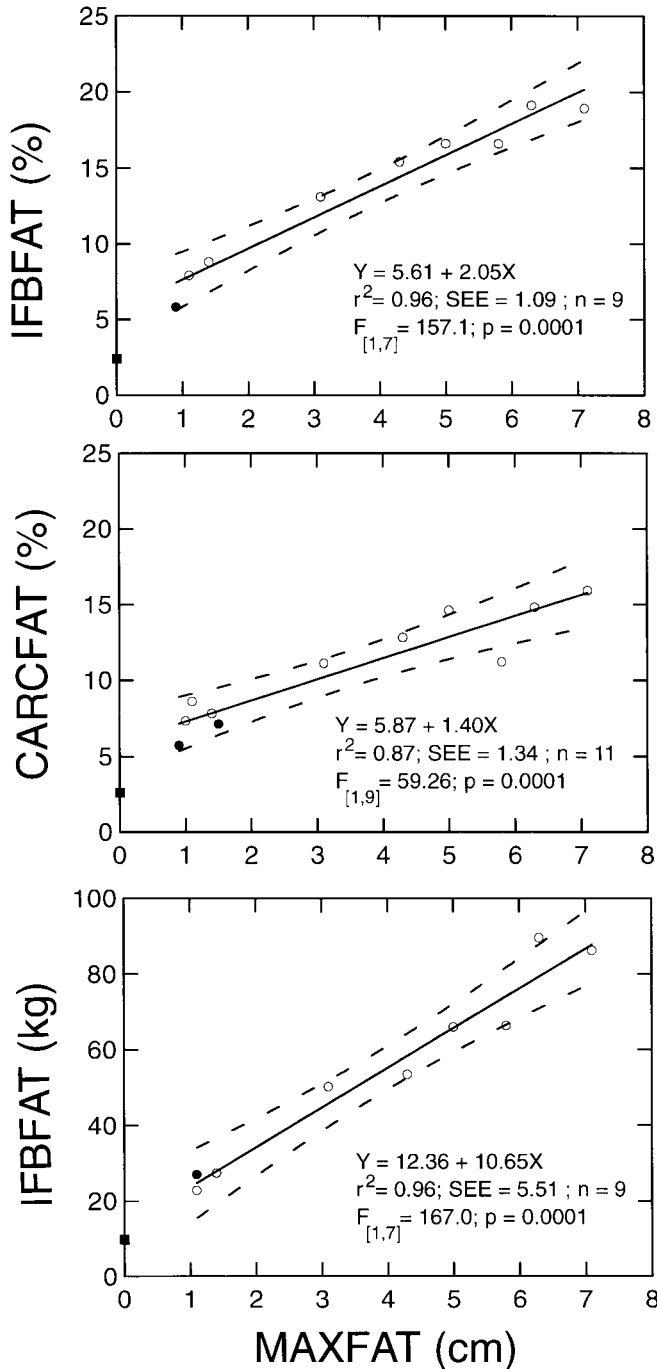
Among predictive equations for IFBFAT, MAXFAT exhibited the lowest variability in predictive value ( $SEE = 1.09$ ). Arcsine transformation of percent IFBFAT failed to improve relationships.

Stepwise multiple regression analysis that included multiple independent variables did not produce significant equations for predicting body mass of adult females. Total length and chest girth were not incorporated into the body mass model ( $p > 0.15$ ). IFBFAT explained 81% of the variability in body mass (Fig. 5). MAXFAT alone predicted body mass using simple linear regression (Fig. 5).

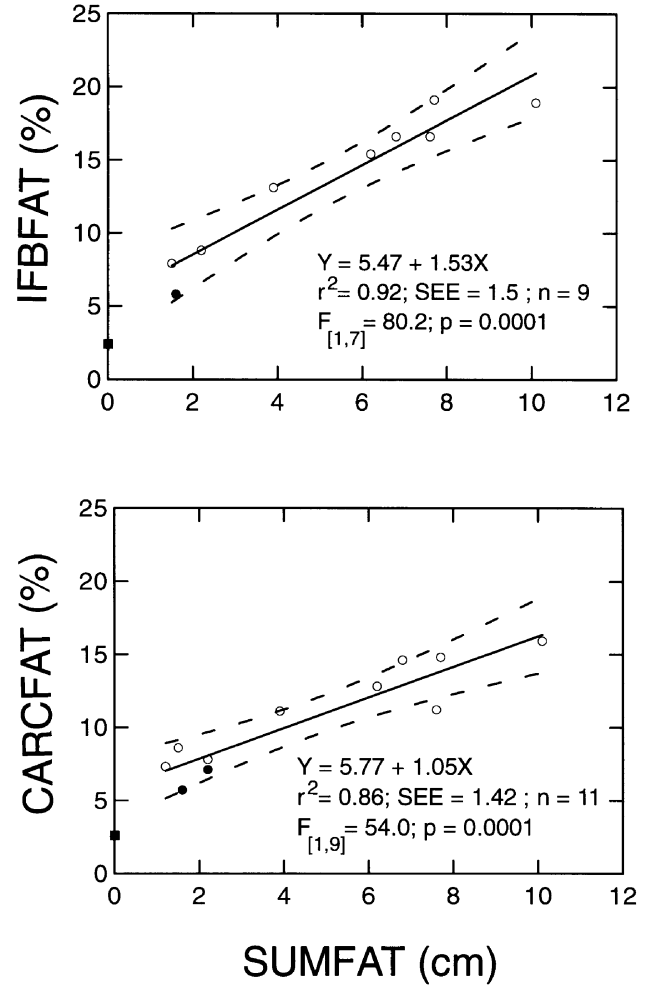
## Discussion

The linear relationship of both CARCFAT and VISC FAT to IFBFAT that we observed supports the argument that lipid deposition and (or) mobilization occur simultaneously in the carcass and visceral deposits (Hundertmark et al. 1994). Riney (1955) indicated that although lipid anabolism and catabolism occurred concurrently among bone marrow, visceral, and subcutaneous depots, the complete disappearance of subcutaneous

**Fig. 1.** Relationships between ultrasonically measured maximum rump fat thickness (MAXFAT) and ingesta-free total body fat (IFBFAT; minus concepta) and carcass fat (CARCFAT) determined by chemical extraction of moose carcasses at the Kenai Moose Research Center, Alaska, in 1993–1995. A male calf (■) with no measurable rump fat was not included in regressions. MAXFAT values of adult males (●) and the calf were scaled (using ratios of mean body mass to that of adult females) to permit the inclusion of different sex and age classes when regressing percent variables against MAXFAT. Broken lines represent 95% confidence intervals.



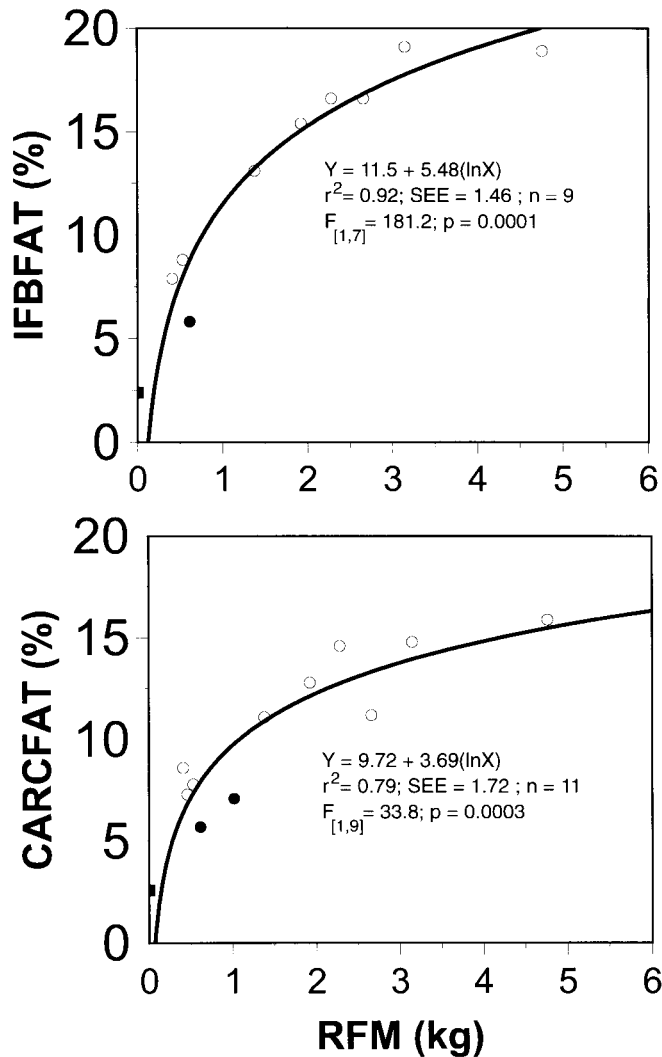
**Fig. 2.** Relationships between ultrasonically measured rump fat index (SUMFAT) and ingesta-free total body fat (IFBFAT; minus concepta) and carcass fat (CARCFAT) determined by chemical extraction of moose carcasses at the Kenai Moose Research Center, Alaska, in 1993–1995. A male calf (■) with no measurable rump fat was not included in regressions. SUMFAT values for adult males (●) and the calf were scaled (using ratios of mean body mass to that of adult females) to permit the inclusion of different sex and age classes. Broken lines represent 95% confidence intervals.



fat occurred first. Berg and Butterfield (1976) noted that in Angus cattle, visceral, intermuscular, and subcutaneous fat reserves varied proportionately during fattening and starving, with subcutaneous fat reserves disappearing first.

In contrast to the findings of Chan-McLeod et al. (1995) for caribou (*Rangifer tarandus granti*) in Alaska, subcutaneous rump fat (termed back fat by Chan-McLeod et al. and most other authors) in moose was measurable at lower total body fat and during more of the annual cycle. One adult male in this study exhibited 1.8 cm rump fat thickness at 5.8% IFBFAT, but a male calf had no measurable rump fat at 2.4% IFBFAT. McGillis (1972) observed measurable levels of rump fat in adult cow moose in a dense population in Alberta during February. Furthermore, Reimers and Ringberg (1983) developed nearly linear predictive regression equations ( $r^2 = 0.968$ )

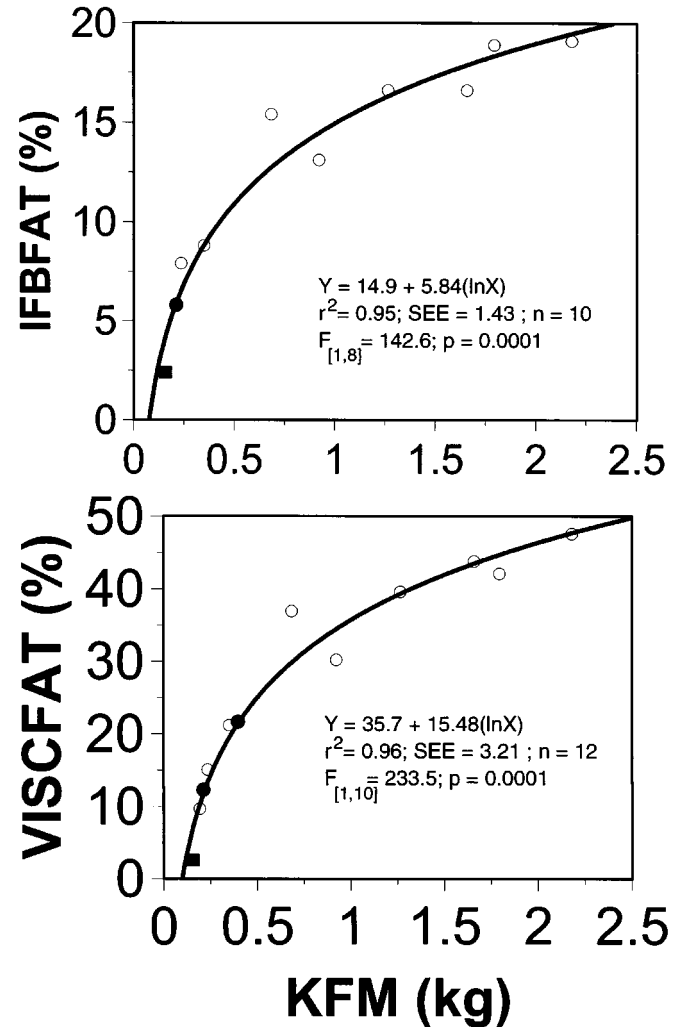
**Fig. 3.** Relationships between rump fat mass (RFM) and ingesta-free total body fat (IFBFAT; minus concepta) and carcass fat (CARCFAT) determined by chemical extraction of moose carcasses at the Kenai Moose Research Center, Alaska, in 1993–1995. A male calf (■) with no measurable rump fat was not included in regressions. RFM values for adult males (●) and the calf were scaled (using ratios of mean body mass to that of adult females) to permit the inclusion of different sex and age classes.



from chemically determined IFBFAT in Svalbard reindeer (*Rangifer tarandus platyrhynchus*), using back fat, which was measurable for IFBFAT < 2.8%. Berg and Butterfield (1976) noted that back fat thickness was the most useful and accurate predictor of total fat, as well as an indirect indicator of muscle mass, in cattle.

For ungulates that rely heavily on large fat reserves for over-winter survival, such as moose (Schwartz 1992) and Svalbard reindeer (Reimers and Ringberg 1983), or have been bred for greater fatness (e.g., domestic cattle), perhaps proportionately more fat is deposited subcutaneously and persists during more of the annual cycle. There are alternative explanations for the measurable levels of rump fat that occurred at low IFBFAT levels in this study. In most other wildlife studies (Riney 1955; McGillis 1972; Reimers and Ringberg 1983;

**Fig. 4.** Relationships between kidney fat mass (KFM) and ingesta-free total body fat (IFBFAT; minus concepta) and visceral fat (VISC FAT; minus concepta) determined by chemical extraction of moose carcasses at the Kenai Moose Research Center, Alaska, in 1993–1995. KFM values for adult males (●) and a male calf (■) were scaled (using ratios of mean body mass to that of adult females) to permit the inclusion of different sex and age classes.

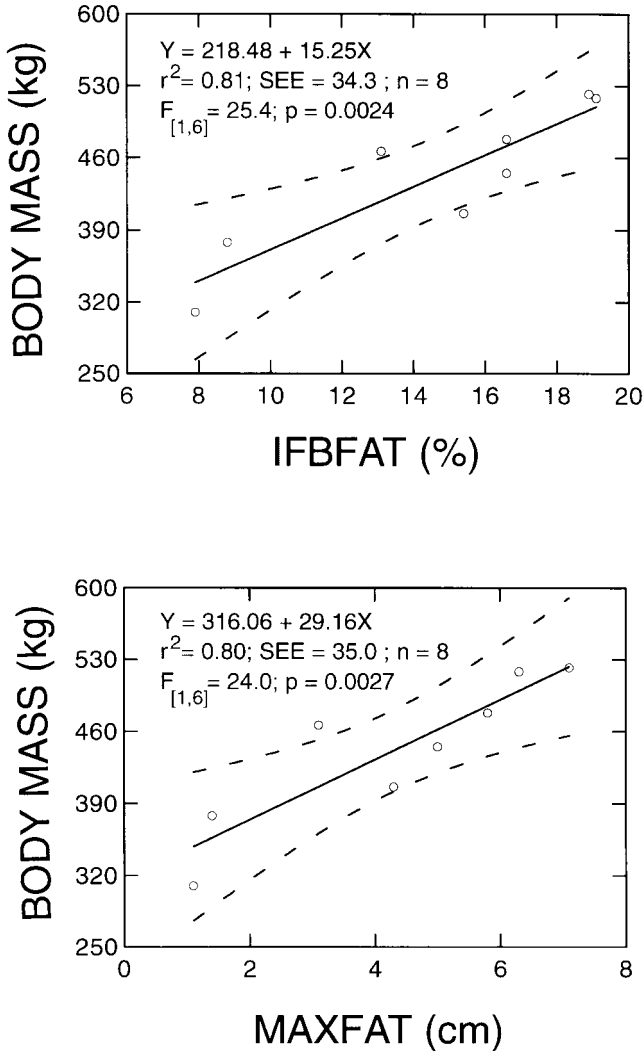


Chan-McLeod et al. 1995), backfat has been measured at a 45° angle cranial from the base of the tail, in contrast to the slightly different location in this study. Perhaps the last remnants of rump fat remained at the sites we measured. Furthermore, because of the difficulty in separating hide from carcass without removing at least minimal amounts of subcutaneous fat, low levels of subcutaneous fat are more difficult to measure using dissection methods. In contrast, nondestructive ultrasonographic measurement permits precise determination of the lowest detectable levels. Although fat thickness can be determined from a carcass, in practice this method appears to be less accurate and subject to greater human error.

Because the kidney fat index can be biased by annual variation in kidney mass (Verme and Ozoga 1980a; Anderson et al. 1990), we used KFM to develop predictive equations. Although the level of predictability of IFBFAT using KFM and RFM was relatively high, the relationships were curvilinear.



**Fig. 5.** Relationships between adult female body mass and ultrasonically measured maximum rump fat thickness (MAXFAT) and ingesta-free total body fat (IFBFAT; minus concepta) determined by chemical extraction of moose carcasses at the Kenai Moose Research Center, Alaska, in 1993–1995. Broken lines represent 95% confidence intervals.



The masses of kidney fat and rump fat, although difficult to determine in dissection methods (Riney 1955; this study), increase disproportionately with increasing levels of fat deposition. In contrast, consistently measuring fat thickness at a single site using ultrasound reduces this tendency.

The linear relationship between IFBFAT and MAXFAT is preferable for use in predictive equations. Robbins (1993) cautioned against using nonlinear predictive equations. Finger et al. (1981) determined that at higher values of the kidney fat index, the precision and predictability of body fat mass became poorer because of decreasing slope and heteroscedasticity. Similarly, the nearly vertical slope at low values of KFM that we observed also reduces predictability.

The lack of a relationship between body mass and both total length and chest girth appears contradictory to results of earlier studies with moose (Franzmann et al. 1978; Haigh et al. 1980). However, in contrast to the broad range of sex and age classes

used to develop body mass equations by other authors, the data we used included only adult females but encompassed a broad range of body masses (Fig. 5). Within a single demographic group, other factors such as differences in fatness, pregnancy status, and quantity of digesta are more influential.

Cameron and Ver Hoef (1994) successfully predicted caribou parturition rates from autumn body mass. The close relationship between IFBFAT and body mass suggests that since they were studying a population of adult females during a single season, Cameron and Ver Hoef (1994) were likely assessing differences in lipid reserves among animals. The use of body mass to predict lipid reserves is biased by variation in gastrointestinal content (Adamczewski et al. 1987) and pregnancy status. Thus, using body mass to predict body fat across a range of seasons and among populations likely will reduce the predictive value of body mass. Albon et al. (1986) demonstrated that body condition, independent of body mass, was important in predicting fertility of red deer (*Cervus elaphus*).

Verme and Ozoga (1980b) cautioned against using body fatness as the sole criterion for assessing nutritional status, particularly in fawns. Although Verme and Ozoga (1980b) suggested that some level of obligate lipogenesis occurred in white-tailed deer (*Odocoileus virginianus*) fawns, moose calves maintained on a low nutritional plane exhibited no subcutaneous fat (this study; Schwartz and Hundertmark 1993). Torbit et al. (1985) observed a concurrent loss of body protein with body fat mobilization in mule deer. Although protein catabolism provides energy, Price and White (1985) also suggested that loss of muscle mass occurs as a response to the reduced work load resulting from loss of body mass.

Knowledge of the level of lipid reserves (body condition) has broad application in wildlife management. In some management applications, condition may indicate proximity of a population to its nutritional carrying capacity without requiring estimates of actual carrying capacity. Hobbs and Swift (1985) pointed out that as population density increases, the optimum nutritional quality of diets will decline progressively. Deterioration in the nutritional status of individuals is expected as density increases, hence the condition of individuals can be monitored to assess diet quality. Furthermore, reliable estimates of total body fat are required for accurately predicting endogenous energy reserves and energy balance. Although in some studies the total caloric value of an individual animal has been calculated (Robbins et al. 1974; Watkins et al. 1991), for energetics modelling it is perhaps more useful to calculate the energy available from catabolized energy reserves (Stephenson 1995). Estimation of body mass and percent body fat permits calculation of the caloric value of lipid reserves available as an endogenous energy source. This ability *in vivo* enables repeated monitoring in both captive and wild individuals, relative to physiological and environmental parameters (e.g., nutrition, reproductive status, weather, disturbance).

Knowledge of the level of body fat reserves also enables prediction of reproductive performance and survival. Threshold levels of fatness may be present that index successful reproduction and these can be monitored. In addition, recent evidence indicates that vulnerability to predation also may be affected by body condition (Sinclair and Arcese 1995). Individuals in superior condition may be more effective at defending themselves against certain predators.

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## References

- Adamczewski, J.Z., Gates, C.C., Hudson, R.J., and Price, M.A. 1987. Seasonal changes in body composition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an arctic island with limited winter resources. *Can. J. Zool.* **65**: 1149–1157.
- Albon, S.D., Mitchell, B., Huby, B.J., and Brown, D. 1986. Fertility in female red deer (*Cervus elaphus*): the effects of body composition, age and reproductive status. *J. Zool. Ser. A*, **209**: 447–460.
- Allen, W.V. 1976. Biochemical aspects of lipid storage and utilization in animals. *Am. Zool.* **16**: 631–647.
- Anderson, A.E., Bowden, D.C., and Medin, D.E. 1990. Indexing the annual fat cycle in a mule deer population. *J. Wildl. Manage.* **54**: 550–556.
- Association of Official Analytical Chemists. 1975. Official methods of analysis. 12th ed. Association of Official Analytical Chemists, Washington, D.C.
- Berg, R.T., and Butterfield, R.M. 1976. New concepts of cattle growth. Sydney University Press, Sydney, Australia.
- Cameron, R.D., and Ver Hoef, J.M. 1994. Predicting parturition rate of caribou from autumn body mass. *J. Wildl. Manage.* **58**: 674–679.
- Chan-McLeod, A.C.A., White, R.G., and Russell, D.E. 1995. Body mass and composition indices for female barren-ground caribou. *J. Wildl. Manage.* **59**: 278–291.
- Farley, S.D., and Robbins, C.T. 1994. Development of two methods to estimate body composition of bears. *Can. J. Zool.* **72**: 220–226.
- Finger, S.E., Brisbin, I.L., Jr., Smith, M.H., and Urbston, D.F. 1981. Kidney fat as a predictor of body condition in white-tailed deer. *J. Wildl. Manage.* **45**: 964–968.
- Franzmann, A.W., and Ballard, W.B. 1993. Use of physical and physiological indices for monitoring moose population status—a review. *Alces*, **29**: 125–133.
- Franzmann, A.W., and Schwartz, C.C. 1978. Moose Research Center report. Federal Aid in Wildlife Restoration Project W-17-10, Alaska Department of Fish and Game, Juneau.
- Franzmann, A.W., LeResche, R.E., Rausch, R.A., and Oldemeyer, J.L. 1978. Alaskan moose measurements and weights and measurement–weight relationships. *Can. J. Zool.* **56**: 298–306.
- Ginther, O.J. 1986. Ultrasonic imaging and reproductive events in the mare. Equiservices, Cross Plains, Wisconsin.
- Haigh, J.C., Stewart, R.R., and Mytton, W. 1980. Relations among linear measurements and weights for moose (*Alces alces*). *Alces*, **16**: 1–10.
- Hall, C.B., Lukaski, H.C., and Marchello, M.J. 1989. Estimation of rat body composition using tetrapolar bioelectrical impedance analysis. *Nutr. Rep. Int.* **39**: 627–633.
- Harder, J.D., and Kirkpatrick, R.L. 1994. Physiological methods in wildlife research. In *Research and management techniques for wildlife and habitats*. 5th ed. Edited by T.A. Bookhout. The Wildlife Society, Bethesda, Md. pp. 275–306.
- Hobbs, N.T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildl. Monogr.* No. 101.
- Hobbs, N.T., and Swift, D.M. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *J. Wildl. Manage.* **49**: 814–822.
- Hundertmark, K.J., Schwartz, C.C., and Shuey, C.C. 1994. Estimation of body composition in moose Federal Aid in Wildlife Restoration Project W-17-10, Alaska Department of Fish and Game, Juneau.
- Huot, J., and Picard, G. 1988. A simplified method for assessment of caribou body composition. *J. Wildl. Manage.* **52**: 606–609.
- McGillis, J.R. 1972. The kidney fat index as an indicator of condition in various age and sex classes of moose. In *Transactions of the 8th North American Moose Conference*, Thunder Bay, Ont., 16–18 February 1972. Edited by R.B. Addison. Ontario Ministry of Natural Resources. pp. 105–114.
- Miquelle, D.G., Peek, J.M., and Van Ballenberghe, V. 1992. Sexual segregation in Alaskan moose. *Wildl. Monogr.* No. 122.
- Price, M.A., and White, R.G. 1985. Growth and development. In *Bioenergetics of wild herbivores*. Edited by R.J. Hudson and R.G. White. CRC Press, Boca Raton, Fla. pp. 183–214.
- Regelin, W.L., Hubbert, M.E., Schwartz, C.C., and Reed, D.J. 1987. Field test of a moose carrying capacity model. *Alces*, **23**: 243–284.
- Reimers, E., and Ringberg, T. 1983. Seasonal changes in body weights of Svalbard reindeer from birth to maturity. *Acta Zool. Fenn.* **175**: 69–72.
- Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. *N.Z. J. Sci. Tech. Sect. B*, **36**: 429–463.
- Robbins, C.T. 1993. *Wildlife nutrition and feeding*. Academic Press, San Diego.
- Robbins, C.T., Moen, A.N., and Reid, J.T. 1974. Body composition of white-tailed deer. *J. Anim. Sci.* **38**: 871–876.
- Schmitt, S.M., and Dalton, W.J. 1987. Immobilization of moose by carfentanil and xylazine and reversal by naltrexone, a long-acting antagonist. *Alces*, **23**: 195–220.
- Schwartz, C.C. 1992. Physiological and nutritional adaptations of moose to the northern environments. *Alces Suppl.* No. 1. pp. 139–155.
- Schwartz, C.C., and Hundertmark, K.J. 1993. Supplemental feeding of moose during winter: can hay serve as an emergency ration? *Alces*, **29**: 135–147.
- Schwartz, C.C., Regelin, W.L., and Franzmann, A.W. 1985. Suitability of a formulated ration for moose. *J. Wildl. Manage.* **49**: 137–141.
- Sinclair, A.R.E., and Arcese, P. 1995. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology*, **76**: 882–891.
- Stephenson, T.R. 1995. Nutritional ecology of moose and vegetation succession on the Copper River Delta, Alaska. Ph.D. dissertation, University of Idaho, Moscow.
- Stephenson, T.R., Hundertmark, K.J., Schwartz, C.C., and Van Ballenberghe, V. 1993. Ultrasonic fat measurement of captive yearling bull moose. *Alces*, **29**: 115–123.
- Thomas, D.C. 1982. The relationship between fertility and fat reserves of Peary caribou. *Can. J. Zool.* **60**: 597–602.
- Torbit, S.C., Carpenter, L.H., Swift, D.M., and Alldredge, A.W. 1985. Differential loss of fat and protein by mule deer during winter. *J. Wildl. Manage.* **49**: 80–85.
- Verme, L.J., and Ozoga, J.J. 1980a. Influence of protein-energy intake on deer fawns in autumn. *J. Wildl. Manage.* **44**: 305–314.
- Verme, L.J., and Ozoga, J.J. 1980b. Effects of diet on growth and lipogenesis in deer fawns. *J. Wildl. Manage.* **44**: 315–324.
- Watkins, B.E., Witham, J.H., Ullrey, D.E., Watkins, D.J., and Jones, J.M. 1991. Body composition and condition evaluation of white-tailed deer fawns. *J. Wildl. Manage.* **55**: 39–51.
- Zar, J.H. 1984. *Biostatistical analysis*. Prentice Hall, Inc., Englewood Cliffs, N.J.