

Research Work Order 30: B. Application of *in vivo* techniques to determine body composition in caribou.

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INTRODUCTION

Among wild ungulates, reproductive success is directly related to body condition (Dauphine 1976, Hamilton and Blaxter 1980, Thomas 1982, Albon et al. 1983, Reimers 1983, Skogland 1984, Albon et al. 1986, White et al. 1989, Cameron et al. 1990, 1992). Monitoring body condition could therefore provide a means of predicting changes in individual and population productivity.

Previous studies relating seasonal changes in body mass and composition of caribou to reproductive performance have been based on analyses of killed animals (Dauphine 1976, Adamczewski et al. 1987, Huot 1989, Allaye-Chan et al. 1991). However, because the reproductive history of specimens was unknown, the influence of past reproduction on current body composition could not be evaluated. In addition, the effects of current body composition on subsequent reproductive success could not be investigated.

Determining the influence of stochastic environmental events on productivity of an ungulate population requires that relationships between individual reproductive performance and body condition be fully understood (Clutton-Brock and Albon 1989). Accurate quantitative field techniques for measuring body condition in live caribou must be developed, so that condition of individuals may be assessed relative to their subsequent reproductive success. Given verification of cause and effect, a means of evaluating condition would be of practical use to caribou managers as a routine tool for predicting herd productivity. In addition, such techniques could be useful in studies of the effects of disturbance, industrial development, or changing population density on body composition and productivity.

Studies involving various mammalian species have demonstrated that a tight inverse relationship exists between percent body fat and percent body water, while the water:protein and water:ash ratios are constant (Pace and Rathburn 1945, Reid et al. 1955, Panaretto 1963, Panaretto and Till 1963, Kodama 1971, Searle and Hilmi 1977, Reimers et al. 1982). Therefore, knowledge of percent body water permits calculation of percent body fat, protein, and ash. In most previous studies, total body water (TBW) (Table 1) has been measured for the prediction of body composition; however, in caribou and other ruminants, the large alimentary water component confounds estimates of body composition from TBW. Therefore, water in the ingesta-free body (IFBW, TBW less alimentary water) is the preferred predictor of caribou body composition.

Ingesta-free body water has been estimated in livestock using a number of markers, such as tritiated water (Byers 1979), deuterated water (Arnold et al. 1985, Lunt et al. 1985), and urea (Kock and Preston 1979, Rule et al. 1986, Bartle et al. 1987). Each marker has its unique advantages and disadvantages.

Tritiated (HTO) and deuterated water equilibrate with the TBW pool, the size of which is estimated by extrapolation of the terminal rate constant to time-zero. However, to estimate the volume of the IFBW pool for determination of body composition, the alimentary water volume must be estimated or measured and subtracted from TBW. In contrast, urea equilibrates with only the IFBW pool, as urea is hydrolyzed by urease to ammonia and carbon dioxide upon entry into the gut.

Table 1. Alphabetized list of abbreviations used in text.

BCS	Body condition score
BIA	Bioelectrical impedance analysis
BRI	Body reserves index
CAH	Central Arctic Herd of caribou
HTO	Tritiated water
IFBW	Ingesta-free body water
IFBWt	Ingesta-free body weight
LARS	Large Animal Research Station
SAAM	Simulation, Analysis, and Modeling program
TBW	Total body water
UREA	¹⁴ C urea

The equilibration time of a given marker in the IFBW pool may determine its potential usefulness in the field, since wild caribou can be restrained for only a short time (< 1 hr). In cattle, the equilibration time for urea is less than that for HTO: 12-15 min (Kock and Preston 1979) versus 6 h (Byers 1979), respectively. Urea would therefore appear to be the preferred marker; however, urea metabolism varies with protein intake (Cocimano and Leng 1967), so that changes in protein intake may affect urea equilibration and turnover. Such changes could complicate the formulation of useful prediction equations and could potentially decrease the precision with which IFBW pool size is measured. Imprecise IFBW estimates will decrease confidence in the prediction of body composition.

Bioelectrical Impedance Analysis (BIA) has been widely used in humans as a simple, non-invasive, portable method of determining total body water, and therefore body fat. The greater electrolyte content of lean tissues allows electrical current to pass through muscle more easily than through fat or bone; thus, the amount of lean tissue is inversely related to impedance (Z). According to electrical theory, impedance to current flow in a cylindrical conductor is a function of the length and configuration of the conductor (the lean body), the cross-sectional area of the conductor, and the signal frequency used. If signal frequency and conductor configuration (i.e., subject position) are held constant, impedance is related to conductor volume:

$$(1) \quad Z = \rho L / A$$

where Z is impedance in ohms, ρ is resistivity in ohms-cm, L is conductor length in cm, and A is cross-sectional area in cm². The volume of the conducting fluid (Vol) can be estimated by multiplying both sides by L and rearranging:

$$(2) \quad \text{Vol} = \rho L^2 / Z$$

We assume that volume is an extremely good index of the TBW pool. Hence, TBW should be a function of resistivity, conductor length, and impedance.

As a measure of TBW, and hence fat, BIA has been validated for few animal models and no ruminants. Because the caribou body is a complex geometrical shape, and not a perfect cylinder, the theoretical basis and application of the above equation may be imperfect. In addition, the

precision of body composition estimates may be reduced by either the use of TBW to estimate body composition or the assumptions necessary to calculate IFBW from TBW.

In addition to BIA and marker dilution, body composition may be estimated through the use of condition indices (e.g., body mass and subjective assessment of muscle and fat reserves). Such indices do not require expensive equipment or prolonged sampling periods, and may be cheap, expedient techniques for studies that do not require great precision or accuracy. Body condition indices have not yet been validated as predictors of fat and lean composition in live caribou. We define the body condition score (BCS) as an index of the amount of soft tissue covering bone (5 being high, 1 low) at each of 3 sites: withers, ribs, and hips. Scores at the 3 sites are summed for an overall BCS (range 3-12). We have also formulated a body reserves index (BRI), which is defined as BCS * live weight, i.e., an index of the total reserve of soft tissue in the animal.

In this study, we evaluate the relative merits of HTO, UREA, BIA, BCS and BRI for determination of caribou body composition, by comparing water, fat, protein, and ash estimates made using the *in vivo* techniques with those obtained through chemical carcass analyses of the same animals. This report includes preliminary data on the efficacy of HTO and UREA in field applications, and analyses of water and fat prediction using the BIA, BCS, and BRI indices.

Female caribou of the Central Arctic Herd (CAH) were among the animals analyzed for chemical carcass composition. Thus, for the first time, estimates of body fat for a small sample of CAH caribou are available for comparison with other herds.

OBJECTIVES

Experiment 1: Marker Kinetics

1. Determine the rate at which the water markers HTO and UREA equilibrate with the IFBW and alimentary water pools.
2. Develop kinetic models of HTO and UREA dilution in caribou for use in determining the size of the IFBW (and TBW) pools with a minimal number of blood samples.
3. Devise a blood sampling regime for HTO and UREA that gives a precise estimate of IFBW pool size within a time window appropriate for field applications.

Experiment 2: Estimation of body composition and validation of *in vivo* techniques

4. Characterize seasonal changes in body composition of adult female caribou of the CAH.
5. Evaluate the efficacy of BIA for estimating TBW and body composition of caribou.
6. Evaluate the efficacy of BCS and BRI as estimators of caribou body composition.

METHODS

Experiment 1: Marker Kinetics

Rumen-fistulated reindeer, maintained at the University of Alaska Fairbanks' Large Animal Research Station (LARS), were used to validate kinetic models and investigate individual and

seasonal variability in HTO and UREA equilibration times. A catheter was inserted into the jugular vein, and background blood and rumen samples were taken. Weighed doses of UREA and HTO were injected into the venous catheter, and in some cases, weighed doses of deuterated water and ^{51}Cr -EDTA were injected into the rumen to give independent measures of alimentary, IFBW, and TBW pool sizes. Blood was sampled at 3-min intervals for 24 min, at 30 and 60 min, and at 1 h intervals thereafter until 6 h post-injection. Rumen samples were taken at 15-min intervals for 1 h, and thereafter at the same time as blood samples. Additional samples were taken at 12 and 18 h, and then at 12 h intervals for 5 d post-injection.

Each reindeer was weighed and BCS and impedance values (see below) were determined. Blood samples were centrifuged, and the plasma collected and frozen. Rumen samples were divided into two sub-samples: one was counted for ^{51}Cr concentrations (when appropriate), the other was strained and centrifuged, and the liquid portion frozen. Tritiated water (HTO) and UREA concentrations in rumen liquor and plasma were determined using a liquid scintillation counter. Deuterium concentration was determined by IR spectrophotometry.

Kinetic models and isotope dilution analyses (Shipley and Clark 1972) were used to differentiate between the alimentary water and IFBW pools, in a manner similar to Judson and Leng (1972) and Byers (1979). The fit of exponential curves and mathematical models to the observed dilution curves was analyzed using the computer program SAAM (Simulation, Analysis, and Modeling, National Institute of Health). This program uses linear differential equations to compute compartmental sizes (e.g., sizes of the IFBW and alimentary water pools) from dilution curves.

The use of 4 markers (^{51}Cr -EDTA, HTO, UREA, and deuterium) and 2 injection sites (jugular and rumen cannulae) allowed 3 independent estimates of TBW, IFBW, and alimentary water, as well as 2 independent estimates of water flow rate between the IFBW and alimentary pools. Pool sizes and flow rates will be used to validate and improve marker dilution models.

While model refinement is incomplete, we have investigated the sensitivity of the existing SAAM models to a reduction in the number of dilution (blood) samples, to examine the efficacy of marker dilution under field conditions. Pool sizes were estimated using 5 d of dilution data for HTO, and 24 h of data for UREA. Data sets were then cut to include only the first 30 min post-injection, and pool sizes were estimated again. For HTO, a final data point at 1-3 d post-injection was included in the data set, and pool sizes calculated a final time.

Experiment 2: Body Composition

Nine captive male reindeer, held at LARS, were used to validate body composition values and body water pool sizes for BIA, BCS, and the marker dilution techniques. Fifteen adult female caribou of the CAH were also used (Table 2).

In the captive trials, *in vivo* body composition was measured using all techniques, then reindeer were placed on diets designed to maximize the range of body weights and condition in the sample. As each reindeer reached its assigned weight and condition, body composition was determined again using each technique. After the final blood sample was taken (5 d post-injection), reindeer were killed and processed for chemical analysis according to Huot and Picard (1988), except that the chemical contribution of hides was not included in the present analysis.

Table 2. Sample sizes, collection season, and *in vivo* body composition techniques (bioelectrical impedance analysis (BIA) and body condition scores (BCS)) applied to caribou and reindeer killed for chemical carcass analysis. Both water marker techniques were applied to all animals.

	Reindeer ^a	Caribou ^b		
		Oct 89	May 90	Jul 90
BIA & BCS	9	0	6	4
BCS only	0	5	0	0

^a Captive male reindeer

^b Female caribou of the Central Arctic Herd

In early May and July 1990, 6 and 4 caribou, respectively, were immobilized using carfentanil (1.5mg) and xylazine (20mg) and fitted with a recapture collar (Wildlink, Inc., Brooklyn Park, MN). After 1-2 d, they were remotely immobilized via a discrete signal to the recapture collar. Marker dilution, BIA, and BCS procedures were conducted as outlined above, except that blood sampling was terminated 30 min post-injection. The drug antagonists yohimbine and naloxone were administered and the animals were released. Animals were relocated 2 d later, shot, weighed, and sampled for blood. They were then field dressed, quartered, and frozen for carcass analysis.

In October 1989, 5 female caribou were collected in a manner similar to the above, except that no recapture collars were used, BIA was not conducted, and animals were killed 30 min post-injection.

Electrical impedance was measured using a bioelectrical impedance analyzer (RJL, Inc., Detroit, MI). Animals were tranquilized, and impedance was determined along 2 paths: down the spine with the animal lying on its chest (Z_c), and on the legs with the animal lying on its side (Z_L) (Fig. 1). Body weight (W, kg), body length (L, cm), metatarsal length (MT, cm), girth (G, cm), and distance between electrodes along the spine (D, cm) were measured.

We expected caribou and reindeer to have similar relationships between body water and other body components, therefore body composition estimates for the two *Rangifer* sub-species were pooled for statistical analyses. The pooled sample was split into 2 groups, one for model-building and another for validation, each comprising the entire range of body conditions (based on BCS) and consisting of roughly half caribou and half reindeer. Stepwise linear regression was used to examine the relationships between the dependent and independent variables (Table 3). Validation of selected variables was a two-fold process: (1) equations derived from the model group were used to predict fat and TBW of the validation group, and predicted values were compared with corresponding estimates based on chemical analyses; and (2) stepwise regressions were run on the validation group to verify that the same variables were selected in both data sets. If no bias was found in the models, the data were pooled for derivation of the final equations.

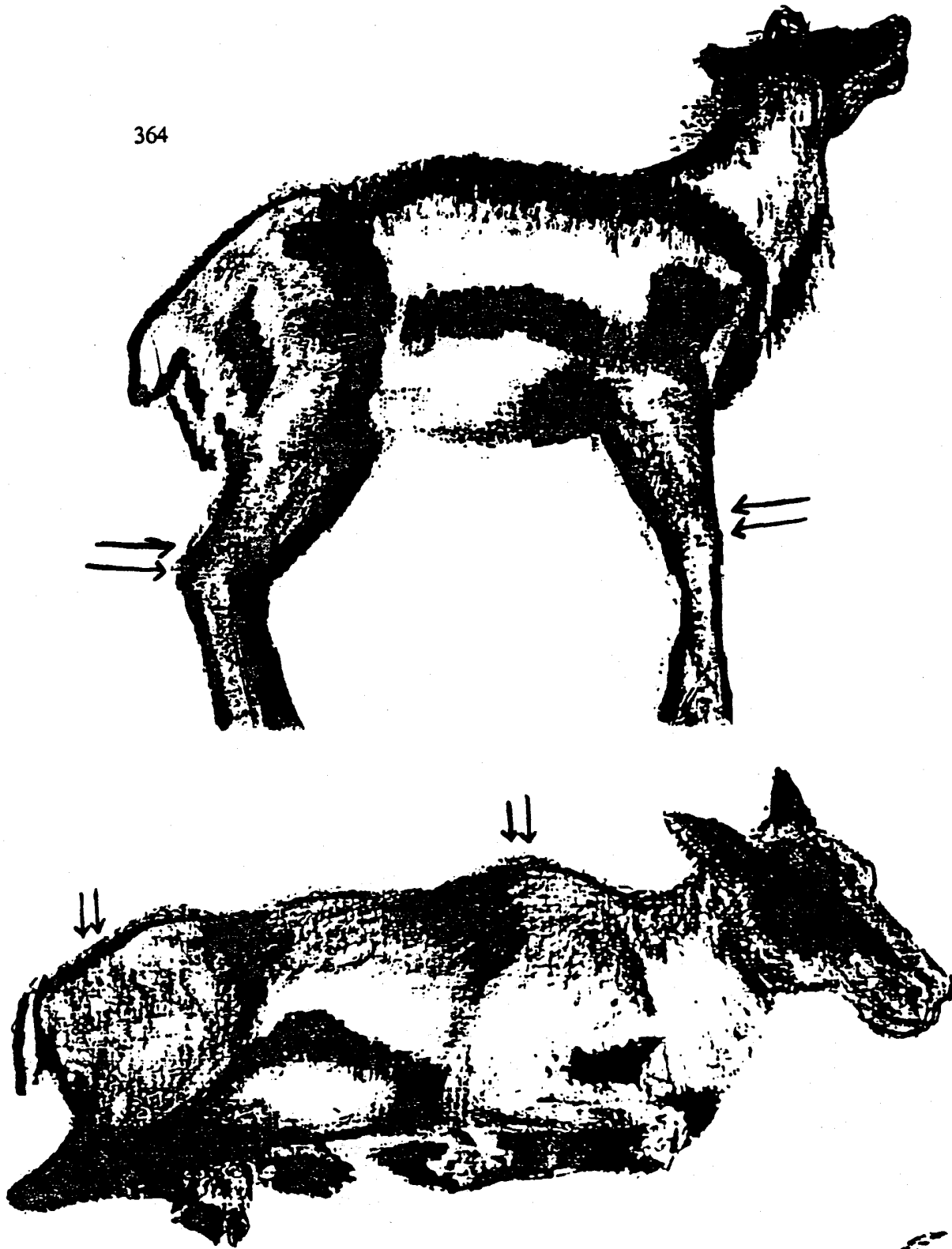


Figure 1. Placement of electrodes for bioelectrical impedance analysis. Impedance was determined in two positions: 1) with a pair of electrodes on the front and hind leg and the animal lying on its side (Z_a), or 2) with a pair of electrodes at two sites along the back and the animal lying on its chest (Z_b).

Table 3. The dependent and independent variables included in the stepwise linear regression model for estimation of body composition in live caribou.

Dependent variables	Independent variables
Total body water (l)	body weight (kg)
Body fat (kg)	BCS = body condition score ^a
	BRI = body reserve index ^b
	L = body length (cm)
	MT = metatarsus (cm)
	chest girth (cm)
	Z _L (ohms)
	Z _s (ohms)
	D = distance (cm) btwn
electrodes (spine)	L ² /(Z _L or Z _s) ^c
	MT ² /(Z _L or Z _s) ^c
	D ² /Z _s ^c

^a BCS = the sum of numerical ratings (1-4, 1 being low) of the amount of soft tissue covering bone at each of 3 sites: withers, ribs, and hips

^b BCS * body weight

^c BIA impedance (Z) is theoretically related to TBW in the form (conductor length)²/Z.

RESULTS

Experiment 1: Marker Dilution

Equilibration time of HTO in captive reindeer varied from 45-90 min in both June and August, while UREA equilibrated in 9-18 min. In both cases, the high degree of variability in equilibration time precluded use of a single blood sample to approximate equilibrium tracer concentration. Seasonal differences in the turnover of both HTO and UREA were demonstrated. Within a season, however, turnover time of each marker was similar between animals.

Total body water (TBW) and IFBW pool sizes calculated using entire data sets (5 d for HTO, 24 h for UREA) were similar to pool sizes calculated using the first 30 min of data (mean differences 3.2 and 3.5%, respectively, Tables 4 and 5). However, the reduction in the number of data points greatly increased the degree of correlation between the parameters of the SAAM model, increasing the likelihood of non-unique solutions. While an estimate of water turnover rate could be used to stabilize the model, the seasonal variation in turnover rate of both markers precluded the use of an estimate unless it was experimentally determined for that season and physiological condition. For HTO, inclusion of an additional data point determined 1-3 d post-injection reduced colinearity substantially, while also reducing variability in the IFBW pool size estimate. Blood samples 1-3 d post-injection could be obtained in the field using the Wildlink recapture system.

Table 4. Ingesta-free body water (IFBW) and total body water (TBW) pool size estimates from the entire tritiated water data set (5 d), from data limited to the first 30 min post-injection and a terminal point at 3 d, and from data limited to 30 min post-injection only.

ANIMAL NO.	TBW*	IFBW*	% Change		
			TBW	IFBW	
180	A	67.6	43.8		
	B	67.0	42.8	0.9	2.3
	C	66.3	40.9	1.9	6.6
40	A	53.4	34.6		
	B	54.5	34.8	2.1	0.6
	C	54.1	33.4	1.3	3.5
192	A	69.4	44.9		
	B	67.8	43.3	2.3	3.6
	C	67.1	41.4	3.3	7.8
193	A	70.8	45.9		
	B	66.6	42.5	5.9	7.4
	C	66.0	40.7	6.8	11.3

A = Entire dilution curve (5 d) used to calculate pool sizes

B = Time-limited set (30 min + 1 point at 3 d)

C = First 30 min post-injection only

* Pools expressed as percent body weight

Table 5. Ingesta-free body water (IFBW) pool size estimates from the entire UREA data set (24 h) and from data limited to 30 min post-injection.

Reindeer	UREA		
	IFBW* total curve	IFBW* 30 min data	% change in IFBW
180	57.95	54.98	5.1
40	51.13	52.18	2.0
07	45.37	43.99	3.0
192	57.90	56.86	1.8
193	54.23	52.03	4.1

* IFBW expressed as % body weight

The estimated IFBW pool size for each animal differed between markers. Mean pool size estimated using UREA was 13% larger than that estimated using HTO. The reason for this difference in estimated IFBW pool size is unknown, and resolution of the discrepancy awaits completion of marker analyses on killed animals.

Experiment 2: Body Composition

Body weight and condition varied between seasons among female CAH caribou (Table 6). Caribou were heaviest and had the largest fat reserves in autumn. Lactating females weighed less and were slightly leaner than non-lactating females. Mean weights were similar in May and July, but females were fatter in May than in July.

While the chemical relations between water and fat were similar between caribou and reindeer (Fig. 2), the 2 sample populations differed in some respects. Ranges of body weight

Table 6. Mean body weights (SE), ingesta-free body weights, and percent fat (as % ingesta-free body weight) for female Central Arctic Herd caribou collected for chemical carcass analysis during 1989 and 1990.

Month	Body Weight	Ingesta-free body weight	%Fat
<u>October 1989</u>			
Lactating (n=3)	81 (4)	64 (3)	6 (2)
Non-lactating (n=2)	92 (1)	78 (2)	7 (2)
Combined (n=5)	85 (4)	70 (4)	6 (1)
<u>May 1990</u>			
Pregnant (n=5)	69 (3)	58 (3)	4.7 (0.7)
Barren (n=1)	65	52	2.9
Combined (n=6)	69 (3)	57 (3)	4.4 (0.6)
<u>July 1990</u>			
Lactating (n=4)	71 (2)	57 (3)	1.2 (0.4)

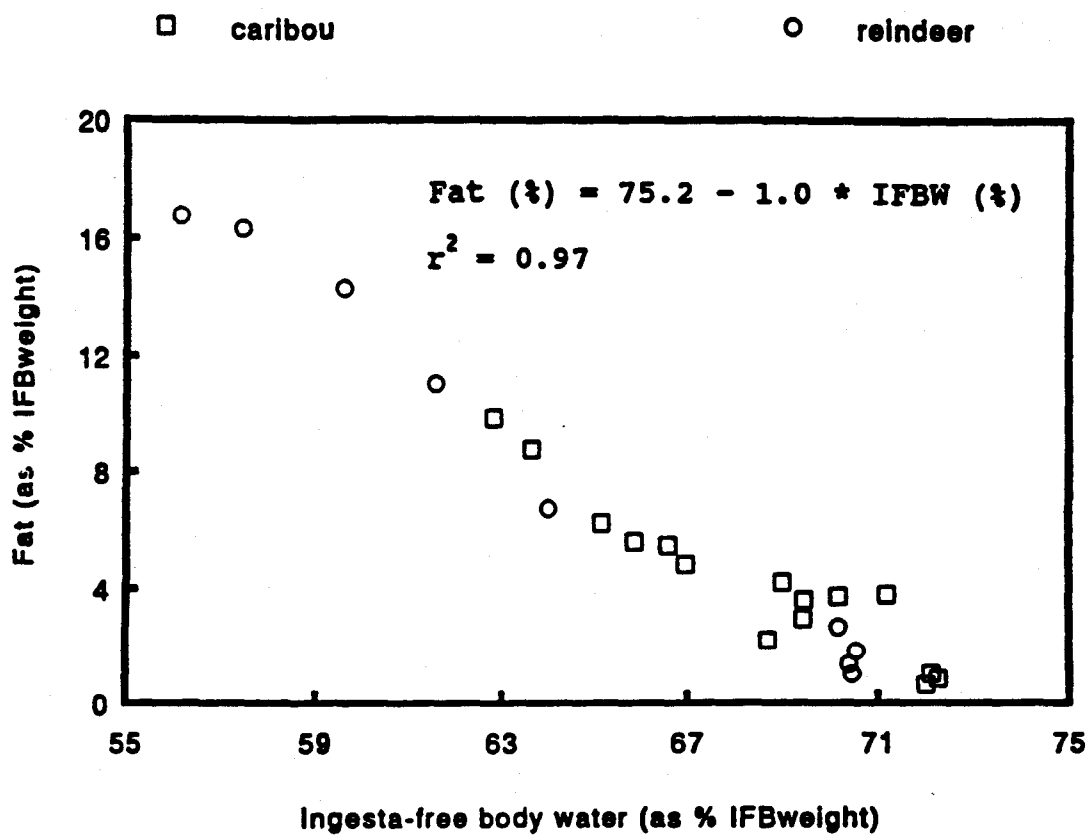


Figure 2. The relation between chemically determined ingesta-free body water and fat (both expressed as a percentage of ingesta-free body weight) in caribou and reindeer.

and body fatness were greater among reindeer than among caribou (Table 7). Differences in metatarsus length and body length existed between the *Rangifer* sub-species. While differences in body length may be related to sex, leg length in *Rangifer* varies between sub-species and between populations (Klein et al. 1987). Impedance values were similar between caribou and reindeer when taken along the spine, but formed 2 discrete populations when taken along the legs, probably because of the differences in leg length. Therefore, the body composition data for the 2 groups, but not necessarily the measurement data, legitimately could be grouped for statistical analyses.

Chemically determined body composition was compared with estimates using *in vivo* techniques. The correlation between TBW and body weight ($r^2 = 0.95$) was stronger than that between TBW and the impedance terms (Figure 3). The impedance term with the strongest correlation to TBW was L^2/Z_L ($r^2 = 0.78$). Impedance along the spine ($1/Z_s$) was not correlated with TBW ($r^2 = 0.00$). Relations between body fat determined by chemical analysis and estimates of body fat made from body weight ($r^2 = 0.78$), BCS ($r^2 = 0.63$), BRI ($r^2 = 0.85$), and BIA ($r^2 = 0.56$) are shown in Figure 4.

Table 7. Means (+/- 1 SE) and ranges of body weight and fat, various body measurements, and BIA parameters for caribou and reindeer collected for chemical carcass analysis.

Estimate		Caribou	Reindeer
Body weight (kg)	mean	75 (3)	101 (8)
	range	59-92	65-132
Fat (%IFB weight)	mean	4.2 (0.7)	8.0 (2.2)
	range	0.7-9.9	1.0-16.8
Metatarsus (cm)	mean	38 (0.2)	33 (1)
	range	37-39	28-37
Body length (cm)	mean	160 (3)	182 (4)
	range	140-172	161-200
Z_s (ohms)	mean	39 (2)	39 (2)
	range	35-50	33-47
Z_L (ohms)	mean	369 (23)	226 (4)
	range	254-468	205-240

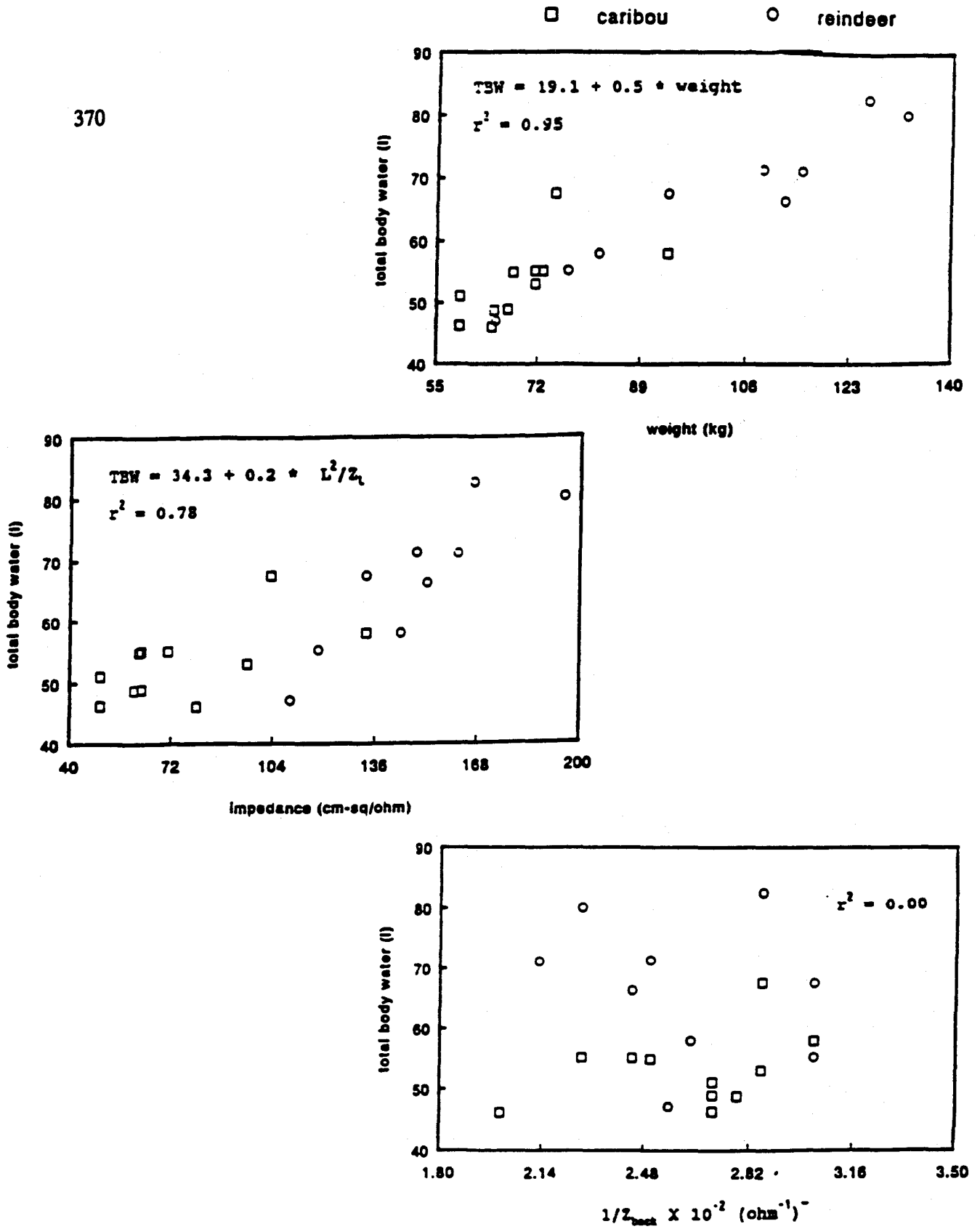


Figure 3. The relation between chemically determined total body water and: 1) body weight, 2) impedance in the form L^2/Z_L , and 3) impedance in the form $1/Z_{tot}$ for caribou and reindeer.

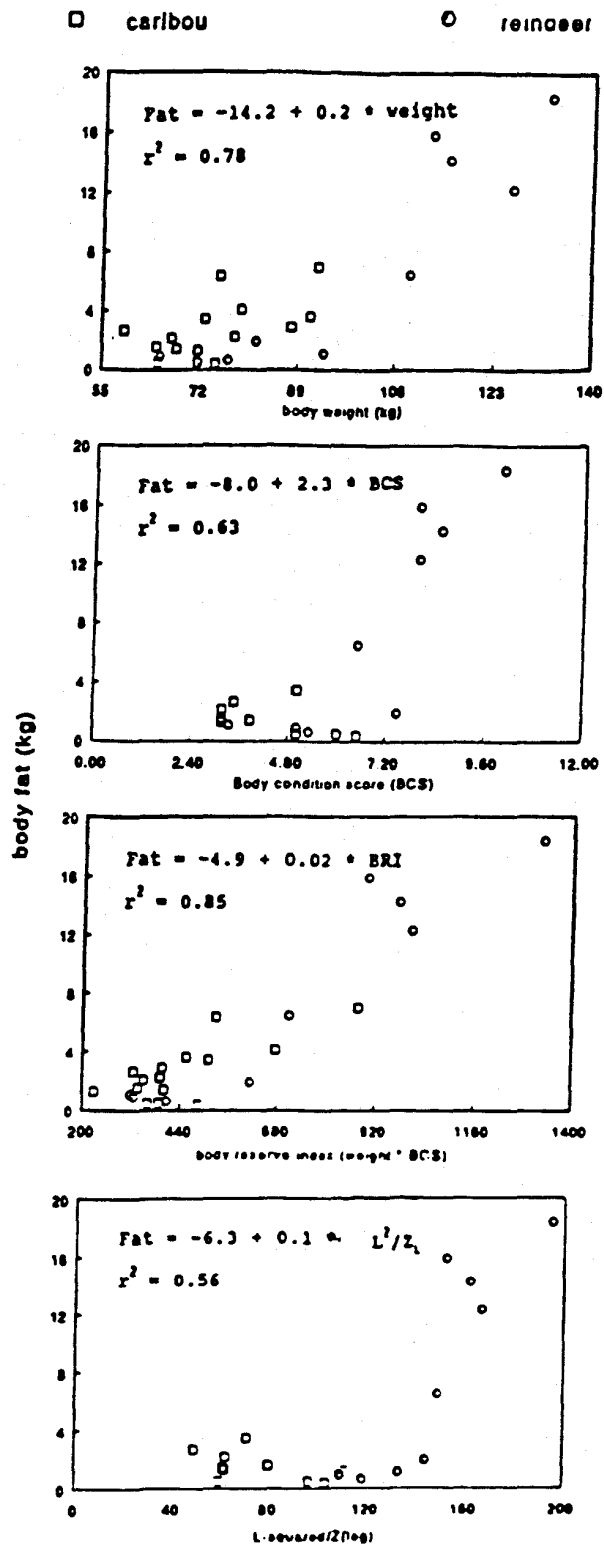


Figure 4. The relation between chemically determined body fat and 1) body weight, 2) body condition scores, 3) the body reserve index, and 4) impedance in the form L^2/Z_1 for caribou and reindeer.

DISCUSSION

Marker Dilution

Both HTO and UREA gave good estimates of body water pool sizes, and may therefore be useful in estimating body composition. However, to calculate IFBW and TBW pool sizes from 30 min of HTO data, the SAAM program required an estimate of TBW turnover. Such estimates were available for the captive animals at LARS, as entire dilution curves had been collected. Turnover could be obtained in the field by using recapture collars to immobilize animals 1-3 d post-injection, allowing collection of an additional blood sample.

UREA shows potential for estimating IFBW in the field. UREA equilibrated with the body water pool within 30 min, thus qualifying it as a useful marker without the use of recapture collars. However, at equilibrium, the tracer concentration was declining markedly, necessitating complex mathematical analyses for estimating IFBW pool size from a series of blood samples taken over 30 min.

Body composition

Body weight and fat of female CAH caribou varied seasonally as in other caribou populations. However, the females in our small sample were lighter than caribou of the (PCH) (Allaye-Chan et al. 1991), George River (Huot 1989), or Coats Island (Adamczewski et al. 1987) herds in fall and spring (see Table 5, Allaye-Chan et al. 1991). In fall, mean ingesta-free body weight (IFBWt) of the CAH (69 kg) was slightly lower than that of the PCH, George River, and Coats Island populations (74-76 kg). Central Arctic Herd (CAH) females, like those of the PCH and George River herds, had low fat reserves (5.2-8.5%) compared with those of Coats Island or Kaminuriak (Dauphine 1976) populations (16-20%). In spring, CAH females were both lighter (57 vs 69-73 kg) and leaner (4.4% vs 7.5-12.4%) than all other herds.

The CAH caribou collected for this analysis tended to be lighter in fall (85 vs 89 kg) and spring (69 vs 77 kg) than the average CAH caribou handled during those seasons (Cameron et al. 1992). To calculate IFBWt for comparison with other herds, we assumed that ingesta was a constant percentage of body weight within a season (determined from the slaughtered CAH females), and subtracted this percentage from the mean weight for each season. The calculated IFBWt of CAH females (73 kg) was similar to that of other herds (74-76 kg) in fall, but CAH females were still lightest in May (65 kg), resembling the Coats Island population (69 kg) more closely than the mainland populations (72-73 kg).

Sampling times were slightly different in the studies noted above. Assuming that pregnant CAH caribou lose fat at an average of 50 g/d between March and June as do PCH females (Allaye-Chan et al. 1991), CAH caribou sampled 40 days earlier (late March/early April) would have 8.5 % fat. This value is above that of Coats Island caribou, but still well below that of mainland herds (11-12%). In fall, CAH females would barely achieve body fat levels similar to those of lactating PCH females (CAH 8% vs PCH 8.5%) if sampled 40 d later (mid-Nov) using the most optimistic rate (39 g/d) of fat gain in female caribou for the period of Sept. through Nov. (Allaye-Chan et al. 1991).

It appears that CAH females were in poor condition in fall 1989 and spring 1990 compared to other mainland herds. The relative importance of summer and winter nutrition in determining these body condition levels is unclear. Inadequate nutrition in summer may affect fall body condition, and have carry-over effects influencing winter condition. Insect harassment in summer and stochastic weather events in winter may play important roles in any given year. Further

study will be necessary to pinpoint the timing and extent of nutritional limitations in the CAH.

Estimation of body composition

Both BRI and body weight are useful predictors of body fat, but the utility of BIA remains unclear. Because of differences in leg length, body length, and impedance values between the caribou and reindeer, construction of a prediction equation for BIA using both groups is not justified. Therefore, further analyses must include calibration of impedance values for caribou.

MANAGEMENT IMPLICATIONS

Our analyses show that BRI (and BCS) are useful for estimating body condition of live caribou. The BIA technique has potential but will require further calibration. Measurements can be made quickly (5-7 min) and we advocate use of these techniques as a management tool to monitor body condition of the Central Arctic and Porcupine Caribou herds. Use of these techniques in experimental research is also promising, but will depend upon the level of precision required. In experimental studies where precise estimates of body composition are required, marker dilution techniques should be used in conjunction with BRI and BCS.

Relatively low rates of calf production in the CAH (Fancy et al. 1990) may be the result of low body weight (Cameron et al. 1992) and, from the present results, low body fat levels. Fat reserves of females at the time of mating are thought to determine the likelihood of conception (Dauphine 1976, Reimers 1983, Allaye-Chan et al. 1991, Crete et al. 1991), and therefore determine parturition rates. Verifying relationships between body fat and fecundity is warranted, as declining productivity has been associated with decreasing body weights in both the CAH (Cameron et al. 1992) and George River (Couturier et al. 1990) herds. Clarification of these processes is necessary to resolve questions regarding density dependent effects on productivity. Such knowledge is critical to effectively manage caribou in the 1002 lands within the Arctic National Wildlife Refuge in the event of oil exploration, and to evaluate restoration protocols for the phase-down period of oil development in the Prudhoe Bay region.

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LITERATURE CITED:

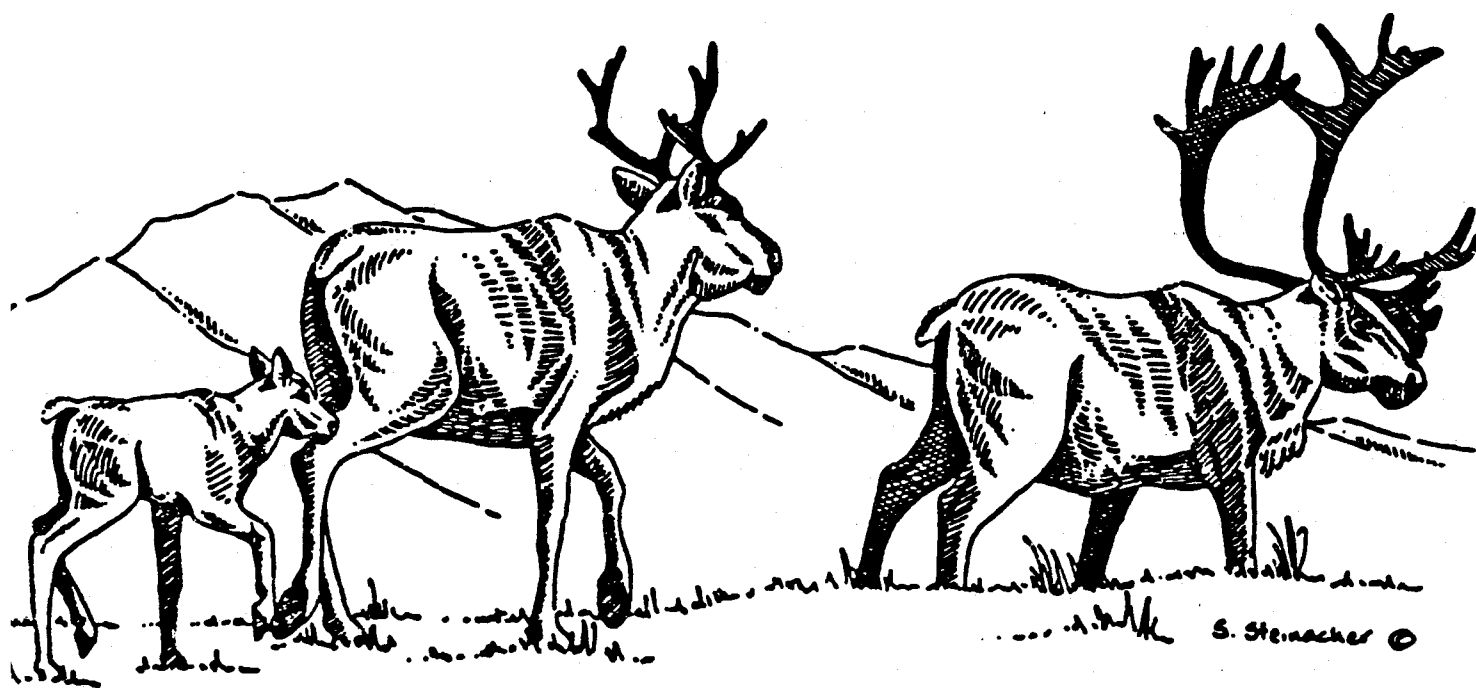
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