SEASONAL CHANGES IN TOTAL BODY WATER; BODY COMPOSITION AND WATER TURNOVER IN REINDEER

Sesongmessige forandringer i totalt kroppsvann, kropps-sammensetning og vannomsetning hos reinsdyr

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Summary: Total body water and water turnover were measured at different times throughout the year in 3 captive Norwegian reindeer, using a tritiated water dilution method (Holleman et al. 1982). Total body water (percent of body weight) increased during late autumn and winter, from 59.1 ± 1.5 % in October to 72.5 ± 2.0 % in April. Using the equatation by Pace and Rathbun (1945) for predicting total body fat (% fat = 100 - % water/0.732), this increase in total body water indicates a concomitant reduction in body fat, from a maximum value of 18.9 ± 2.6 % (of body weight) in October to a minimum of 0.9 ± 2.7 % in April. During summer, on the other hand, fat content increased at the expense of a reduced percentage of body water. Water turnover was low in winter (December - April), ranging between 30.8 ± 5.2 and 43.6 ± 13.5 $ml.d^{-1}. kg^{-1}$, but increased nearly fourfold during summer (June - August) with a maximum of 117.7 ± 5.9 $ml.d^{-1}. kg^{-1}$ in August. Positive correlations between water turnover and food intake and between water turnover and ambient temperature were found, the latter probably resulting from an incidental correlation between food intake and ambient temperature.

Key words: Rangifer, fattening, tritiated water.

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Sesongmessige forandringer i totalt kroppsvann, kropps-sammensetning og vannomsetning hos reinsdyr.

Sammendrag: Totalt kroppsvann og vannomsetning av vann ble målt til forskjellige årstider i 3 norske reinsdyr ved hjelp av utvasking av tritiert vann (Holleman et al. 1982). Totalt kroppsvann (prosent av kroppsvekt) økte utover høsten og vinteren, fra 59.1 ± 1.5 % i oktober til 72.5 ± 2.0 % i april. Ved hjelp av en ligning som er gitt av Pace og Rathbun (1945) for beregning av totalt kroppsfett (% fett = 100 - % vann/0.732), fant en at denne økningen i vanninnhold tilsvarte en samtidig reduksjon i fettinnhold, fra en maksimums-verdi på 18.9 ± 2.6 % av kroppsvekt i oktober til et minimum på 0.9 ± 2.7 % i april. Utover sommeren økte derimot innholdet av fett på bekostning av vanninnholdet. Omsetningen av vann var lav vinterstid (desember - april), varierende mellom 30.8 ± 5.2 og 43.6 ± 13.5 $ml.d^{-1}.kg^{-1}$, men økte nesten fire ganger i løpet av sommeren (juni - august) til et maksimum på 117.7 ± 5.9 $ml.d^{-1}.kg^{-1}$ i august. Det ble funnet positive korrelasjoner mellom vannomsetning og fôrinntak og mellom vannomsetning og omgivelsestemperatur. Sistnevnte korrelasjon kan muligens skyldes en tilfeldig sammenheng mellom fôrinntak og omgivelsestemperatur.

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Vuodenaikaiset muutokset poron ruumiin kokonaisvesimäärässä, ruumiin koostumuksessa ja vesiaineenvaihdunnassa.

Yhteenveto: Ruumiin kokonaisvesimäärää ja vesiaineenvaihduntaa mitattiin eri vuodenaikoina 3 norjalaisella porolla käyttämällä apuna tritioitua vettä (Holleman et al. 1982). Ruumiin kokonaisvesimäärä (prosenttia ruumiinpainosta) lisääntyi syksyllä ja talvella lokakuun 59.1±1.5%:sta 72.5±2.0%:i huhtikuussa. Käyttämällä Pacen ja Rathbunin (1945) ruumiin kokonaisrasvapitoisuude laskukaavaa (rasva % = 100 - vesi %/0.732) huomattiin tämän vesimäärän lisääntymis johtuvan samanaikaisesta rasvapitoisuuden vähenemisestä. Rasvapitoisuus laski lokakuun maksimiarvosta 18.9±2.6% ruumiinpainosta huhtikuun minimiarvoon, joka oli 0.9±2.7% ruumiinpainosta. Kesällä rasvapitoisuus lisääntyi puolestaan vesipitoisuuden kustannuksella. Talvella jäkäläravinnolla (joulu-huhtikuussa) veden käyttö vaihteli välillä 30.8±5.2 ja 43.6±13.5 ml vrk^{-1}·kg^{-1}, mutta se kohosi melkein nelinkertaisesti kesällä (kesä-elokuussa) maksimiarvoonsa 117.7±5.9 ml·vrk^{-1}·kg^{-1} elokuussa. Veden käytön ja ravinnon oton sekä veden käytön ja ympäristön lämpötilan välillä oli positiivinen korrelaatio. Viimeksi mainittu korrelaatio voi johtua väliaikaisesta riippuvuudesta ravinnonoton ja ympäristön lämpötilan välillä.

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INTRODUCTION

The tritiated water dilution method has been widely used for the in vivo determination of total body water in experimental animals (Panaretto 1963, Cameron and Luick 1972, Holleman et al. 1982). The determination of this parameter is particularly useful in studies of body composition, since it permits body weight changes to be partitioned into solid and aqueous component changes. Moreover, it is well established that body water and body fat are inversely related (Longhurst et al. 1970). This relationship has been used to develop equations for estimation of body fat content (Pace and Rathbun 1945, Panaretto 1963) based on measurement of body water.

Both in nature and in captivity reindeer and caribou exhibit a cyclic growth pattern (Mc Evan 1975, Ryg and Jacobsen 1982). This pattern is characterized by net deposition of large amounts of body fat in summer, when energy intake is far in excess of maintenance requirements (Larsen et al. 1985). In winter, on the other hand, food intake is markedly reduced and the reindeer enter a state of negative energy balance. In this situation mobilization of the body fat stores is activated to compensate for the low energy intake. The purpose of the present study was to determine the seasonal changes in total body water for the prediction of the accompanying changes in total body fat in captive Norwegian reindeer. Measurements of water turnover were also included, and the influence of food intake and ambient temperature on this variable investigated.

MATERIALS AND METHODS

Procedures

Three female Norwegian reindeer (Rangifer tarandus tarandus) aged 2-3 years at the start of the experiment, were used in the study. Two of the animals gave birth to a calf in May, while the third was barren. Throughout the experimental period the animals were kept under outdoor conditions at the Department of Arctic Biology at the University of Tromsø (70°N) With ad. lib. access to food and water. The diet consisted of RF-71[1] a commercially available, pelleted reindeer feed (Jacobsen and Skjenneberg 1979). The animals were weighed at intervals by use of a Sauter® KOM-AZ/N2E platform scale (accuracy ± 20 g).

Total body water (TBW, percent of body weight) and water turnover were determined at intervals throughout the year using tritiated water (TOH) following the principles and calculations outlined by Holleman et al. 1982. A stock solution was prepared by adding tritiated water (New England Nuclear, specific activity 100 mCi/ml) to a sterile, isotonic solution of sodium chloride to a specific activity of 100 μCi/ml. Body weight of each reindeer was recorded immediately prior to injection of the radiotracer, and these values were used for calculations of TBW. A venous cannula (Venflon ®) was inserted into the jugular vein, and a 10 ml preinjection sample for determination of background activity obtained. A preweighed dose of TOH (500 - 600 μ Ci) was then injected. The syringe was rinsed several times with venous blood to ensure complete administration of the tracer. At

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[1] Composition of feed (% of dry matter): crude protein 13.7, ether extract 7.2, crude fiber 11.0, nitrogen free extract 62.4, ash 5.7.

regular intervals during the following 10 day period blood samples were taken into 5 ml heparinized tubes, centrifuged and the plasma stored at −20°C.

Preparation of samples was started within a few days following the sampling program. Plasma proteins in a 1 ml plasma sample were precipitated by 2 ml 0.6N perchloric acid. Following centrifugation duplicate aliquots of 0.5 ml of the supernatant were counted (Packard Tri-Carb Liquid Scintillation) in 10 ml scintillation solution (Insta-Gel®). TOH standards were prepared from the stock solution (diluted 1:10^3) in exactly the same way as the plasma samples and counted simultaneously.

Calculations.

Plasma water specific activity decreased exponentially with time and can be described by the single exponential equation $A_t = A_O \cdot e.^{-kt}$. A_t is the plasma water specific activitiy ($cpm.ml^{-1}$). at any time (t) after the injection of TOH and A_O the specific activity at the time of injection. The rate constant, K, is the daily fractional turnover of body water. A_O was calculated by extrapolation of the linear log A_t versus time curve, while K was obtained from the slope of the curve. The regression line was constructed by use of the least squares method. Total body water, which was equated with the TOH distribution space, was computed using the equation $TBW = {}^{I}/A_O\text{-}A_B$, where I is the dose of TOH (cpm) injected and A_B the specific activity ($cpm.ml^{-1}$). of the preinjection sample. The total injected activity was calculated by the equation, $I = St \times V \times D \times 0.93$ where St is the activity of the standard solution ($cpm\ ml^{-1}$)., V the volume of TOH injected (ml), D the dilution factor of the standard, and 0.93 is to correct for plasma water content (Oddershede and Elizondo 1980). The biological halftime ($t_{1/2}$)., which is the time (days) required for the body to eliminate one half of an injected dose of TOH is given by the expression $t_{1/2} = 0.693/k$. The water flux rate ($ml.kg^{-1}d^{-1}$). expresses the amount of water entering or leaving the body water pool per unit time and was calculated from the equation $F = k \cdot TBW\ (\text{body weight})^{-1}$

The amount of body fat was calculated using the relationship of Pace and Rathbun (1945): % fat = 100 - TBW/0.732, where 0.732 is the suggested proportion of water by weight in a lean mammal.

The water flux rate obtained at the different times of the year was correlated to the corresponding mean ambient temperature, and to the mean food intake values of the same animals, previously published by Larsen et al. (1985). Finally, mean food intake was correlated to mean ambient temperature. The regression equations were calculated by least squares method, using a standard computer program (MINITAB, Statistics Dept., Penn. State Univ.).

RESULTS

The changes in body weight of the animals are shown in Fig. 1. For all three reindeer body weight increased some 3-4 kg during November. For the pregnant reindeer this was followed by a moderate decline (2-3 kg) to a minimum in January. Thereafter body weight was fairly constant, or even increased (one of the animals), while it from April on there was a marked weight gain until calving took place in May. The non-pregnant reindeer lost 5.5 kg from November to January, followed by a two-month period where virtually no weight changes could be detected, while during late March and April a new reduction to approximately 9 kg below the November value occurred. During summer body weight increased considerably for all animals, starting at the end of April for the non-pregnant, non-lactating reindeer. For the lactating animals, however, there was no weight gain until July. Maximum body weight was reached in late August or in early September.

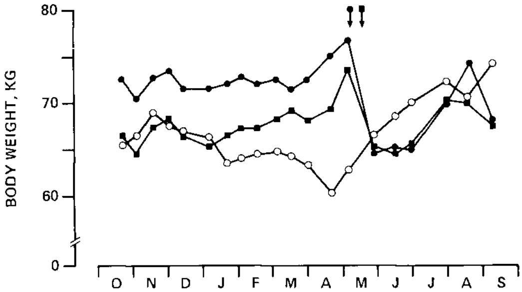

Fig. 1. Seasonal changes in body weight of 3 individual ad lib. fed Norwegian reindeer. Two of the animals were pregnant (filled symbols) and calved in May (arrows), while one animal was barren.

Fig. 1. Sesongmessige forandringer i kroppsvekt hos 3 individuelle ad lib. fôrede norske reinsdyr. To av dyrene var drektige (fylte symboler) og kalvet i mai (piler), mens ett dyr var uten kalv.

Total body water (TBW), body water volume (I), biological halflife ($t_{1/2}$) of the injected TOH dose

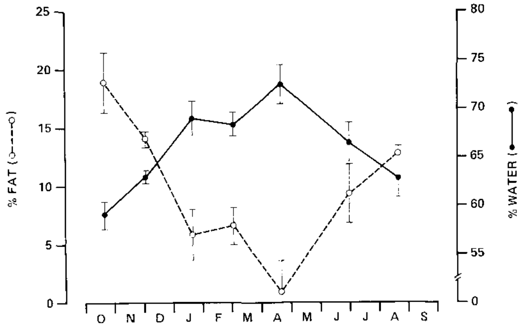

Fig. 2. Seasonal changes in total body water (o — o) and body fat (o----o) of ad lib. fed Norwegian reindeer. Total body water is equated with the distribution space of the injected dose of tritiated water, while body fat content was calculated using the formula of Pace and Rathbun (1945): % Fat = 100% - % water/0.732. The symbols indicate mean values ± SD (n=3).

Fig. 2. Sesongmessige forandringer i totalt kroppsvann (o — o) og kroppsfett (o----o) hos ad lib. fôret norsk rein. Totalt kroppsvann tilsvarer distribusjonsvolumet til den injiserte dosen av tritiert vann, mens fettinnholdet ble beregnet ut fra ligningen til Pace og Rathbun (1945): % fett = 100 - % vann/0.732. Symbolene angir gjennomsnittsverdier ± S.D. (n=3).

and water flux rates are listed in Table 1. TBW increased significantly during autumn and winter, from a mean value of 59.1 ± 1.5 % of body weight in late October to 72.5 ± 2.0 % (mean ± S.D.) in late April (Fig. 2). The increase in total body water during this period can be described by the linear relationship $y = 2.1x + 60.0$ ($r = 0.932$), where y = TBW (%) and x the time (months), indicating that TBW increased by an average value of 2.1 % every month in the period between October and April. During late spring and summer, on the other hand, TBW decreased to a mean value of 62.8 ± 2.0 % in August. The seasonal changes in total body fat which are derived from the changes in total body water, are illustrated by the broken line in Fig. 2. The highest fat value was found in October, being 18.9 ± 2.6 % (mean ± S.D.) of body weight. The fat content dropped markedly during autumn and winter to 5.8 ± 2.3 % in January. From January to March, however, there was no evident change in the fat content, while the value in late April was only 0.9 ± 2.7 %. In fact the calculated April fat value for one of the reindeer (No. 22/78) was negative. During summer TBW

Table 1. Seasonal changes in body water volume (l), total body water (percent of body weight), biological halflife, of the injected TOH dose (t½) and water flux rate (ml.d.$^{-1}$kg^{-1}) of ad lib. fed Norwegian reindeer.

Tabell 1. Sesongmessig forandring i volum (l) av kroppsvann, totalt kroppsvann (prosent av kroppsvekt), biologisk halveringstid av den injiserte TOH dose (t½) og vannomsetning (ml.d.$^{-1}$kg^{-1}) hos ad lib. fôret rein.

	Body water volume (l)			Total body water (%)				t½-days				Water flux rate (ml.kg.$^{-1}$d^{-1})			
Reindeer No. month	2/79	22/78	33/78	2/79	22/78	33/78	mean ± S.D.	2/79	22/78	33/78	mean ± S.D.	2/79	22/78	33/78	mean ± S.D.
October	41.9	38.9	42.1	60.8	58.5	58.1	59.1±1.5	11.2	13.4	14.7	13.0±1.9	40.0	30.3	27.5	32.6± 6.6
December	42.3	42.9	46.1	62.6	62.9	63.3	62.9±0.4	12.0	16.9	14.5	14.5±2.5	36.2	25.8	30.0	30.8± 5.2
January	44.2	46.8	48.9	69.6	70.3	67.1	69.0±1.7	8.2	14.7	12.0	11.6±3.3	58.9	33.1	38.9	43.6±13.5
March	43.7	47.5	49.3	67.4	69.6	68.0	68.3±1.1	10.5	16.8	16.7	14.7±3.6	44.6	28.8	28.3	33.9± 9.3
April	42.9	51.8	53.6	71.3	74.8	71.4	72.5±2.0	10.8	8.5	8.7	9.3±1.3	45.7	61.4	57.1	54.7± 8.1
June	44.9	44.9	43.7	64.1	67.8	67.2	66.4±2.0	5.2	6.7	4.5	5.5±1.1	85.9	70.6	104.3	86.9±16.7
August	45.5	42.3	47.3	64.1	60.5	63.9	62.8±2.0	4.4	3.6	3.7	3.9±0.4	111.1	122.4	119.6	117.7± 5.9

decreased. This indicates an increase in body fat, and in August a calculated fat value of 12.8 ± 0.4 % was obtained.

Biological halflife (Table 1) of the injected TOH dose was highest from late October (11.6 ± 3.3) (mean ± S.D.) to the end of March (14.7 ± 3.6 days). During spring and summer it declined markedly, however, to reach the lowest value of 3.9 ± 0.4 days in August. Water flux, accordingly, was lowest in autumn and winter, changing only negligibly between October and March (range: 30.8 ± 5.2 - 43.6 ± 13.5 ml.d^{-1} kg^{-1}). A 3-4 fold increase was, however, seen during summer with a maximum in August of 117.7 ± 5.9 ml.d^{-1}kg^{-1}

In Fig. 3 we have illustrated the (linear) relationship between water flux rate and ambient temperature (A), between water flux rate and food intake (B) and also between food intake and

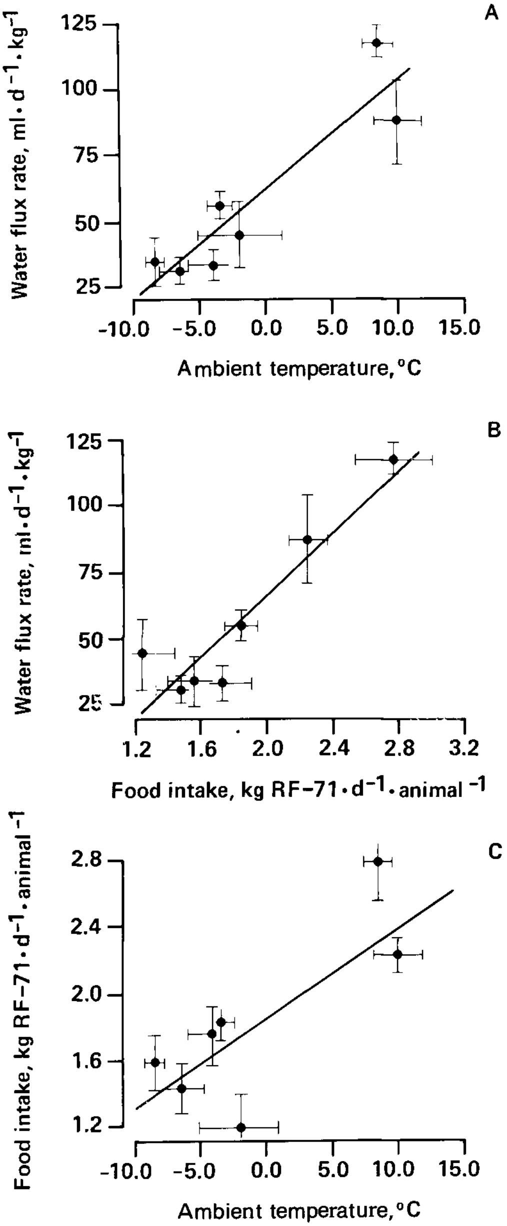

Fig. 3. A. Water flux rate related to ambient temperature. Water flux rates (mean values) were taken from Table 1, while the corresponding temperature values represent the local mean ambient temperature (± SD) for the sampling period following injection of tritiated water. Temperature data were provided by the Norwegian Insitute of Meterology.

B. Water flux related to food intake of ad lib. fed Norwegian reindeer. Again water flux rates were taken from Table 1, while the corresponding food intake values were obtained from another study (Larsen et al. 1985) involving the same animals as used in the present study. The symbols indicate mean values ± S.D. (n=3).

C. Food intake related to ambient temperature. The symbols are defined in A and B.

Fig. 3. A. Vannomsetning relatert til omgivelsestemperatur. Vannomsetningsdata (gjennomsnittsverdier) er tatt fra Tabell 1, mens tilsvarende verdier for omgivelsetemperatur representerer den lokale gjennomsnittstemperatur (± S.D.) i prøvetakningsperioden etter injeksjon av tritiert vann. Temperaturdata ble gitt av Norsk Meterologisk Institutt.

B. Vannomsetning relatert til fôrinntaket hos ad lib. fôret norsk rein. Igjen er vannomsetningsdata tatt fra Tabell 1, mens tilsvarende fôrinntaksverdier er tatt fra en annen undersøkelse (Larsen et al. 1985) hvor en benyttet de samme dyrene som inngikk i dette studiet. Symbolene angir gjennomsnittsverdier ± S.D. (n=3).

C. Fôrinntaket relatert til omgivelsestemperatur. Symbolene er definert under A og B.

ambient temperature (C). These relationsships can be described by the following equations: $y = 4.2x + 61.3$ (x = ambient temperature in °C, y = water flux rate in $ml.d^{-1}kg^{-1}$), $y = 59.1x - 51.7$ (x = food intake in kg RF-71.d^{-1} $animal^{-1}$, y = water flux rate in $ml.d^{-1}kg^{-1}$) and $y = 0.06x + 1.90$ (x= ambient temperature in °C, y = food intake in kg RF-71·d^{-1}·$animal^{-1}$). The correlation coefficients were 0.919, 0.923 and 0.808, respectively and the slopes of regression lines were all significantly different from zero at the 95% confidence interval.

DISCUSSION

The present study has demonstrated marked seasonal changes in body composition and body fluid dynamics as evaluated by the tritiated water dilution technique. One objection to this method is that injected tritium exchanges to some degree with labile hydrogen atoms of organic body constituents, thereby increasing the apparent distribution volume of tritiated water. Values for exchangable hydrogen space have been reported to vary between 0.5 to 5.0 % of the body weight (Panaretto and Till 1963). However, the main purpose of the present study was to examine relative changes in total body water (TBW) and related parameters and we have therefore found it acceptable to equate the uncorrected tritiated water spaces with total water volume.

In accordance with earlier observations on reindeer (Cameron and Luick 1972) we found that TBW increased significantly during late autumn, winter and spring, reaching maximum values at the end of April (Fig.2). In the non-pregnant reindeer the increase in TBW was accompanied by a considerable reduction in body weight (Fig. 1). Since total body water volume changed only negligibly in this period (Table 1), the increase in TBW may be explained by a reduction in body solids. In the two pregnant reindeer on the other hand, body weight (Fig. 1) was fairly constant during winter (November - April), suggesting that the increase in TBW in this case is caused by an increase in body water volume (Table 1), which approximately equals the reduction in body solids. The increase in body water volume may in part be a consequence of water retention during pregnancy. Conversely, TBW decreased during late spring and summer, and was accompanied by an increase in body weight, reflecting an increase in body solids. The finding of higher TBW values at the end of June in the two lactating reindeer compared to that of the non-lactating one, fits well with the delayed weight gain (fattening) observed for these two animals (Fig. 1). Retarded growth of the lactating reindeer very likely is the result of increased energy demands due to high milk production during early lactation.

Seasonal changes in TBW of reindeer have previously been studied by Cameron and Luick (1972). The TBW values reported in their study varied within a much wider range than in the present study. This discrepancy may be explained by the fact that in the former the animals were allowed to forage on natural vegetation, and that the seasonal changes in body weight in that case were much more pronounced than in our study, where the animals had free access to a high quality diet throughout the whole experiment.

An inverse relationship between TBW and total body fat has been established in ruminants by several investigators. Direct analysis of carcass preparations following in vivo determination of body water have been used to derive equations for the indirect estimation of body fat in domestic livestock (Panaretto and Till 1963, Searle 1970). No such equation has been establised for reindeer, and we therefore used the formula suggested by Pace and Rathbun (1945) for the calculation of total body fat, where lean body mass is assumed to contain all body water in a constant proportion equal to 0.732. According to Sheng and Huggins (1979) the ratio of TBW to fat-free weight (0.732) may vary, both among individuals and between species, and result in significant errors in the calculated body fat. It is assumed that the largest potential error in the prediction of body fat by the tritiated water method is in the estimation of TBW. For this reason, we have found it acceptable to assume a constant ratio of TBW to fat-free weight of 0.732.

Maximum fat content was found in October, accounting for nearly 20 % of the total body weight. This value probably represents an underestimate since TBW is likely to be slightly overestimated. However, it nevertheless is within the upper range of directly measured fat values of other ruminants (Panaretto and Till 1963), and illustrates the importance of fat as an energy source in these animals. The marked drop in the predicted fat content from end of October to end of January (Fig. 2) indicates that fat mobilization is most pronounced during the darkest part of the year. Thereafter the catabolic processes within the adipose tissue are retarded, most likely due to slightly increasing food intakes during late winter and spring (Larsen et al. 1985). It should also be noted that the predicted reduction in the fat content during autumn and winter is an agreement with the observed reduction in adipocyte size (Larsen et al. 1985). However, the calculated April fat values were extremely low, in fact the fat value of one of the pregnant animals turned out to be negative. This is most likely due to the fact that our 0.732 value for assumed water content of lean body mass is lower than the real value at this time of the year. Elevation of the fraction of water in the lean body mass might be explained in terms of water retention during pregnancy and nutritional stress.

Previous studies have suggested that water flux is influenced both by climatic and nutritional factors. Cameron and Luick (1972) found that the biological halflife of TOH tended to decrease with increasing ambient temperature, suggesting a direct influence of temperature and water turnover. In accordance with their results we obtained a positive correlation between water flux rate ($ml.d^{-1}kg^{-1}$) and ambient temperature (°C), which in part may result from higher evaporative water loss in summer (Fig. 3 A). We also obtained a postive correlation between food intake and ambient temperature (Fig. 3 C). This correlation may be incidental (food intake is believed to be governed mainly by photoperiod) and unlike Cameron and Luick (1972), we suggest that the increase in water flux with increasing ambient temperature simply is a consequence of the higher food intake in summer.

A relationship beween food intake and water turnover has previously been demonstrated in domestic animals. Forbes (1968) studying non-pregnant ewes found a positive correlation between total water intake and dry matter intake for three different feeds. Similarly, Siebert and Macfarlane (1969) noted a higher water turnover in cattle in response to increased food supply. In reindeer on natural pastures the effect of food intake on water turnover is difficult to evaluate, because seasonal temperature changes and snow cover strongly influence the availability and quality (protein, mineral and water content) of the forage. Data by Cameron et al. (1982) indicate, however, that at low ambient temperatures (−14 to - 20°C) water turnover is primarily a function of protein and mineral intake. In the present study, the animals were fed a diet of constant composition ad lib. Moreover, the fact that reindeer in captivity (like free living animals) voluntarily restrict their food intake in winter (Ryg and Jacobsen 1982, Larsen et al. 1985), makes our model a very suitable one for examination of the impact of food intake on water turnover in the reindeer. The linear relationship between the two variables, (Fig. 3 B) demonstrates that food intake may be an important determinant of the water turnover in reindeer. Most likely, the production of nitrogenous wastes, and thus the urinary losses, changes in parallel with the seasonal changes in food intake. High water flux rates in summer may therefore in part reflect the water requirements needed to balance the urinary losses. The low food intake of reindeer during winter will, on the other hand, allow a low water turnover rate, which is further diminished due to an increased recycling of urea (Hove and Jacobsen 1975).

In conclusion, the present investigation has shown that in reindeer an increase in total body water takes place during late autumn and winter, accompanied by a concomitant reduction in total body fat. Water flux rate was positively correlated both with ambient temperature and food intake at all times of the year. It is suggested that the present and previously published correlations between water flux rate and ambient temperature in reindeer are resulting from incidental correlations between food intake and ambient temperature.

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