Seasonal variations in glucose metabolism of reindeer (*Rangifer tarandus* L.) estimated with [U-^{14}C]glucose and [3-^{3}H]glucose

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1. The pool size, space and rate of irreversible loss of glucose were estimated with primed infusions of [U-^{14}C]glucose in reindeer cows within 6 h of being taken from outdoor pens or from free grazing in the field.

2. In conjunction with primed infusions of [U-^{14}C]glucose, single injections of [3-^{3}H]glucose were also used to estimate pool size, space, transfer rate, and turnover time of glucose.

3. Except in a period of severe undernutrition, the concentration of glucose in plasma was higher (range 0·76–1·40 mg/ml) than that recorded for other ruminants.

4. The size of the glucose pool (range 8–35 g) varied in parallel with plasma glucose concentration and was generally distributed in a space in excess of the extracellular fluid volume.

5. The lowest rates of irreversible loss of glucose (approximately 1·7 mg/min per kg$^{0·75}$) were measured when cows were in mid pregnancy and when available food was scarce; the highest rate (5·5 mg/min per kg$^{0·75}$) was found in cows during mid summer.

6. Changes in irreversible loss and transfer rate of glucose are interpreted in relation to changes in body composition (estimated in a parallel study), subjective assessment of available food and factors known to control glucose metabolism in other ruminants.

7. The difference between glucose transfer rate and rate of irreversible loss of glucose was used as an index of the rate of resynthesis of glucose from products of glucose catabolism. The rates of glucose resynthesis were highest during a period of rapid growth (4·52 mg/min per kg$^{0·75}$ or 45% of the glucose transfer rate) and in mid and late pregnancy (respectively 4·14 and 4·28 mg/min per kg$^{0·75}$ or 71 and 59% of the transfer rate).

The habitat of *Rangifer tarandus* L., the domesticated reindeer and wild caribou, is characterized by marked changes in climatic conditions and availability of food (Scotter, 1965; Kelsall, 1968; Skuncke, 1969). These factors probably impose regulations on growth and reproduction of the species, for during late winter and early spring, harsh climatic conditions are common and the main food source, lichen (Karaev, 1961; Kelsall, 1968), is low in crude protein ($\leqslant 3\%$) and is usually covered by snow. Some nutritional relief may be obtained by supplementation with frozen grasses (Karaev, 1961; Skoog, 1968) and mushrooms which in turn may increase the digestibility of lichen (Scotter, 1964).

Although there are now many studies on the type of food consumed by reindeer and caribou throughout the year in the North American subarctic, changes in the nutritional status of these animals has not been widely investigated although rates and patterns of growth have been reported for mature animals (Klein, 1968; McEwan, 1968*a*) and calves (Krebs & Cowan, 1962; McEwan & Wood, 1966; McEwan, 1968*a*). Glucose is an important intermediate of metabolism and growth of animals in general and is particularly important for foetal growth and development. The exogenous precursors of glucose for grazing ungulates are mainly propionate absorbed from the rumen-reticulum and amino acids absorbed from the small intestine (for reviews see

Armstrong, 1965; Ballard, Hanson & Kronfeld, 1969; Leng, 1970). In summer when herbage is lush and abundant, the supply of these precursors probably exceeds the animals' requirements for glucose.

This paper reports seasonal changes in the amounts of glucose synthesized by domesticated reindeer immediately after feeding on natural vegetation. Isotope-dilution techniques were used to study glucose synthesis. The total rate of glucose formation (the 'transfer rate') was estimated by single exponent analysis following single injection of [3-^{3}H]glucose. The rate of net formation (rate of *de novo* synthesis or irreversible loss of glucose (White, Steel, Leng & Luick, 1969)) was estimated from primed-infusion experiments using [U-^{14}C]glucose. The rate of resynthesis of glucose (that is, the rate of recycling of glucose carbon or rate of formation of glucose from products of glucose metabolism) was then estimated as the difference between total and net formation.

Some of the results of this work have been reported in preliminary forms (Luick, Person, Cameron & White, 1971; Person, Luick, Cameron & White, 1971).

EXPERIMENTAL

Experimental animals and feeding and grazing regimens

Nine female reindeer (1·5–2·5 years of age in January 1969) were obtained from the Bureau of Indian Affairs Model Herd, Nome, Alaska. On arrival at the University of Alaska, the reindeer were given commercial cattle food (Purina Cattle Starter 2, Ralston-Purina Corp., St Louis, Mo., USA) containing about 12% crude protein.

At least 5 months before these experiments the animals were taken to the Reindeer Research Station at Cantwell, Alaska and were allowed to graze naturally occurring vegetation. Occasional supplementary feeding (see Fig. 1) was necessary to conserve lichen pastures and to ensure survival of the animals. However, in all instances supplementation was stopped at least 2 months before any experiment. No animals were pregnant during the 1969 trials; all except one were pregnant during the January and April 1970 trials.

Composition of summer pasture. Summer pastures were predominantly shrub (including glandular birch *Betula glandulosa* Michx. and willows – *Salix* spp.) low heath shrubs (including *Vaccinium* spp. and *Ledum* spp.) grasses (mostly *Festuca altaica* Trin.) and sedges (*Carex* spp.), lichens and plant litter. At all times scattered stands of white spruce (*Picea glauca* (Moench) Voss) were available for shelter. A typical botanical composition of two areas is shown in Table 1; samples were taken by the point frame method (Levy & Madden, 1933) from 1386 readings on each pasture. During most of autumn, winter and early spring, the pastures were covered with snow and reindeer were observed to eat from food craters which they dug in the snow.

Climatological data. Summary sheets of local climatological data for Summit, Alaska, were obtained from the US Department of Commerce, Environmental Science Services Administration. Summit is located 16 km south of the University of Alaska Cantwell Reindeer Research Station.

Table 1. *Vegetative composition of two pastures grazed by reindeer during summer. Analyses were based on* 1386 *readings on each pasture*

	Pasture A		Pasture B	
	No. of samples	Percentage* composition	No. of samples	Percentage* composition
Trees				
Spruce	2	0·14	5	0·36
Shrubs				
Birch	182	13·0	514	37·1
Willow	42	3·0	20	1·4
Low canopy				
Heaths	598	43·1	593	42·8
Grass-sedge	498	35·9	147	10·6
Carpet				
Moss	649	46·8	535	38·6
Lichen	344	24·8	634	45·7
Litter	392	28·3	217	15·7

$$* \text{ Percentage} = \frac{\text{no. of samples}}{1386} \times 100.$$

Fig. 1 shows a summary of the meteorological records for the Cantwell district. The temperature recordings agree closely with independent, but less complete, records from the reindeer station. The first 4 months of 1970 were characterized by a greater snowfall than that recorded in the same months in 1969. High rates of snowfall in February and March 1970 were associated with higher mean temperatures ($-6·7$ and $-5·6°$) than those recorded for February and March 1969 (-15 and $-9·4°$). Lowest mean temperature (approximately $-22°$) was recorded during the experimental period in January 1970. The area is generally subjected to gusty winds averaging 4–12 m/s but no consistently abnormal wind speeds were recorded in 1969 or 1970. Grazing areas were generally free of snow cover between June and September of each year.

Experimental procedures

Treatment of animals. Reindeer were accustomed previously to handling, blood sampling by jugular puncture and to the experimental regimen. On the day of the experiment all animals were brought in and three animals were held in stalls in an animal house. Isotope experiments (injections or infusions) were started within 45 min and were continued routinely for 3–5 h. After these experiments a second group of three animals was placed in stalls and experiments were commenced within 4 h of yarding. Routine measurements of body-weight and vegetative and climatic conditions were recorded during the experimental periods. Temperature in the animal house was between 5 and 15° in winter and spring, and between 15 and 22° in summer.

For primed infusion experiments, catheters were inserted in one jugular vein 15 min before the experiments began. Isotope was infused through the catheter at a constant rate and the priming dose was given into the opposite jugular vein by venepuncture. Ratios of amount of isotope injected to the amount infused per min were between 81:1 and 119:1. Infusions were made with battery-powered solenoid pumps (Lambda

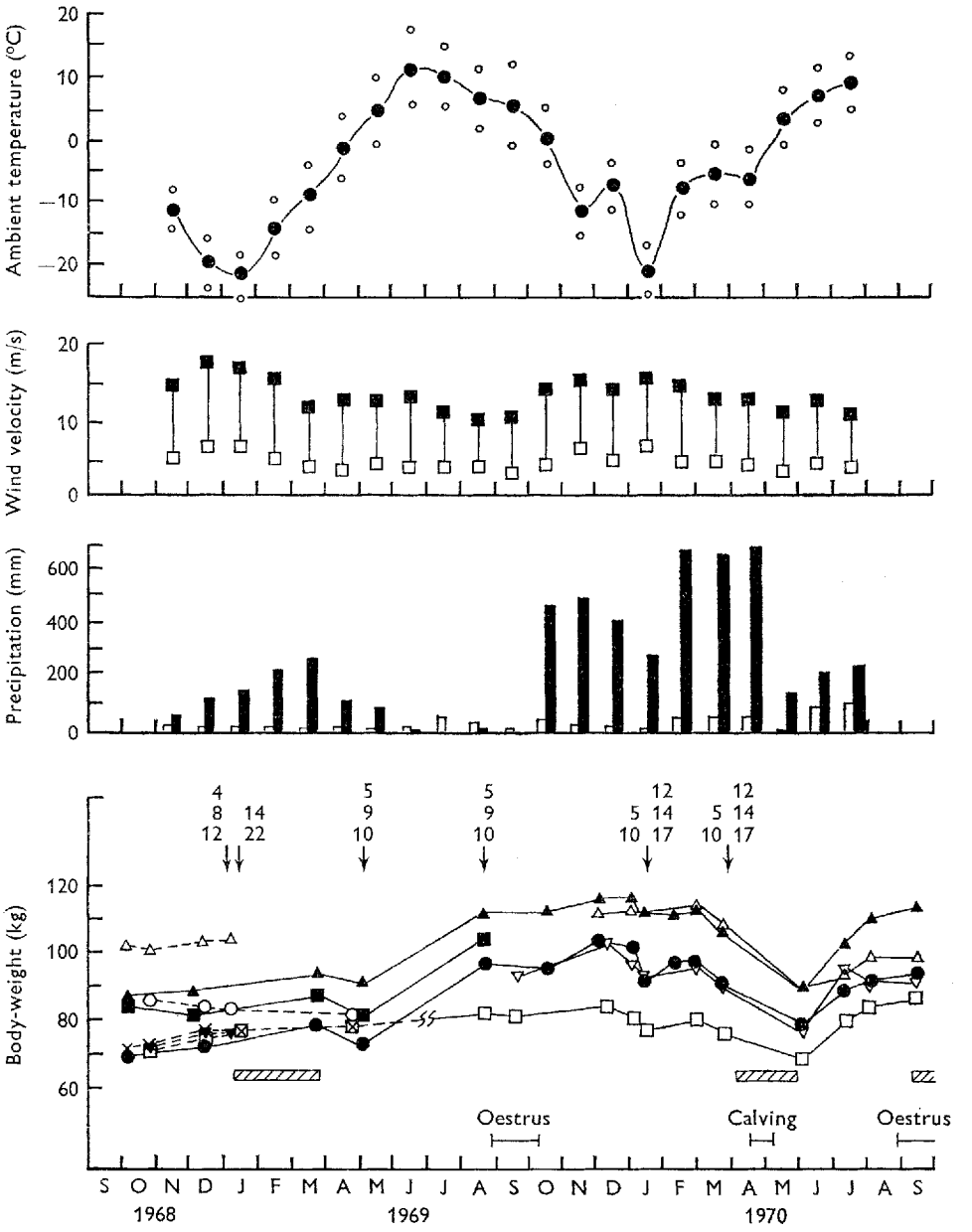

Fig. 1. Summary of climatological data for the Cantwell district (see p. 247). ●, mean monthly average temperature; ○, maximum and minimum temperatures; □, ■, mean monthly average and maximum wind speed; □, ■, mean monthly precipitation as rain and snow respectively; and bodyweight changes in reindeer cows from October 1968 to September 1970. ↓, start of experimental period and animals used; – –, penned animals; —, grazing animals; ▲, △, ●, ○, ■, □, ▽, ×, ▼, individual body-weights for animals numbers 10, 12, 5, 4, 9, 14, 8, 22 and 17 respectively: ▨, supplementary feeding period.

Pump, Harvard Apparatus Co., Mass., USA) that were calibrated before and after each experiment.

In most experiments blood was taken by jugular puncture into evacuated test tubes containing sodium heparin as an anticoagulant. Blood samples were taken 60 min after starting infusions or injections and then at 30 min intervals.

Chemical methods and radioactivity assay. Concentration of reducing sugars in plasma was determined by an automated potassium ferricyanide method (Hoffman, 1937). For twelve samples analysed in duplicate by this method and that of Huggett and Nixon (1957) the difference in the means was $0{\cdot}6 \pm 1{\cdot}0\%$. Glucose was assayed for radioactivity by liquid scintillation counting with a Nuclear Chicago Scintillation Spectrometer (mark I) after isolation as the pentaacetate derivative (Jones, 1965). Recoveries of glucose pentaacetate were approximately 50% of the carrier glucose added.

^{14}C and ^{3}H were assayed separately by dual channel counting; external standardization was used for quench correction.

Radioactive compounds. [U-^{14}C]glucose and [3-^{3}H]glucose were obtained from Amersham/Searle Corp., Des Plaines, Ill., and solutions for infusion and injection were made up in 9 g NaCl/l. Solutions of [^{14}C]- and [^{3}H]-glucose were assayed for radioactivity after preparation of the glucose pentaacetate derivative.

Calculation of results

Glucose transfer rate, pool size and space were calculated according to the method described by Kronfeld, Tombropoulos & Kleiber (1959). A single exponential component was observed between 60 and 300 min after injecting [3-^{3}H]glucose.

Irreversible loss, pool size, and space of glucose were calculated from primed infusion experiments according to the method of Steele, Wall, deBodo & Altszuler (1956) using [U-^{14}C]glucose. If a plateau was not achieved, that is specific radioactivity was increasing or decreasing with time, a plateau specific radioactivity was obtained by extrapolation assuming the asymptote was the product of a single exponential process (see equation 1, Steele *et al.* 1956).

RESULTS

Body-weight changes of grazing reindeer

Fig. 1 shows changes in body-weight of the reindeer during these experiments. All animals were at a peak body-weight during December 1969 and early January 1970; lowest body-weights were recorded in May 1969 and June 1970. All animals exhibited similar trends in body-weight throughout the period of this study.

Estimation of glucose transfer rate and irreversible loss

Dual isotope experiments. Experiments in August 1969 were designed to investigate the feasibility of making simultaneous estimates of glucose transfer rate and irreversible loss of glucose. Estimates of glucose transfer rate invariably exceeded those of irreversible loss of glucose in each reindeer; the mean difference was 4·52 mg/min

Table 2. *Measurement of glucose metabolism estimated with single injection of [3-^{3}H]glucose and primed-infusion of [U-^{14}]glucose in reindeer*

Date	Reindeer No.	Reindeer Wt (kg)	Glucose turnover time (min) ^{3}H	Glucose entry rate (mg/min per kg$^{0.75}$) ^{3}H*	Glucose entry rate (mg/min per kg$^{0.75}$) ^{14}C†	Difference in entry rate (mg/min per kg$^{0.75}$)‡	ΔW (g/d)	Packed cell volume (%)	Plasma glucose concentration (mg/ml)
January 1969 (pen-feeding)	4	83	150	9·30	—	—	−31	49	1·23
	12	103	124	9·50	—	—	0	39	1·02
	14	76	—	—	2·92	—	+5	41	1·13
	12	103	—	—	2·22	—	0	35	0·76
	8	74	—	—	6·21	—	0	—	1·55
	14	—	—	—	5·39	—	—	—	1·08
	22	77	—	—	4·58	—	0	—	1·17
	8	—	159	3·54	—	—	—	38	0·84
	14	—	134	4·81	—	—	—	36	0·98
	22	—	134	6·12	—	—	—	39	1·40
Mean	—	—	140	6·65	4·26	—	—	40	1·12
SEM	—	—	6	1·19	0·75	—	—	2	0·08
May 1969	5	72	113	3·13	—	—	0	—	0·52
	9	80	88	3·68	—	—	0	—	0·53
	10	90	101	2·55	—	—	0	—	0·54
Mean	—	—	101	3·12	—	—	—	—	0·53
SEM	—	—	7	0·33	—	—	—	—	0·01
August 1969	9	104	112	9·26	5·39	3·87	0	40	1·31
	5	96	99	10·72	5·69	5·03	0	39	1·21
	10	111	114	10·00	5·33	4·67	0	36	1·35
Mean	—	—	108	9·99	5·47	4·52	—	38	1·29
SEM	—	—	5	0·42	0·11	0·34	—	1	0·04
January 1970	5	90	121	5·13	—	—	−150	48	1·26
	10	110	115	5·00	—	—	−165	45	1·15
	12	101	110	5·51	—	—	0	44	1·20
	14	77	102	6·71	—	—	−30	50	1·11
	5	90	—	—	1·42	—	−150	41	1·37
	10	110	—	—	2·15	—	−165	45	0·97
	12	101	—	—	1·34	—	0	40	0·99
	14	77	—	—	1·09	—	−30	43	1·30
	17	91	—	—	2·52	—	−100	46	1·40
Mean	—	—	112	5·58	1·70	—	—	45	1·19
SEM	—	—	4	0·39	0·27	—	—	1	0·05
April 1970	5	88	121	6·20	2·81	3·39	−190	48	1·01
	10	104	102	6·83	2·12	4·71	−290	45	0·92
	12	96	99	6·37	3·54	2·83	−290	42	0·87
	14	74	98	7·80	2·85	4·95	−180	43	1·05
	17	87	117	7·16	2·85	4·31	−110	43	1·06
Mean	—	—	107	6·87	2·83	4·04	—	44	0·98
SEM	—	—	5	0·29	0·22	0·40	—	1	0·04

SEM, standard error of mean; ΔW, approximate changes in body-weight during experimental period.

* Glucose transfer rate (total formation). † Rate of irreversible loss of glucose (net formation). ‡ Glucose transfer rate minus irreversible loss (resynthesis).

Table 3. *Estimates of seasonal changes in resynthesis of glucose in grazing reindeer cows; comparisons are made with pen-fed controls*

Date	Glucose transfer rate (mg/min per $kg^{0.75}$) A		Irreversible loss of glucose (mg/min per $kg^{0.75}$) B		Glucose resynthesis (mg/min per $kg^{0.75}$) (A − B)	Glucose resynthesis (%) C	Glucose resynthesis (%) D
	Mean	SE	Mean	SE			
January 1969* (pen-fed controls)	6·65	1·19 (5)	4·26	0·75 (5)	2·39	36	56
May 1969*	3·12	0·33 (3)			—	—	—
August 1969*	9·99	0·42 (3)	5·47	0·11 (3)	4·52	45	83
January 1970*	5·58	0·39 (4)	1·70	0·27 (5)	3·88	70	228
April 1970*	6·87	0·29 (5)	2·83	0·22 (5)	4·04	59	43

A, mean of estimate for single injection of [3-^{3}H]glucose; B, mean of estimates for primed infusion of [U-^{14}C]glucose; C, resynthesis index (A − B) expressed as a percentage of glucose transfer rate; D, resynthesis index (A − B) expressed as a percentage of irreversible loss.

* Combined estimates from Table 2.

per $kg^{0.75}$ or 45% of the transfer rate (Table 2). In a later series of experiments, in April 1970, the same trends were noted and the mean difference was 4·04 mg/min per $kg^{0.75}$ or 59% of the glucose transfer rate (Table 2).

Single isotope experiments. Unfortunately both single injection and primed infusion experiments were not made at all seasons. Where comparisons of these two techniques were made, the responses were similar. Therefore, highest transfer rates and irreversible losses of glucose were noted in August 1969 when the cows were increasing markedly in body-weight. The lowest estimate of glucose transfer rate was noted in May 1969 (Table 3) when cows were at their lowest body-weights (Fig. 1) and glucose concentrations were generally less than half those recorded at other times of the year (see Table 2).

Seasonal changes in both transfer rate and irreversible loss of glucose are shown in Table 3 for both grazing and pen-fed cows. Statistical analysis of these means was by Student's *t* test. Individual mean estimates of glucose transfer rate for grazing cows were not significantly different from the mean for penned cows ($P > 0.05$). Of the mean estimates of glucose transfer rate for grazing cows, those for August 1969 and April 1970 were significantly greater ($P < 0.001$ and $P < 0.01$ respectively) than that for May 1969; the mean transfer rate for January 1970 was significantly less ($P < 0.001$) than that for August 1969.

Only the mean irreversible loss of glucose for January 1970 was significantly different ($P < 0.05$) from that of the pen-fed cows (January 1969). Of the grazing groups, mean values for August 1969 and April 1970 were significantly different from each other ($P < 0.01$) and the former was significantly greater ($P < 0.001$) than the mean for January 1970.

Changes in glucose concentration, pool size and space

Glucose concentration was relatively constant during experiments (CV, 4–26% of mean) and the mean concentrations for these periods are shown in Table 2.

Table 4. *Comparison of estimates of glucose pool size (g) and space (% body-weight) measured with single injections of [3-^{3}H]glucose or simultaneous injection of [3-^{3}H]glucose and primed infusions of [U-^{14}C]glucose*

(Mean values with their standard errors; numbers of observations in parentheses)

Date		Single injection		Primed infusion	Significance of difference between individual paired estimates
		Mean	SE		
January 1969 (pen-fed)	Pool	35·5	2·7 (2)	—	—
	Space	36·5	0·5	—	—
May 1969	Pool	8·4	0·5 (3)	—	—
	Space	19·2	2·0	—	—
August 1969	Pool	35·2	1·9 (3)	30·6 ± 0·5 (3)	NS
	Space	25·9	1·1	22·9 ± 1·5	NS
January 1970	Pool	18·6	0·5 (4)	—	—
	Space	17·0	1·2	—	—
April 1970	Pool	21·5	0·7 (5)	12·3 ± 0·7 (5)	$P<0·01$
	Space	24·5	0·6	13·9 ± 0·7	$P<0·01$

NS, not significant.

Except for results from trials in May 1969, glucose concentration in grazing reindeer exceeded 0·90 mg/ml (Fig. 2). Errors in estimating concentration of glucose (see p. 249) were eliminated as possible influencing factors. Although no strictly controlled experiments have been made to verify our subjective assessment of the docile manner of these reindeer, we have results for two reindeer cows held in metabolism stalls for over 3 months and given lichen containing 3–4% crude protein. These animals were as docile as sheep under similar conditions (White *et al.* 1969), yet the mean glucose concentrations (1·09 and 1·11 mg/ml) were in excess of those for the sheep (0·60 mg/ml; White *et al.* 1969) but were within the range reported for reindeer taken from the field (Table 2).

Mean estimates of glucose pool size and space are shown in Table 4. Seasonal trends in the size of the glucose pool of grazing reindeer were similar to those shown for glucose concentration and were highest in August 1969 (35·2 g) and lowest in May 1969 (8·4 g).

In April 1970 a significant difference was noted between estimates of glucose pool size and space using the two isotope-dilution techniques. In these primed infusion experiments, although the ratio of priming dose to infusion rate was not inordinately high (105:1), a decline in specific radioactivity with time was noted between 30 and approximately 150 min of the infusion. If the intercept of zero time is underestimated, a spuriously low estimate of the size of the glucose pool and space could result. However, we have no evidence for this nor have we any evidence for an overestimate of pool size using the single-injection technique. Thus, for further discussion on the results for April 1970 the mean estimates of glucose pool size (16·9 g) and space (19·2%) for both techniques has been used.

Correlations between criteria of glucose metabolism

A significant linear relationship between irreversible loss of glucose (I, mg/min per $kg^{0.75}$) and glucose transfer rate (T, mg/min per $kg^{0.75}$) was given by

$$I = 0.574\,T - 0.680 \ (r = 0.679,\ 0.05 > P > 0.01). \qquad (1)$$

However, the rate of resynthesis of glucose was not significantly correlated ($P > 0.05$) with glucose transfer rate or irreversible loss. Likewise, no significant relationship ($P > 0.05$) was noted between the rate of resynthesis of glucose expressed as a percentage of the transfer and the transfer rate. These relationships were computed from a total of nine observations, eight on the pooled results where measurements were made in the same animal (August 1969 and April 1970, Table 2) plus one based on group means (January 1970, Table 3).

DISCUSSION

In our studies it was expected that values obtained for measurements of glucose metabolism would reflect those which would be measured in free-grazing reindeer. Lack of suitable automated equipment for taking blood samples throughout the year under the range of climatic conditions experienced by reindeer and caribou at Cantwell limited the freedom given to animals during measurements. However, even though Leng (1970) shows that irreversible loss of glucose declines after feeding, his summarized findings (Leng, 1970, Table 2) indicate it does not decline markedly during the first 5–8 h. Therefore, provided adequate training of animals is undertaken, and provided measurements are made within 5–8 h of being taken from pasture, meaningful measurements of glucose metabolism can be made. The reindeer cows used in the experiment were subjected to routine handling during the 6 month period before the first trials in January 1969. We have only subjective evidence that these reindeer were not unduly excited during the experiments (see *Changes in glucose concentration, pool size and space*, p. 252). The interpretation of results will remain a matter of conjecture until many aspects of the study are confirmed under controlled conditions in an animal house where effects of diet, temperature and pregnancy on glucose metabolism can be investigated.

The many factors which control glucose metabolism by ruminants have been reviewed recently by Ballard *et al.* (1969), Leng (1970) and Lindsay (1970). For comparisons with these and other studies on sheep, measurements of glucose metabolism in reindeer, such as irreversible loss and transfer rate, have been expressed as a function of metabolic body size. Empirical relationships supporting interspecies comparison of glucose entry rate based on body-weight to the 0·75 power have been inferred by Armstrong (1965) and proposed by Ballard *et al.* (1969). Although Kleiber (1961) proposed $kg^{0.75}$ as a factor for comparing metabolic rates of animals in the postabsorptive state within their thermoneutral ranges, it is not at all clear that the relationship holds for feeding animals given varying levels and types of food. Therefore, some of our interpretations may prove inadequate as we learn more of the influence of changing physiological and nutritional states on the metabolism of glucose by reindeer and caribou.

Growth and nutrition of reindeer

The body-weight curves for grazing reindeer as shown in Fig. 1 are similar to previous reports (Druri, 1960; Krebs & Cowan, 1962; McEwan & Wood, 1966; Klein, 1968; McEwan, 1968*a*; Skjenneberg & Slagsvold, 1968) and are characterized by a rapid increase in body-weight in early summer and marked decrease during late winter to early spring. Growth curves of the genus *Rangifer* cannot be interpreted simply in relation to food availability and quality, as even when food of medium-high protein content is made available, reindeer and caribou restrict their intake during winter and their body-weights are maintained about constant (McEwan, 1968*a*). This winter 'growth dormancy' was noted during the January 1969 trials and has been confirmed in reindeer calves at the University of Alaska (White, Luick and Reimers, unpublished observations).

Glucose metabolism in reindeer

Concentration of plasma glucose. The high-glucose concentrations recorded in January 1969 exceed values for blood reducing sugars of 0·59 and 0·71 mg/ml for captive and wild caribou (*Rangifer tarandus*) reported by McEwan (1968*b*). However, the glucose content of reindeer erythrocytes is low (0·18–0·37 mg/ml, White, unpublished observations); so when the concentration of glucose in whole blood reported by McEwan is corrected for erythrocyte(s) dilution, the resultant plasma concentration is within the range now reported.

Concentrations of glucose in plasma of both grazing and penned reindeer are about 1·5 times that of sheep at maintenance (Reid, 1950; Leng, 1970) and are closer to that for tame white-tailed deer (Ullrey, Youatt, Johnson, Fay, Purser, Schoepke & Magee, 1971), horses (Evans, 1971), non-herbivores (Ballard *et al.* 1969), preweaned calves (Webb, Head & Wilcox, 1969) and preweaned lambs (House & Phillips, 1968). The high concentrations of plasma glucose are not associated with inordinately high spaces as has been found for young lambs (Jarrett, Jones & Potter, 1964; House & Phillips, 1968). In reindeer, the glucose pool is distributed in a space of approximately 31% of body-weight, which is within the range of reports of 17–35% for sheep and cattle (see Leng, 1970, Tables 2 and 3). This glucose space is considerably in excess of the extracellular fluid space of 10–19% body-weight in grazing reindeer as measured with $Na_2{}^{35}SO_4$ (Cameron & Luick, 1972). The difference between the volume of distribution of glucose and the extracellular fluid may be due to techniques of estimating glucose space. Recent work has shown that in comparison with estimates based on multi-exponential analysis of the isotope dilution curve, both mono-exponential and primed infusion analyses overestimate glucose pool size and space in sheep (White *et al.* 1969) and cows (Kronfeld, Ramberg & Shames, 1971).

The factors controlling the concentration of plasma glucose in these animals is not known. In other ruminants, several factors may control the level of plasma glucose, for example time after feeding (Leng, 1970), pregnancy (Bergman, 1963) and variation in hormone concentration (Lindsay, 1960) including insulin (Boda, 1964; Kronfeld & Raggi, 1964; Dash & Lindsay, 1967; Kronfeld *et al.* 1971) and catecholamines (Setchell & McClymont, 1955; Bassett, 1970).

The packed cell volumes (PCV) noted in the present experiments are higher than those generally reported for ruminants, but are similar to other reports for domesticated reindeer (McEwan, 1968*b*; Dieterich & Luick, 1971) as well as for some other arctic mammals (Dieterich, 1970). Again we suggest that the generally high PCV is not the result of excitement; many of the present blood samples were taken through jugular catheters and most animals appeared undisturbed by our activity.

Comparison of penned and grazing animals. For the first experiments (i.e. January 1969), reindeer cows were placed in outdoor pens and were offered commercial cattle food *ad lib.* Body-weight records during this period (Fig. 1) suggest that the five cows were regulating their food intake to maintain constant body-weight. The rate of irreversible loss or net formation of glucose averaged 4·26 mg/min per $kg^{0·75}$, and the rate of resynthesis of glucose (2·39 mg/min per $kg^{0·75}$) (Table 3) was 36% of the glucose transfer rate.

Rates of irreversible loss of glucose in these animals may reflect the availability of dietary glucose precursors. Since glucose is being formed over and above this *de novo* rate it is possible that the dietary intake of glucose precursors is insufficient to meet the animal's requirements for glucose. Therefore, glucose carbon could be conserved by recycling, for example through gluconeogenesis from lactate (Annison, Lindsay & White, 1963; Leng, 1970), to satisfy the animal's need for glucose.

Estimates of glucose metabolism in grazing reindeer varied with season of the year. In May 1969, a period of extremely low feed availability, estimates of glucose transfer rate were the lowest recorded for the study (3·12 mg/min per $kg^{0·75}$) and were associated with a low glucose concentration. Unfortunately, the contribution made by resynthesis of glucose during May 1969 could not be calculated, since no estimates were made of the rate of irreversible loss of glucose at this time.

In our studies the rates of irreversible loss, total entry and resynthesis of glucose were high in August 1969 (Table 3) when cows were at, or close to, maximum body-weight (Fig. 1). Food and water were readily available, and limited analyses of typical forage species indicate they are high in protein at this time of year (Klein, 1965; Kubota, Rieger & Lazar, 1970); so the rates of glucose metabolism presumably reflect the high quality of food eaten by the cows.

Associated with the presumed decline in food quality and availability due to an increase in snow depth, body-weight declined, and both irreversible loss and transfer rate of glucose were lower in January 1970 than in the preceding August. In addition, irreversible loss (net formation) of glucose was less than that for reindeer at maintenance in January 1969 (1·70 compared with 4·26 mg/min per $kg^{0·75}$), suggesting that the intake of glucose precursors was insufficient to meet the animals' requirement. In contrast, glucose transfer rate (total formation) was similar to estimates for reindeer at maintenance (5·58 compared with 6·65 mg/min per $kg^{0·75}$), suggesting that an adequate supply of glucose was available for tissue metabolism. The increased availability of glucose was brought about by resynthesis of glucose at approximately 2·3 times the rate of net formation from exogenous (i.e. dietary) precursors.

A similar phenomenon was noted in April 1970 when the plane of nutrition was

probably as low as in January 1970 and a decline in body-weight was noted in all animals. With one exception, in April 1970, the cows were heavier than in the previous May, and all cows were pregnant. Although non-pregnant cows were not available for comparison with the pregnant ones in April 1970, differences between results for May 1969 and those for April 1970 may reflect some of the effects of pregnancy. The differences discussed below could also be due to variations in the quantity and quality of ingested food.

As in January 1970, irreversible loss of glucose in April 1970 (2·83 mg/min per $kg^{0·75}$) was low compared with reindeer at maintenance (4·26 mg/min per $kg^{0·75}$). Although in May no estimate of irreversible loss was made, it could be no greater than the glucose transfer rate (3·12 mg/min per $kg^{0·75}$), which would again indicate a low level of nutrition. In contrast, the mean glucose transfer rate in April 1970 was 6·87 mg/min per $kg^{0·75}$ which is more than twice that recorded for the previous year and 1·5 times that in the preceding January. Steel & Leng (1968) and J. W. Steel (cited by Leng, 1970) have shown that pregnancy *per se* stimulates the rate of irreversible loss of glucose in sheep given a fixed ration. Our results suggest that under conditions of limited food availability and consequent low rates of *de novo* synthesis of glucose, pregnancy may also stimulate a mechanism for conserving glucose carbon, resulting in total synthesis at a rate at least as high as female reindeer at maintenance.

Comparison of the nutrition and glucose metabolism of reindeer and other animals

The rate of irreversible loss or net formation of glucose in penned non-pregnant reindeer cows was similar to estimates of 3·9–4·5 mg/min per $kg^{0·75}$ for penned, non-pregnant sheep at or about maintenance (Bergman, Roe & Kon, 1966; Bergman & Hogue, 1967; Judson, Anderson, Luick & Leng, 1968; White *et al.* 1969), however, our estimate of glucose transfer rate (rate of total formation) (6·65 mg/min per $kg^{0·75}$) was greater than those of Kronfeld & Simesen (1961) and Jarrett *et al.* (1964) measured with [U-^{14}C]glucose in sheep (4·2–6·1 mg/min per $kg^{0·75}$). These latter estimates are probably minimum since they were made between 16 and 24 h after feeding, and the single exponential analysis of the isotope dilution curve using [U-^{14}C]glucose tends to underestimate the rate of total formation of glucose (G. J. Judson and R. A. Leng, personal communication). A more realistic comparison with transfer rate in reindeer may be the estimates of total entry rate of glucose in fed sheep at maintenance (73 mg/min or 4·8 mg/min per $kg^{0·75}$) reported by White *et al.* (1969). Again the estimates are less for sheep than reindeer. Since there is no difference between these species in irreversible loss of glucose, it is concluded that at maintenance reindeer cows resynthesize more glucose than sheep.

Recent work in this laboratory (Cameron, White & Luick, unpublished observations) shows the daily maintenance energy requirement of non-pregnant reindeer held in a winter photoperiod is about 46 KJ/$kg^{0·75}$. Assuming metabolizable energy (ME) is 82% of digestible energy (Blaxter, 1964), the estimated daily maintenance requirement (38 KJ ME/$kg^{0·75}$) is similar to that for penned sheep of 33–39 KJ ME/$kg^{0·75}$

(calculated from the results of Coop, 1962; Langlands, Corbett, McDonald & Pullar, 1963; Langlands, Corbett, McDonald & Reid, 1963). Thus at maintenance, non-pregnant, non-lactating reindeer and sheep have similar intakes of ME and synthesize *de novo* about the same quantities of glucose.

The highest rates of irreversible loss of glucose (5·47 mg/min per $kg^{0·75}$ in August, 1969) probably reflect an intake of food above maintenance. This observation is based on published work showing that the rate of irreversible loss of non-pregnant, non-lactating sheep, is equal to or exceeds 5 mg/min per $kg^{0·75}$ on highly productive rations such as *ad lib.* pelleted lucerne chaff (Kronfeld & Simesen, 1961), 800 g lucerne chaff + 100 g maize (Annison, Brown, Leng, Lindsay & West, 1967) and *ad lib.* pasture + hay + concentrate (Ford, 1963). Recently, it has been shown that the rate of irreversible loss of glucose increases with increasing intake of protein (Ford, 1965; Reilly & Ford, 1971) and digestible energy (Judson & Leng, 1968; Leng, 1970; Lindsay, 1970).

The irreversible loss of glucose estimated for grazing pregnant reindeer cows near term (experiments in April 1970) (mean of 2·83 mg/min per $kg^{0·75}$) is low compared with estimates for pregnant sheep of 4·7 (Bergman, 1963), 3·2 (Ford, 1963) and 4·3–6·7 (Steel & Leng, 1968) mg/min per $kg^{0·75}$. If the foetal requirement for glucose is the same for reindeer as for sheep (6·5 mg/min per $kg^{0·75}$ foetus, Kronfeld, 1958), then the net synthesis in these pregnant reindeer is probably insufficient to meet the maternal and foetal requirement. However, glucose transfer rate of these reindeer cows (6·87 mg/min per $kg^{0·75}$) was within the range of glucose transfer rates reported for normal pregnant sheep 2–4 d before lambing (131–256 mg/min, equivalent to 6·1–10·5 mg/min per $kg^{0·75}$) (Kronfeld & Simesen, 1961) suggesting they were synthesizing enough glucose for normal metabolism. Again, this difference is apparently brought about by resynthesis of glucose from products of glucose metabolism.

Glucose resynthesis has generally been expressed as a fraction of the rate of total formation of glucose. Kronfeld *et al.* (1971) have shown that glucose resynthesis is not increased over control values of 10–22% in response to fasting or insulin treatment of cows. Our studies show that resynthesis varies throughout the year and can be correlated with pregnancy, the nutritional status of the reindeer, or both. Similarly in postabortive humans, glucose resynthesis is only 12–20% of total formation (Reichard, Moury, Hochella, Patterson & Weinhouse, 1963) but increases markedly to 15–41% during fasting (Cahill, Herrera, Morgan, Soeldner, Steinke, Levy, Reichard & Kipnis, 1966). Cahill & Owen (1967) and Cahill (1970) suggest that glucose carbon is conserved during prolonged starvation in man by recycling through lactate and pyruvate in the Cori and alanine cycles respectively. Our tentative suggestion is that in periods of undernutrition in reindeer, pregnancy may stimulate conservation of glucose by resynthesis in one or both of these cycles.

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