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ENERGY FLOW THROUGH THE LICHEN – CARIBOU – WOLF FOOD CHAIN DURING WINTER IN NORTHERN ALASKA

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ABSTRACT

The fallout radiocesium method was used to estimate energy flow through the lichen-caribou-wolf food chain during winter in northern Alaska. Lichen dry matter intake estimated for free-ranging caribou ranged from 3.0 to 7.0 kg/day for an 80 kg caribou. The mean lichen intake rate was 4.9 ± 0.8 kg/day which corresponded to a metabolizable energy intake of approximately 38 MJ/day. Estimates of caribou intake by wolves ranged from 2.2 to 3.1 kg/day of wet muscle for a 40 kg wolf. The mean intake was 2.8 ± 0.2 kg/day or a metabolizable energy intake of approximately 20 MJ/day. The estimated metabolizable energy intakes were compared with expected energy requirements for free-ranging caribou and wolves. Nitrogen, phosphorus and calcium intakes were calculated.

1. INTRODUCTION

The food habits of caribou and wolves in the northern arctic during winter are well known. Throughout winter and early spring, when forage is often in short supply, lichens are consumed extensively by caribou. Winter-killed non-lichen vegetation is consumed, but to a lesser extent (Kelsall 1968). Wolves prey primarily on large ungulates, however small mammals, birds and/or fish may be important supplements (Murie 1944, Kelly 1954, Stephenson and Johnson 1972, Stephensen 1978). Although the qualitative food habits of caribou and wolves are well known, little quantitative data for free-ranging caribou and wolves are available. Estimates of lichen intake by caribou have been made using penned reindeer or caribou (see review in Kelsall 1968) and esophageal fistulated reindeer (Holleman et al. 1979). However, these methods moderate the animals exposure to environmental extremes, i.e. to stresses of cold and wind, predators, and to difficulties in obtaining forages covered with snow or ice. Estimates of prey consumption by free-ranging wolves have been computed for wolf packs of known size by estimating the amount of prey consumed from observed kills and scavenged carcasses (Kolenosky 1972, Mech 1977). The number of prey taken and the actual percent of prey consumed are difficult to measure and therefore, often poorly defined.

This paper reports estimates of food intake or energy flow for free-ranging caribou and wolves as derived from the application of the fallout radiocesium method. The radiocesium method was first proposed by Holleman et al. (1971) and some preliminary lichen intake estimates for caribou were determined. Hanson et al. (1975) applied the radiocesium method to data collected in northern Alaska during 1963–70 and estimated lichen intake by free-ranging caribou. Alldredge et al. (1974) used the fallout radiocesium method to determine forage intake of mule deer. Recently, estimates of food intake for free-ranging caribou (Holleman et al. 1979) and wolves (Holleman and Luick 1978) have been made using the method.

2. METHODS AND RESULTS

The amount of label transferred from a labeled food source to a consumer of that food source is related to the quantity of food consumed. The equation relating the food intake rate (R) to the label body burden of the consumer (Q) may be written as follows:

$$R = Q/(c \cdot a \cdot C_0) \qquad (1)$$

where c equals the concentration of label in the food source, a equals the absorption factor for the ingested label and C_0 equals the in vivo kinetic parameter for the absorbed label. The relationship assumes that both the concentration of label in the food source (c) and the food intake rate (R) remain constant. In the application of the methods, the label body burden of the consumer (Q) and the concentration of label in the food source (c) are measured directly from field samples. The absorption factor (a) and the kinetic parameter (C_0) are determined from controlled experiments. The derivation of equation (1) has been given previously (Holleman et al. 1971).

Eleven adult female caribou and 2 adult male caribou were collected in mid-March 1976 in the Brooks Mountain Range in northern Alaska. Approximately 1-kg samples of skeletal muscle was taken from each animal. Radiocesium concentrations in skeletal muscle ranged from 5950 to 11270 picocuries (pCi)/kg of wet muscle, a mean of 8190 (s = 1690) pCi/kg. The radiocesium body burden of each caribou was calculated using constants derived earlier with 4 reindeer (Holleman et al. 1971), i.e., skeletal muscle equals 41 $\pm$ 0.8% of body weight and the fraction of radiocesium in skeletal muscle was 78.9 $\pm$ 1.2% of the total body burden.

Lichen and other plant samples were collected and radioassayed for radiocesium. The radiocesium concentrations in dry grasses and leaves were less than 0.05 that in lichens while the radiocesium concentrations in older and more slowly growing plant parts such as twigs and buds were about 0.1 that of lichens. Therefore, we assume in our calculations that lichens were the only source of radiocesium in the dietary regimes of reindeer and caribou during winter. Values for the kinetic parameter and the absorption factor were taken from controlled experiments using reindeer (Holleman et al. 1971).

The lichen intake estimate derived from the fallout radiocesium method was 4.9 $\pm$ 0.8 kg/day dry weight for an 80-kg caribou or 61.3 $\pm$ 10 g/day per kg body weight. Lichen intake estimates ranged from 3 to 7 kg/day for an 80-kg caribou.

A total of 14 wolves from 4 different packs were collected in the Brooks Mountain Range in northern Alaska during January and February of 1977 in connection with a wolf control program. Approximately 1 kg of skeletal muscle was taken from each wolf for radiocesium analysis. Radiocesium concentrations in skeletal muscle ranged from 21600 to 31500 pCi/kg wet muscle, a mean of 25800 (s = 2560) pCi/kg. The radiocesium body burden of each wolf was calculated from the radiocesium concentration in skeletal muscle by assuming that 43% of the body weight was skeletal muscle and that 80% of the radiocesium body burden was located in skeletal muscle.

Samples of skeletal muscle were collected during winter from potential prey species of the wolf, including caribou, moose, sheep and snowshoe hares. Radiocesium concentrations in caribou (5950 – 14700 pCi/kg) were high while concentrations in moose (80 – 140 pCi/kg), sheep (300 – 390 pCi/kg) and hares (160 – 460 pCi/kg) were low. In the calculation of prey intake it was assumed that the entire radiocesium body burden of the wolf was derived from ingestion of caribou. Radiocesium kinetic parameters and the absorption factors were taken from earlier controlled experiments on wolves and other arctic carnivores (Holleman and Luick 1976).

The caribou intake estimate using the radiocesium method was 2.8 $\pm$ 0.2 kg/day of wet muscle for a 40 kg wolf – or 70 $\pm$ 5 g/day per kg body weight. Values ranged from 2.2 to 3.1 kg/day for a 40 kg wolf.

The food intake estimates derived from the application of the radiocesium method were used to calculate energy and nutrient values available to free-ranging caribou and wolves during winter (Tab. 1). The daily food and nutrient intakes were expressed on the bases of body weight (80 kg caribou and a 40 kg wolf) and metabolic body weight (body weight$^{0.75}$). Nitrogen, phosphorus and calcium intake were calculated from measured mineral content in lichen or wet muscle and the daily food intake estimate.

3. DISCUSSION AND CONCLUSION

The lichen intake estimate of 4.9 $\pm$ 0.8 kg/day for a 80 kg caribou was significantly greater than previous estimates based on feeding trials (1.4 kg/day) and for esophageal fistulated reindeer (2.9 kg/day) (Holleman et al. 1979). However, intake estimates obtained with pen-fed or tethered, esophageal fistulated reindeer may underestimate the lichen intake for free-ranging caribou since both experimental protocols moderate the animals' exposure to environmental extremes, i.e., stresses of cold and wind, predators, and to difficulties in obtaining forages covered with snow or ice. In contrast, the fallout radiocesium method minimizes disturbances to the animal and its environment and, in this respect, circumvents some of the undesirable features of measurements obtained with pen-fed and fistulated reindeer.

The mean energy content for the most important reindeer and caribou lichen species as measured in March was 19.0 MJ/kg dry weight (Pegau 1969). A reasonable digestibility of lichen is 50% (Cameron 1972). For other ruminants, namely cattle and sheep, approximately 82% of the digested dry matter is metabolizable (Blaxter 1962). Using these data, the metabolizable energy intake (MEI) equivalent to a lichen intake of 4.9 kg/day can be computed as 38 MJ/day or 1.4 MJ/kg$^{0.75}$ per day. The present estimated MEI for free-ranging caribou is 3.5 times the standard fasting energy expenditure of 0.40 MJ/kg$^{0.75}$ per day for caribou (McEwan 1970) and 4.6 times the interspecific mean basal metabolic rate of 0.3 MJ/kg$^{0.75}$ per day (Kleiber 1961). The maintenance metabolizable energy requirement of penned ruminants is approximately 2 times the standard fasting energy

Tab. 1. Estimates of energy and nutrient intakes for free-ranging caribou and wolves during winter in northern Alaska.

	Caribou		Wolves	
Body Weight	80kg		40kg	
Daily Food Intake	4900g(1)	$180 g/kg^{0.75}$(1)	616g(1)	$39 g/kg^{0.75}$(1)
			2800g(2)	$180 g/kg^{0.75}$(2)
Gross Energy	93 MJ	$3.5\ MJ/kg^{0.75}$	24 MJ	$1.5\ MJ/kg^{0.75}$
Metabolizable Energy Intake (MEI)	38 MJ	$1.4\ MJ/kg^{0.75}$	20 MJ	$1.3\ MJ/kg^{0.75}$
Basal Metabolic Rate (BMR)	11 MJ	$0.4\ MJ/kg^{0.75}$	4.6 MJ	$0.29\ MJ/kg^{0.75}$
MEI/BMR	3.5		4.1	
Nitrogen Intake (NI)	17g	$0.64 g/kg^{0.75}$	80g	$5.0 g/kg^{0.75}$
Nitrogen Requirement (NR)	17-29	$0.64\text{-}1.1 g/kg^{0.75}$	30g	$1.9 g/kg^{0.75}$
NI/NR	1.0 - 0.58		2.7	
Phosphorus Intake	1.5g	$0.55 g/kg^{0.75}$	5.0g	$0.31 g/kg^{0.75}$
Calcium Intake	4.0g	$0.15 g/kg^{0.75}$	0.28g	$0.018 g/kg^{0.75}$

(1) Intake estimate in dry matter

(2) Intake estimate in wet matter

expenditure (Brody 1945) while the added energy expenditure for ruminants at pasture has been estimated as 1.5 to 1.6 times the maintenance energy requirements for penned ruminants (Webster 1967, Young and Corbett 1968). Hammel et al. (1962) estimated an energy expenditure for a reindeer pulling a sled to be approximately 4 to 5 times greater than the resting metabolism of the same animal. Therefore a reasonable estimate for the energy expenditure of a free-ranging caribou may be 1.2 to 1.3 $MJ/kg^{0.75}$ per day (3.0 to 3.2 times the standard fasting metabolism). Using data derived from a 70 kg female and male caribou, McEwan and Whitehead (1970) estimated that a grazing caribou would require over 33 MJ of metabolizable energy per day or 1.4 $MJ/kg^{0.75}$ per day. The present lichen intake rate (4.9 kg/d) or MEI (38 MJ/d) exceeds most estimates for energy expenditures for free-ranging reindeer and caribou however most methods to date fail to adequately account for an increase in food intake in response to the energy cost of free existence in extreme environmental conditions of the arctic winter. Further, such a high intake of lichens would support speculations that caribou lose little fat reserves in the first half of winter and that under favorable winter feeding conditions reindeer may actually fatten (Steen 1966, Westerling 1970).

The metabolizable energy of caribou muscle was calculated to be 7.2 MJ/kg wet muscle by assuming: a 10% fat content for muscle, a 30% dry matter content of fat-free wet muscle, an 84% protein content of fat-free dry muscle, a 3% carbohydrate content of fat-free dry muscle and, digestibility coefficients and gross energy values as recommended by the Committee on Animal Nutrition (1974). Using this data, the present estimate of 2.8 kg of caribou per day per 40 kg wolf would equal to a MEI of 20 MJ/day or 1.3 $MJ/kg^{0.75}$ per day.

The maintenance energy requirement for an adult dog as given by the Committee on Animal Nutrition (1974) is 0.553 $MJ/kg^{0.75}$ per day. Working dogs may require 2 to 3 times more energy than would be required for maintenance i.e. 1.1 to 1.7 $MJ/kg^{0.75}$ per day (ibid). In a review of published diets for working dogs in both the Arctic and Antarctic, Orr (1965) concluded that working sled dogs (body weight 38—44 kg) require 13 to 25 MJ/d in order to maintain body weight, morale and efficiency. The present MEI estimate for wolves is within the range of energy requirements given for working dogs during arctic winters.

Nitrogen, phosphorus and calcium intakes for caribou and wolves were computed from the food intake rates and the respective elemental content in their diet, namely lichen or caribou muscle. It is likely that these intake rates are underestimations for free-ranging animals since both caribou and wolves may supplement their diet with food components other than lichen or caribou muscle which have higher nitrogen and/or mineral content, e.g. caribou during winter consume non-lichen vegetation of higher mineral content than lichen. Estimates of the amount of digestible nitrogen required for maintenance for reindeer and/or caribou ranges from 0.46 $gN/kg^{0.75}$ per day (McEwan and Whitehead 1970) to 0.8 $gN/kg^{0.75}$ per day (Cameron 1972). For reindeer and caribou over one year of age, the mean digestibility for nitrogen was 74% (McEwan and Whitehead 1970) resulting in a maintenance intake requirement of 0.64 — 1.1 $gN/kg^{0.75}$ per day. However, extrapolating these data to free-ranging animals may not be valid since the nitrogen requirement for maintenance depend upon the composition of the diet, i.e. increasing amounts of roughages in the diet increase the nitrogen maintenance requirement (Elliott and Topps 1964). Although the data suggest that free-ranging caribou may be in a negative nitrogen balance during winter there are too many uncertainties to permit more than speculation. Mineral intake estimates for free-ranging caribou may be equally questionable not only due to the possible consumption of non-lichen foods but also the possible use of mineral licks by caribou.

The nitrogen and mineral content of lean muscle (Committee on Animal Nutrition 1974) was used to compute the intake estimates for wolves. The ratio of 2.7 for the nitrogen intake to nitrogen requirement suggests that the nitrogen requirements are adequately met for a 40 kg wolf consuming 2.8 kg/day of lean muscle. The phosphorus and calcium intakes were substantially lower than the requirements of 9 g/day and 11 g/d, respectively (ibid). However, it would be questionable to conclude that a phosphorus or calcium deficiency exist, since wolves consume bone and other tissues having high mineral content.

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