# RUMEN FUNCTION AND ENERGY PRODUCTION OF MOOSE IN INTERIOR ALASKA

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Abstract: Variations in seasonal characteristics of rumino-reticular contents were analysed in a preliminary study to evaluate nutritional status and estimate energy production of moose from Interior Alaska. Weight, percent dry matter, pH, botanical and nutrient composition of rumino-reticular contents from several moose were measured. Production rates of volatile fatty acids (VFA) were measured using two different incubation techniques. Molar proportions of individual VFA's were determined.

VFA production rate per milliliter of rumen liquor was higher in four moose collected in early summer (May ) than in one moose collected in early winter (October). However, greater rumen volume of moose in winter resulted in similar VFA production rates per animal during summer and winter. Energy derived from VFA production ranged from 68 to 136 percent of theoretical basal metabolic rate.

Botanical and nutrient composition of rumino-reticular contents and molar proportions of individual VFA's supported the hypothesis that higher quality food was consumed during summer than during winter.

As the management of wildlife species becomes more intensive, the study of wildlife nutrition becomes more critical. Food habits data were once the only food resource information considered important. However, while useful in many respects, certain deficiencies in this approach have promoted studies of greater scope to better understand relationships between wild herbivores and their food resources. Wildlife nutrition must be concerned not only with availability and utilization of forage species, but also with the ability of herbivores to convert plant to animal tissue. For example, ungulates consuming high quality diets grow larger, are more vigorous and healthy, and usually have higher rates of reproduction and lower rates of mortality than those consuming low quality diets.

Numerous and diverse techniques for investigating nutritional aspects of wild ungulates have been recently reviewed (Abrams, 1968; Bruggemann, et al., 1968; Van Dyne, 1968; Korschgen, 1969; Regelin, 1969; USDA, 1970). Basically, these nutritional studies have dealt with botanical, chemical, and microbial composition of rumen (and/or fecal) contents, observations of food consumed by wild and tame animals, in vitro and in vivo digestion of forage species, and use of whole rumen contents to estimate overall rumen function.

Whole rumen contents are probably best suited for evaluating total rumen activity, since they contain microorganisms, forage, and endproducts of fermentation. Volatile fatty acids (VFA) are important endproducts of microbial fermentation which provide the major energy source for ruminant species (Carroll and Hungate, 1954; Bergman, et al., 1965; Gray, et al., 1967). The concentration of VFA's in rumino-reticular (R-R) contents at any given

time is determined by the rate of microbial fermentation and by the rate of VFA passage from the rumen to the blood.

Seasonal changes in microbial populations and fermentation endproducts of wild species seem largely due to variations in the physical nature and nutrient composition of the diet (Kistner, 1965; Pearson, 1965; Warner, 1965; Hungate, 1966). Other factors affecting rumen microbes and their endproducts are amount and time of food intake, adaptation of the animal to its environment, climatic conditions, and physiological status of the animal.

Changes in VFA concentration reflect the availability and nutritive value of forage and have been recorded for several wild ruminants (Ullrey, et al., 1964, 1969; Short, et al., 1966, 1969; Nagy, et al., 1967). However, rates of VFA production, reflecting the rate at which energy is produced from ingested forage and the relative contribution of fermentation endproducts to the energetic needs of the ruminant, have been reported for few wild species (Hungate, et al., 1959). Both concentration and production of VFA's in domestic ruminants of economic importance have been studied and these studies have been reviewed by Church (1970).

The purpose of this study was to develop a useful and reliable field sampling technique for determining VFA production rates in wild ruminants and to relate preliminary measurements on moose to the type and quality of forage consumed.

## STUDY AREA

The Tanana Flats study area, located south of Fairbanks, Alaska, is an alluvial lowland bounded on the south by the Alaska Range, on the north and east by the Tanana River, and on the west by the Wood River. This study area is approximately 3400 square kilometers (1300 square miles) in size with little relief, and is underlain by permafrost of varying thickness (Black, 1958). Drainage is poor, resulting in numerous small, shallow ponds, extensive bogs, and old, dry stream beds.

Regional vegetation types have been strongly affected by permafrost and drainage patterns (Lutz, 1956; Viereck, 1970). Black spruce (Picea mariana), larch (Larix laricina), and various ericaceous and bog species occur on the poorly drained areas, while stands of white spruce (P. glauca), paper birch (Betula papyrifera), and quaking aspen (Populus tremuloides) are restricted to the relatively well-drained soils. Willow (Salix spp.) and alder (Alnus spp.) occur throughout the area but are most abundant along ponds and water courses.

## METHODS

Five female adult moose were collected by shooting from a helicopter in May and one female adult and one female calf were collected by shooting from the ground in October and February, respectively. VFA production rates were determined for the above moose as well as for a captive fistulated reindeer by the "zero time rate method" described

by Carroll and Hungate (1954) and modified by Gasaway (unpublished data). The procedure involves *in vitro* incubation of a R-R content sample under conditions approximating those in the rumen as closely as possible. Isolation of the R-R sample prevents absorption of bacterial endproducts while allowing fermentation to continue for a period of time (Hungate, 1966). Subsamples were collected at intervals for total VFA determination.

The "zero time rate method" was also applied to three of the above moose by "subsampling" directly from the total R-R contents *in situ*.

The pH of isolated samples and of R-R contents *in situ* was monitored using pH paper. Samples of mixed R-R contents were collected for dry matter determination.

Body weights of moose killed in May were determined with a spring scale attached to a helicopter. Body weight of the moose killed in February was measured with a spring scale attached to a tripod, while that of the moose killed in October was estimated from heart girth measurements. Weights of R-R contents were determined by weighing in a large plastic bag attached to a spring scale.

After collection by stream distillation, total VFA's were determined by a modified titration technique using 0.01 N sodium hydroxide (Gray and Stevens, 1966). Individual VFA's were identified by gas:liquid chromatography. Percent dry matter of R-R contents was determined by lyophilization to constant weight.

Proximate analyses of washed R-R contents retained by a 9.423 mm opening sieve were performed by WARF Institute, Inc., Madison, Wisconsin. Hungate (1966) reports that most microflora are not closely associated with large plant fibers and therefore the washed material was

considered to be representative of forage consumed (see Klein and Schønheyder, 1970). Botanical composition of one liter samples of R-R contents was determined by a technique of macroscopic examination (Cushwa, et al., unpublished ms.).

All linear regression lines fitted to VFA production rates were compared by analysis of covariance. The null hypothesis was rejected at a probability level of 0.05.

## RESULTS

1. VFA Production Rate:

VFA production rates determined from isolated in vitro samples were significantly greater in four moose killed during May (Figure 1) than in one moose killed in October (Figure 2). Initial concentration of VFA's extrapolated to time of death were not significantly different among the five animals. VFA production rates were not significantly different among the four moose killed during May.

The duration of in vitro subsampling was extended from approximately 30 minutes in May (Figure 1) to approximately 240 minutes in October (Figure 2) to increase accuracy of estimating VFA production rates. The production rate remained relatively linear for 140 minutes after death, after which linearity appeared to decrease as acidity increased (Figure 2). PH of R-R content samples remained stable at six during subsampling from all moose in May (Figure 1), but began to decrease from six to five approximately two hours after death of the animals in October (Figure 2). Linearity of the VFA production rate was also maintained for approximately 120 to 140 minutes in the R-R sample obtained from the fistulated reindeer

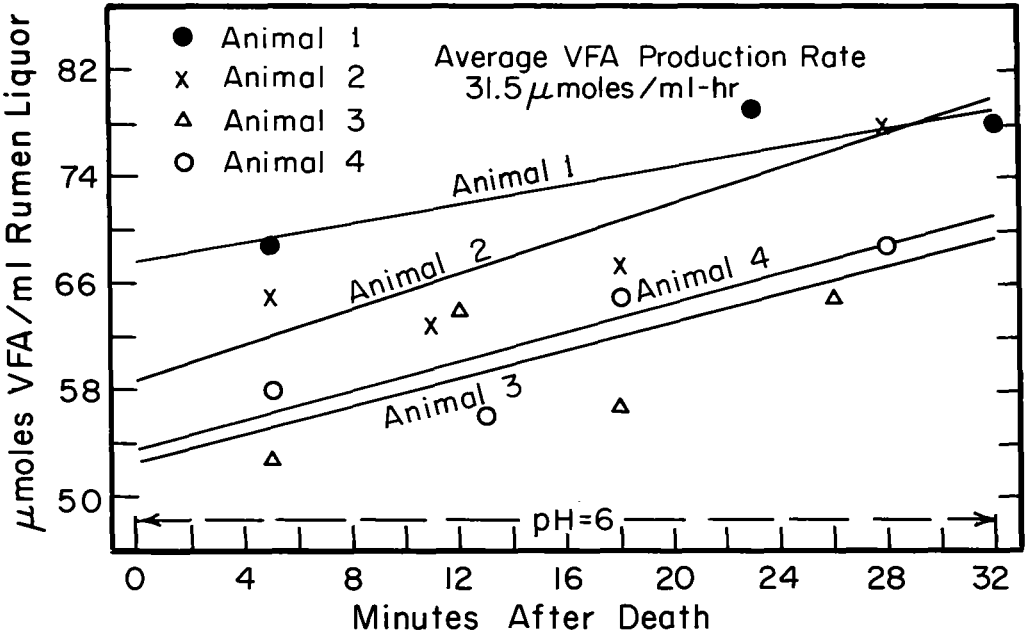


Figure 1. IN VITRO VFA PRODUCTION RATE IN R-R CONTENTS OF FOUR MOOSE COLLECTED DURING MAY

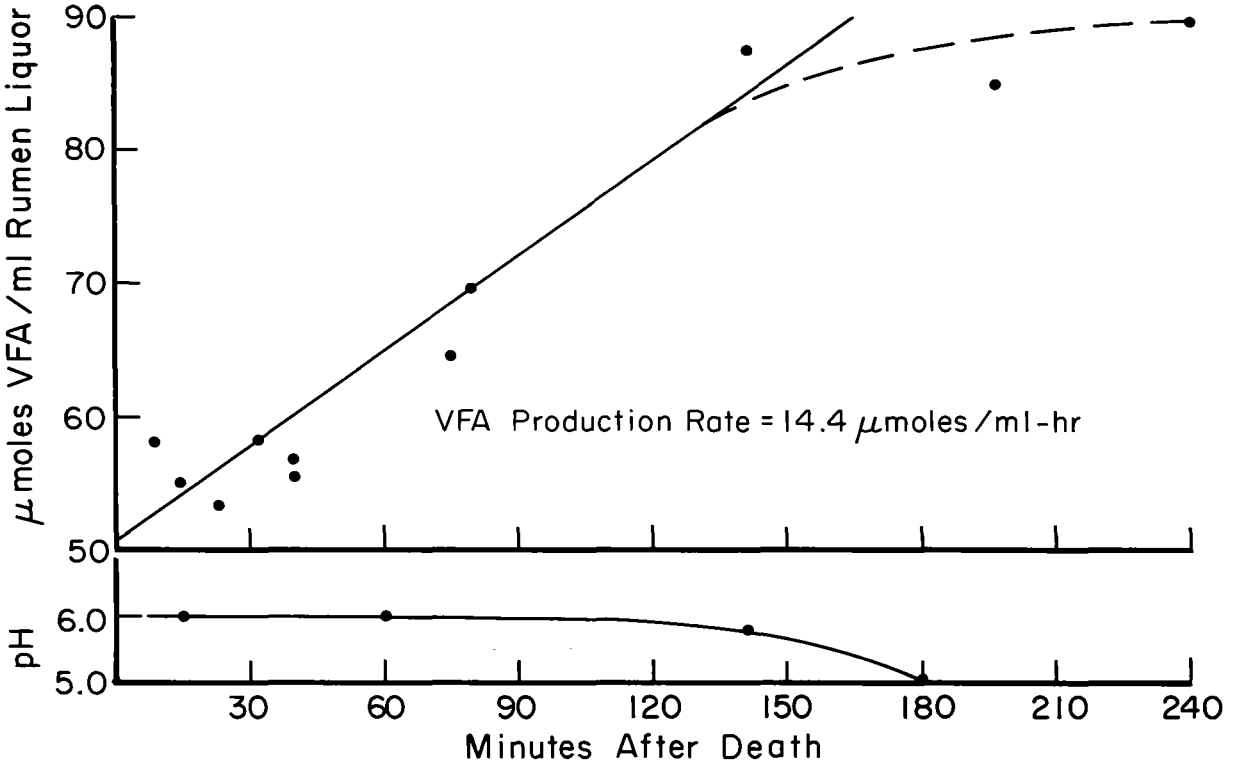


Figure 2. IN VITRO VFA PRODUCTION RATE IN R-R CONTENTS OF ONE MOOSE COLLECTED IN OCTOBER

(Figure 3).

Zero (February and May) or negative (October) VFA production rates were obtained from three moose in which "subsamples" were collected directly from R-R contents *in situ* (Figure 4). The moose subsampled in May was killed on the same day and in the same area as four others showing a positive production rate (cf. Figure 1), while the animal subsampled in October was the same individual from which positive production rates were obtained from R-R samples isolated *in vitro* (cf. Figure 2). PH of R-R content samples *in situ* of all three moose remained near six.

2. VFA Molar Proportions:

Only molar proportions of individual VFA's from the moose killed in February and one moose killed in May have been analysed (Table 1).

Table 1: MOLAR PROPORTIONS OF INDIVIDUAL VFA'S IN R-R LIQUOR FROM MOOSE COLLECTED DURING FEBRUARY AND MAY

| Month of Kill | Acetate | Propionate | Butyrate | Others |
|---|---|---|---|---|
| February | 74.3 | 16.9 | 7.5 | 1.3 |
| May (#3) | 67.0 | 21.3 | 11.1 | 0.6 |
| (#1) | 69.7 | 20.4 | 8.9 | -- |
| (#2) | 78.3 | 14.9 | 6.9 | -- |
| (#4) | 75.8 | 16.1 | 7.8 | -- |
| (#5) | 74.5 | 15.8 | 8.0 | -- |

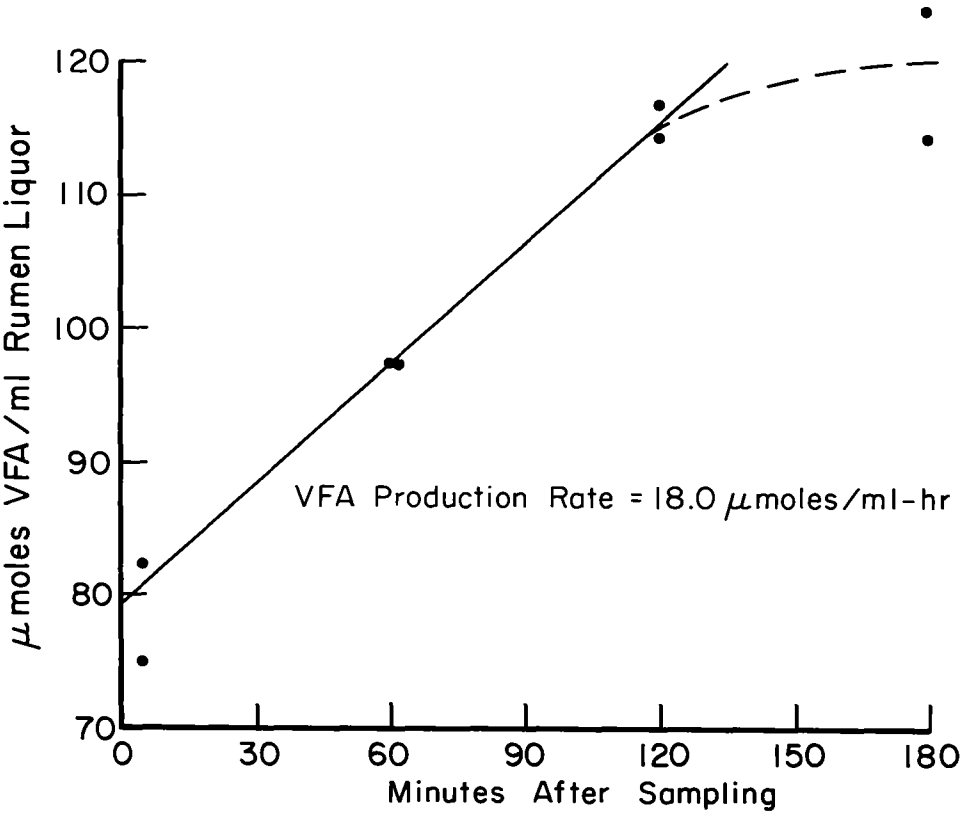


Figure 3. IN VITRO VFA PRODUCTION RATE IN R-R CONTENTS OF CAPTIVE REINDEER

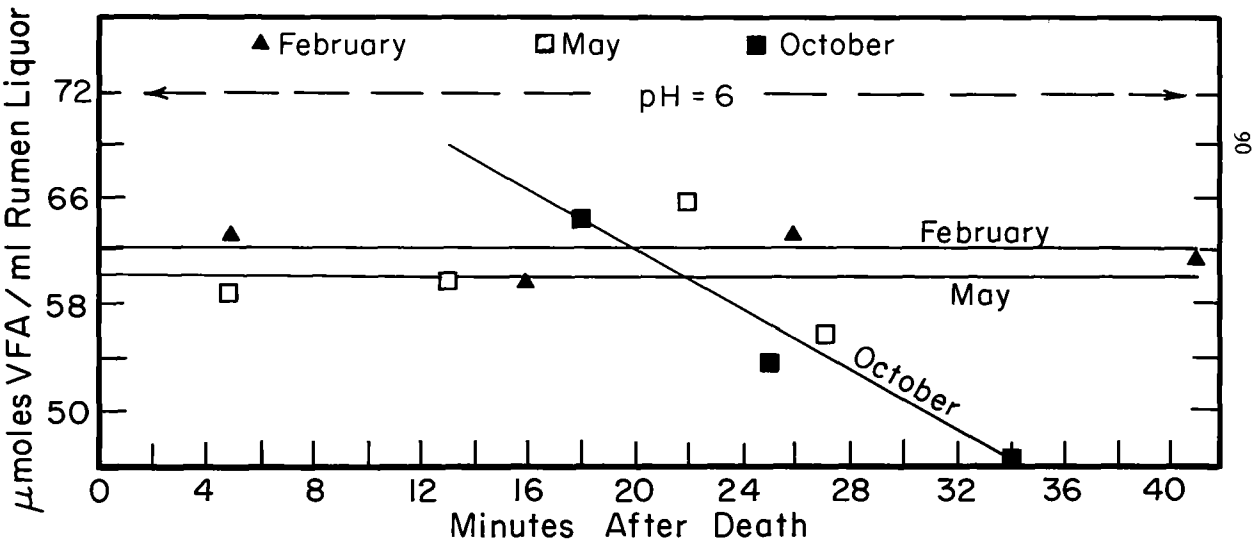


Figure 4. IN SITU VFA PRODUCTION RATES IN R-R CONTENTS OF MOOSE COLLECTED DURING FEBRUARY, MAY AND OCTOBER

The moose collected in May had a lower proportion of acetate and higher proportions of propionate and butyrate than did the animal killed in February.

3. Nutrient and Botanical Analysis of R-R Contents:

Proximate analysis was performed on washed R-R contents from four of the five moose collected in May and from the one moose collected in October, as well as from five animals killed accidentally on highways near Fairbanks in February (Table 2).

Table 2: AVERAGE AND ONE STANDARD DEVIATION OF CRUDE PROTEIN, FIBER AND FAT OF WASHED R-R CONTENTS FROM MOOSE KILLED DURING THREE MONTHS

| Month of Kill | No. of Samples | Protein | Fiber | Fat |
|---|---|---|---|---|
| October | 1 | 7.5 | 46.6 | 3.5 |
| February | 5 | 6.3 $\pm$ 0.97 | 46.6 $\pm$ 2.54 | 3.1 $\pm$ 1.56 |
| May | 4 | 10.0 $\pm$ 2.03 | 35.6 $\pm$ 2.36 | 4.3 $\pm$ 0.36 |

Protein and fat were higher and fiber was lower in washed R-R contents from moose killed during May than from moose killed during October or February.

Botanical analysis of rumen samples indicated that animals in May were beginning to feed on succulent forage while those in February and October were feeding largely on woody browse.

4. R-R Content Weight and Percent Dry Matter:

R-R content weight and percent dry matter were determined from moose collected for VFA studies and from animals killed accidentally on highways near Fairbanks during February (Table 3). Both the average weight of R-R contents as a percent of body weight and the percent dry matter in R-R contents were greater from animals killed during October and February than from those killed during May.

## DISCUSSION

1. In Vitro versus In Situ Incubation Techniques:

As might be imagined, a number of methods have been utilized to measure VFA concentration and production. Since rumen absorption of VFA's is thought to stop at death (Olson, 1969), it was assumed that direct "subsampling" from R-R contents in situ would be a simple and valid technique for measuring VFA concentration and production rate. However, comparison of results using the in situ and the in vitro incubation techniques on moose killed during May and especially during October, when both techniques were used with R-R contents from the same individual, illustrates that difficulties are associated with measuring VFA production in R-R contents incubated in situ.

It seems unlikely that any appreciable passage of VFA's from the rumen would occur after death, since circulation would be curtailed.

Table 3: BODY AND R-R CONTENT WEIGHTS OF MOOSE

COLLECTED DURING THREE MONTHS

| Month of Kill [1] | Sex, Age | Body wt. (kg) | R-R Content Wt. (kg) | % R-R Contents of Body wt. | % Dry Matter in R-R Contents |
|---|---|---|---|---|---|
| October | ♀Adult | 408[2] | 59 | 14.5 | 18.7 |
| February | ♀Calf | 154 | -- | ---- | ---- |
| | ♀Yearl | 186 | 32 | 17.2 | ---- |
| | ♂Adult | 363 | 54 | 14.8 | 17.3 |
| | ♀Adult | 379 | 58 | 15.2 | 17.8 |
| | | | | $\bar{x}$=15.7±1.29 | $\bar{x}$=17.6±0.35 |
| May | ♀Adult (#1) | 340 | 30 | 8.7 | 14.3 |
| | ♀Adult (#2) | 329 | 34 | 10.2 | 12.0 |
| | ♀Adult (#3) | 295 | 28 | 9.5 | 12.5 |
| | ♀Adult (#4) | 386 | 25 | 6.5 | 11.9 |
| | ♀Adult (#5) | 351 | -- | ---- | 14.1 |
| | | | | $\bar{x}$=8.7±1.60 | $\bar{x}$=13.0+1.16 |

[1] All moose were collected for VFA studies except for one yearling and two adults, which were accidentally killed on highways in February.

[2] Weight estimated from heart girth measurements.

Apparently either VFA metabolism was altered or eliminated in the rumen-reticulum immediately post mortum or our technique for "subsampling" and/or quantifying total VFA's in R-R contents incubated in situ was inadequate.

Since VFA concentration is related to the rate of VFA production (Church, 1970), workers have measured VFA concentration in R-R contents of dead ruminants as an index of fermentation rate (Short, et al., 1966; Nagy and Williams, 1969). However, results presented in this report suggest that studies utilizing VFA measurements from in situ R-R contents should be interpreted with caution until aspects of post mortum microbial fermentation and VFA metabolism are better understood.

2. VFA Production Rates versus Forage Quality:

Initial concentration of VFA's in R-R contents of moose killed in October, February and May were not significantly different. Rates of VFA production in R-R samples incubated in vitro did, however, reflect seasonal and/or dietary changes. High rates of VFA production in moose killed in May (Figure 1) were associated with high protein and low fiber in the diet (Table 2), while low rates of VFA production in the moose killed in October (Figure 2) were related to low protein and fat and high fiber in the diet (Table 2). The decrease in R-R VFA production rate in moose (Figure 2) and reindeer (Figure 3) after approximately two hours is presumably related to a decrease in R-R pH at this time, since small changes in pH can greatly alter the pattern of microbial fermentation (Hungate, 1966).

As was indicated previously, the quantity of VFA's present in

the R-R contents is a reflection of microbial activity, and this activity is affected primarily by the quality of forage and the amount of and time since food was consumed. Relatively frequent feeding by moose during daylight hours (see LeResche and David, 1971) and rumination during inactive periods, especially coarse, fibrous material, probably tends to reduce, although certainly not eliminate, diurnal variation in microbial activity. Short, et al. (1969a), found only minor diurnal fluctuations in R-R VFA concentration in white-tailed deer. Therefore, time of collection is probably not a major source of variation in VFA concentration in this study.

Studies and reviews by Klein (1962, 1964, 1968, 1970) leave little doubt as to the positive influence of high protein, low fiber diets on the productivity and survival of wild ruminants. The effects of different diets on VFA concentration in R-R contents of wild ruminants have been studied by many workers (Short, 1963; Short, et al., 1967). These studies, unlike results presented here, indicate that high concentration of VFA's in the R-R contents are positively correlated with forage quality. Our results do agree, however, with studies of domestic ruminants indicating greater VFA production rates in animals with increasing protein and/or decreasing fiber in the diet (see Church, 1970).

3. Nature of R-R Contents versus Forage Quality:

The ratio of R-R content weight to total body weight appears to be primarily a function of stomach fill and percent dry matter in the R-R contents. Both larger R-R contents and higher percent dry matter found in

moose killed in October and February compared with those killed in May (Table 2) were apparently related to the high proportion of fibrous, low digestible material in the diet, and subsequent greater retention time in the rumen (Hungate, 1966). Short, et al. (1966) found a lower proportion of dry matter in R-R contents of mule deer killed during late spring and summer than during late fall and winter. This was apparently related to the greater digestibility of the summer forage.

4. Total VFA Production:

Although there has been an appreciable amount of research relating to the production of VFA's by domestic ruminants fed various diets, almost no information of this nature exists for wild species. Aside from academic interest in the subject, it is useful to know the relative contribution of VFA's to the energetic needs of ruminants.

The total contribution of VFA's to the energy requirements of ruminants depends on the molar proportions and production rates per milliliter of R-R liquor, and on the total amount of R-R liquor. Rates of VFA production in moose during May and October (Figures 1 and 2) and total rumen liquor calculated from total R-R content weight and percent dry matter (Table 2) can be used to calculate the total energy produced by VFA's.

Caloric equivalents for individual VFA's are: acetate, 209.4 Kcal/mole; propionate, 367.2 Kcal/mole; and butyrate, 524.3 Kcal/mole. Molar proportions of individual VFA's from one moose killed in May (Table 1) were used in calculations for all four animals from that month, while molar proportions of individual VFA's from the moose killed in February (Table 1) were used in calculations for the animal killed in October.

Theoretical basal metabolic rate (BMR) was calculated from the equation given by Kleibur (1961), where BMR - 70 (body weight in kg) 3/4. The total contribution of VFA's to theoretical BMR was estimated.

A sample calculation of total VFA production and its contribution to theoretical BMR of the moose killed in October is given below:

Total R-R Content Weight (Table 2) = 59.0 kg
% Dry Matter of R-R Contents (Table 2) = 18.7%
Thus, Total R-R Liquor = 47.97 kg

VFA Production Rate (Figure 2) = 14.4 moles/ml-hr

Total VFA Production Rate =

$$\frac{14.4 \text{ moles}}{\text{ml-hr}} \times 47970 \text{ ml} = 690770 \text{ moles/hr}$$

$$= 16.57 \text{ moles/day}$$

Molar Proportions of Individual VFA's (Table 1):

Acetate = 74.3
Propionate = 16.9
Butyrate (plus Others) = 8.8

Total Proportion of Individual VFA's in R-R Liquor =

Acetate = (0.734)(16.57 moles/day) = 12.15 moles/day
Propionate = (0.169)(16.57 moles/day) = 2.80 moles/day
Butyrate (plus Others) = (0.088)(16.57 moles/day) = 1.62 moles/day

Total Caloric Value of Individual VFA's =

Acetate = (12.15 moles/day)(209.4 Kcal/day) = 2544.2 Kcal/day
Propionate = ( 2.80 moles/day)(367.2 Kcal/day) = 1028.2 Kcal/day
Butyrate (plus Others) = ( 1.62 moles/day)(524.3 Kcal/day) = 849.4 Kcal/day

Total Energy from VFA Production = 4421.8 Kcal/day

Theoretical BMR = 70 (W) 3/4 = 70 (408 kg) 3/4 = 70 (90.8) = 6356 Kcal/day

Thus, total VFA contribution to theoretical BMR $= \frac{4421.8}{6356} = 70\%$

Total VFA energy production and its contribution to the theoretical BMR of moose was not significantly different between animals killed in October and those killed in May (Table 4). However, larger sample sizes would very likely reveal seasonal differences in total production.

Table 4: TOTAL VFA ENERGY PRODUCTION AND ITS CONTRIBUTION TO THEORETICAL BMR OF MOOSE COLLECTED DURING TWO MONTHS

| Month of Kill | Total Energy Derived from VFA Production (Kcal/day) | Theoretical BMR (Kcal/day) | VFA Contribution to Theoretical BMR (%) |
|---|---|---|---|
| October | 4421.8 | 6356 | 70 |
| May (#1) | 3765.9 | 5544 | 68 |
| (#2) | 7356.9 | 5407 | 136 |
| (#3) | 5264.7 | 4984 | 106 |
| (#4) | 4877.9 | 6083 | 80 |

Although BMR clearly underestimates energy requirements for free-ranging ruminants by 25 to 100% (Brody, 1945; Blaxter, 1962), estimates of VFA contribution to theoretical BMR nevertheless indicate, in general terms, whether the animal is in negative or positive energy balance and the magnitude of that balance. Since VFA's are the major source of energy to ruminants (Carroll and Hungate, 1954; Church, 1970), their relative contribution to the energetic needs of the ruminant largely reflect the overall nutritional status and physiological conditions of the animal. Additional energy is obtained by assimilation of

unformented material through the abomasum and small intestine.

## SUMMARY

1. VFA production rates were measured in moose collected during February, May, and October using the "zero time rate method". Zero or negative production rates were obtained from R-R contents incubated *in situ*, whereas positive production rates were obtained from R-R contents incubated *in vitro*. Unknown difficulties associated with *in situ* incubation of R-R material should be resolved before it can be used confidently in VFA measurements.

2. Average VFA production rates in four moose collected in May and one moose collected in October were 31.5 and 14.4 moles per ml of R-R liquor per hour, respectively.

3. R-R content weight and percent dry matter were greater in moose killed in October and February than in May.

4. Seasonal differences in production rates and molar proportions of VFA's as well as in the physical nature of the R-R material were related to the nutrient and botanical composition of the forage. Protein was higher and fiber was lower in washed R-R contents from moose killed in May than from moose killed in October or February.

5. The relative contribution of VFA's to the energy requirements of moose was estimated to range between 68 and 136 percent of the theoretical BMR. Since VFA's represent the major source of energy to ruminants, estimates of VFA contribution to the energy budget of ruminants are useful as a measure of the nutritional and energetic status of those animals.

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