Predicting energy expenditures for activities of caribou from heart rates

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Abstract: Highly significant (P<0.001) linear relationships between oxygen comsumption (VO_2) and heart rate (HR) were found for six caribou (*Rangifer tarandus granti*) at several times during the year. The standard error of the estimate for predicting VO_2 from HR was within 10% of the mean VO_2 for 9 of 13 caribou/season combinations. Energy expenditures by caribou while feeding on grain at a trough, grazing, browsing and walking within a large enclosure were 12%, 17%, 18% and 46% higher than the cost of standing. HR's recorded during a given activity decreased sharply during September and October, and reached a minimum in January. An abrupt increase in HR's of female caribou occurred 3 weeks prior to parturition. Heart rate telemetry can be used to determine the relative energy expenditures of free-ranging caribou with reasonable accuracy.

Key words: caribou, oxygen consumption, heart rate, metabolic rate, *Rangifer tarandus*, energetics

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Introduction

Measurements of energy expenditures by large animals are frequently made using closely-confined animals encumbered by equipment that restricts their behavior. Development of the CO_2 entry rate technique (Young *et al.*, 1969) and the doubly labeled water method (Lifson *et al.*, 1955) provided the methodology for estimating energy expenditures by free-ranging animals, but these methods are complex and expensive. Heart rate is common used to estimate energy costs by humans because it is easily measured and the measurements do not interfere with the subject's normal acitivites (Bradfield *et al.*, 1969; Acheson *et al.*, 1980). Some investigators working with ruminants have found poor agreement between heart rate and energy expenditure; the relationship is known to be affected by individual differences, season, time since the last feeding, type of activity, ambient temperature, excitement or stress, and other factors (Webster, 1967; Brockway and McEwan, 1969; Johnson and Gessaman, 1973; Holter *et al.*, 1975, 1976; Robbins *et al.*, 1979). However, other researchers, by controlling some of these factors, established relationships which predicted energy expenditure within 10% for individually-calibrated animals (Yamamoto *et al.*, 1979; Pauls *et al.*, 1981; Renecker and Hudson, 1983; Nilssen *et al.*, 1984; Richards and Lawrence, 1984; Fancy and White, 1985a). We investigated the heart rate/energy expenditure relationship for six caribou (*Rangifer tarandus granti*) throughout the annual cycle and used heart rate to estimate energy expenditures for activities as the caribou ranged within a large enclosure. Energy expenditures of caribou while cratering in snow are reported elsewhere (Fancy and White, 1985a).

Methods

Hand-raised caribou were kept within a 19-ha enclosure at the University of Alaska Large Animal Research Station in Fairbanks, Alaska, where they had *ad libitum* access to natural forage and a commercial livestock ration (Quality Texture, Fisher Mills, Seattle, WA). At the time of the experiments, the caribou were 16 - 35 months of age and weighed between 85 and 123 kg. A heart rate transmitter (J. Stuart Enterprises, Grass Valley, CA; see Follmann *et al.* (1982) for transmitter design) was implanted subcutaneously on either side of each caribou adjacent and approximately parallel to the sixth rib. The pulsed signals were received by a Telonics (Mesa, AZ) TR-2 receiver and were either plotted on a chart recorder or counted directly.

The relationship between O_2 consumption (VO_2, l·min^{-1}) and heart rate (HR, beats·min^{-1}) was determined for each caribou at several times during the annual cycle using an open-circuit respirometry system (Fancy, 1986). VO_2 and HR were measured concurrently once the caribou reached a steady state of O_2 consumption (i.e., when the rate of O_2 consumption was relatively constant) while walking or standing on a treadmill, or while standing in a respiration chamber. Caribou were taken directly from the enclosure prior to measurements.

Data from trials on the same caribou conducted within a 4 - 5 week period were combined to develop regression equations predicting VO_2 from HR for that season. These equations were then used to estimate VO_2 from HR of each caribou at the same time of year as
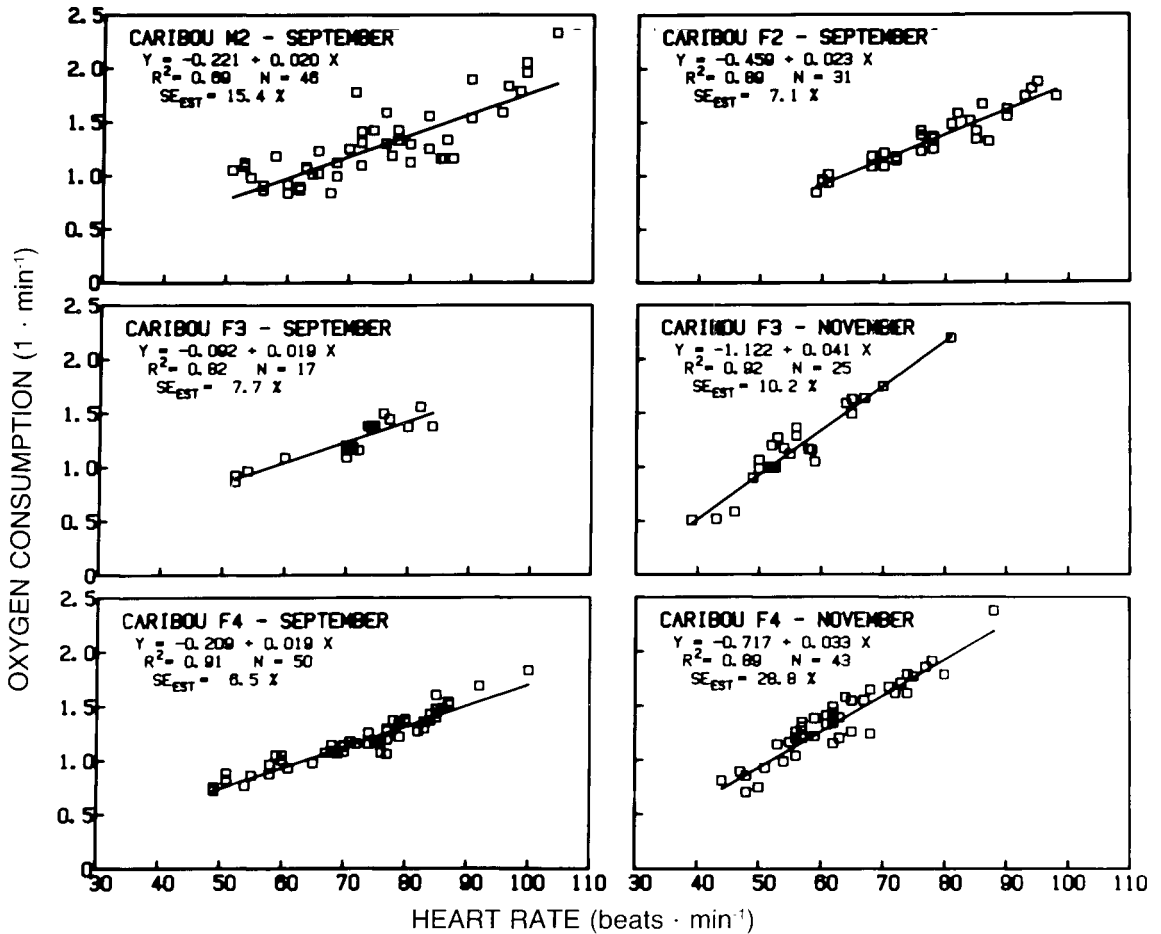

Fig. 1. Regressions of O_2 consumption on heart rate for caribou in late summer (September) and early winter (November). Data were collected while the caribou were standing or walking. The standard error of the estimate is for a new observation at the mean HR, expressed as a percentage of the mean O_2 consumption.
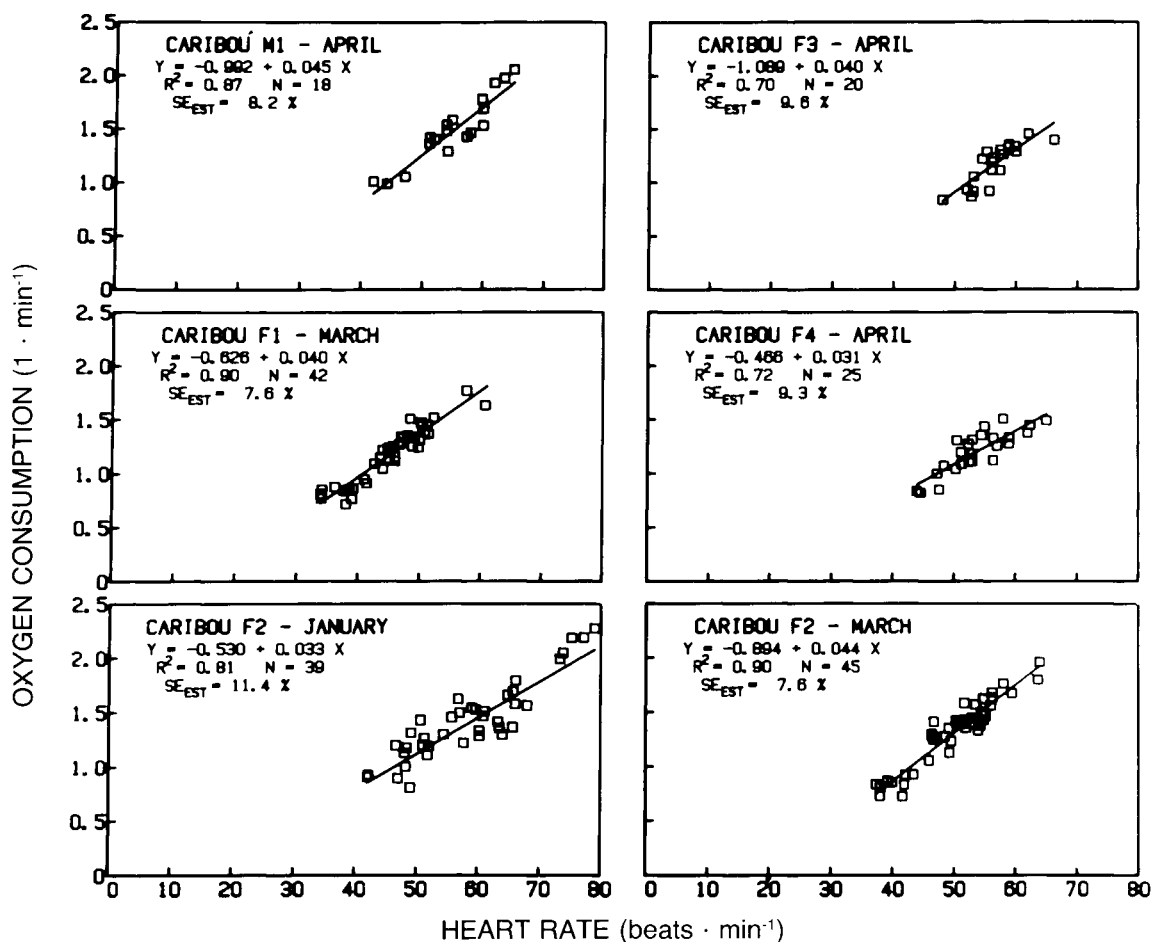
Fig. 2. Regressions of O_2 consumption on heart rate for caribou in winter.

they ranged within the 19-ha enclosure. Energy costs of individual activities of caribou in the enclosure were expressed as a multiple of the predicted energy cost of standing, thereby adjusting for seasonal differences in metabolic rates, time of day and other factors. An energy equivalent of 20.6 kJ·l O_2^{-1} (Brody, 1945) was used to convert VO_2 to energy expenditure. This value was based on a respiratory quotient of 0.90 determined from air samples taken from caribou while in the enclosure.

Eight activity categories were recognized: lying with head on the ground, lying with the head up but not ruminating, lying and ruminating, standing quietly, feeding on grain at a trough, grazing (without walking), browsing, and walking. Mean HR's were calculated from 30 sec counts taken continuously while the caribou was engaged in each activity. Statistical comparisons between regression lines were made by analysis of covariance (Zar, 1973; Neter and

Wasserman, 1974). The standard error of the estimate for predicting VO_2 from one additional measurement of HR (at the mean HR) was calculated according to Zar (1973) as:

$$SE_{est} = \sqrt{S_{y \cdot x}^2 \cdot (1 + 1/n)}. \qquad (1),$$

where n is the sample size and $S_{y \cdot x}^2$ is the residual mean square.

Results

Highly significant (P<0.001) linear relationships between VO_2 and HR were found for all six caribou (Figs. 1 - 3). In 4 of the 13 cases, correlation coefficients increased about 1% when exponential equations were used, but these small improvements did not justify the transformations. Significant differences were found between the slopes of the regression lines (O_2 pulse, l O_2·beat^{-1}) between seasons for individual caribou, and among caribou within a season (Table 1). For example, the O_2 pulses of four

FASTED Y = -0.967 + 0.040 X
R^2 = 0.92   N = 24
SE_{est} = 6.6%

FED Y = -0.957 + 0.036 X
R^2 = 0.87   N = 68
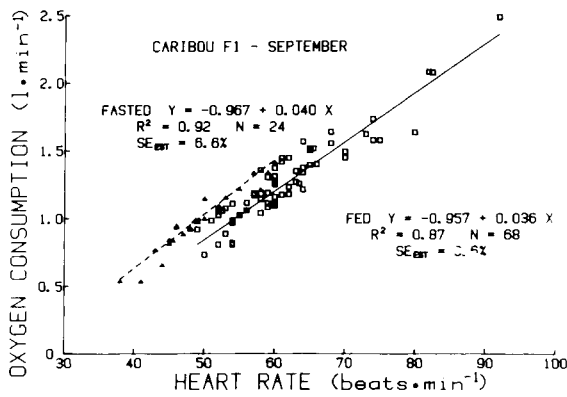SE_{est} = 5.6%

CARIBOU F1 - SEPTEMBER

Fig. 3. Regressions of O_2 consumption on heart rate for caribou F1 in September when fed and following a 15 h fast. Measurements were made as the caribou stood or walked on a treadmill.

females averaged 69% higher in late winter (March - April) than in late summer (September). Four of the five caribou had the same O_2 pulse in late summer, but the elevations of the regression lines were significantly different (Table 1). The high O_2 pulse of caribou F1 in summer may be a result of pooling data collected throughout the month of September when HR's were decreasing rapidly (Fig. 4).

Significant differences were also found between the VO_2/HR relationships calculated for the same individual during a season. Although the O_2 pulses of caribou F3 and F4 in November were the same as those calculated 6 months later, the elevations of the two regression lines calculated for caribou F4 were significantly different (Table 1). In contrast, the O_2 pulse of caribou F2 in March was significantly greater than that calculated 3 months earlier. Some of these differences can be attributed to differences in the time since feeding, as fasting increases the elevation of the regression and lowers the range of HR's observed for the same activities (Fig. 3).

Heart rates of caribou decreased sharply during September and October, and reached a minimum in January (Fig. 4). Mean HR's of all female caribou increased by approximately 15 beats·min^{-1} during the 3 weeks preceeding parturition, then decreased sharply within 3 days following parturition (Fig. 4). The calves of caribou F1 and F2 died within 3 days of birth; therefore, these females lactated for only a few days.

The lowest energy expenditures occurred when the caribou were lying with their heads on the ground (Table 2). The expenditure of feeding at a trough was 12% higher than that while

Table 1. Summary of analyses of covariance comparing regression lines relating VO_2 to heart rates of caribou.

Comparison	No. of lines	Degrees of freedom	F-values		
			Lines[1]	Slopes[2]	Elevations
Among individual caribou during summer	5	4, 202	65.2†	17.7†	63.8†
Among individuals during summer, excluding F1	4	3, 136	3.2*	0.8	3.4*
Among individuals during winter	8	7, 241	60.8†	3.4†	66.1†
Summer vs. Winter, Caribou F1	2	1, 106	128.3†	1.2	255.4†
Summer vs. Winter, Caribou F2	2	1, 72	222.3†	60.1†	384.6†
Summer vs. Winter, Caribou F3	2	1, 33	18.6†	11.2†	25.9†
Summer vs. Winter, Caribou F4	2	1, 71	103.5†	11.6†	195.4†
January vs. March, Caribou F2	2	1, 80	26.1†	8.4§	43.8†
November vs. April, Caribou F3	2	1, 41	0.8		
November vs. April, Caribou F4	2	1, 64	8.0†	0.2	15.8†
Fed vs. Fasted, Caribou F1	2	1, 88	10.7†	0.5	21.0†

[1] Test for equality among regressions (Neter and Wasserman, 1974:160)
[2] Test for equality of slopes and elevations among regressions (Zar, 1973).
* p<0.05.
§ p<0.01.
† p<0.001.

Table 2. Energy costs of activities relative to the cost of standing, as estimated from heart rates of caribou[1].

Caribou	Month	Body-weight, kg	Standing cost kJ/kg·h	Ratio[2]						
				LHD	LHU	LR	FT	GRZ	BRW	WAK
F1	September	100	11.14	0.87	1.02	1.00	1.00		1.32	
F2	September	105	11.38	0.93	0.95	1.07				
F2	September	105	9.76	0.72			1.22	1.22	1.14	
F1	November	103	11.64				1.16	1.16		
F1	December	102	10.97		0.96	0.93	1.03	1.06		1.45
F2	December	120	9.02	0.78		0.89	1.04			
F1	January	102	7.09				1.17			1.68
F2	January	120	7.08				1.02	1.18		1.41
F2	January	120	7.02	0.77		0.86	1.03			1.36
F2	January	120	7.64	0.83	0.88	0.88	1.12	1.13		
F1	March	104	10.12	0.84	0.92	0.88	1.03	1.23		1.33
F1	March	104	10.83	0.62	0.95	0.99	1.14	1.17	1.23	1.47
F2	March	120	7.36	0.89		0.91	1.19	1.25		1.60
M1	April	111	7.92	0.71	0.85	0.91	1.15	1.10		1.49
M1	April	111	9.52	0.77	0.91			1.10		
F2	April	122	8.19	0.85		0.97	1.00			
F3	April	95	7.67	0.83		0.90	1.37	1.46		
F4	April	108	8.72	0.89		0.97				
F4	April	108	9.61		0.91	0.94	1.20	1.25		
F4	April	108	11.18	0.86	0.93	0.87	1.06	1.11	1.16	
Mean ratios				0.80	0.91	0.92	1.12	1.17	1.18	1.46
Standard errors				0.02	0.01	0.02	0.02	0.04	0.03	0.04

[1] Estimates are bases on regressions developed for each caribou at the same time of year as its application.
[2] Activity codes are: LHD=lying with the head down; LHU=lying with the head up; LR=lying and ruminating; FT=feeding at a trough; GRZ=grazing without walking; BRW=browsing; WAK=walking
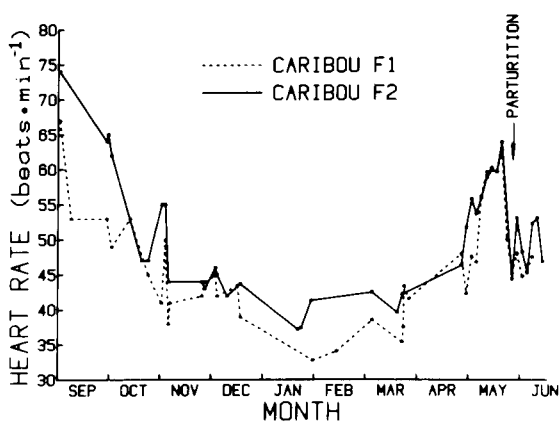

Fig. 4. Seasonal trends in heart rates of two female caribou feeding on grain at a trough.

standing. The highest energy expenditures involved locomotion; the energy cost of walking was 46% above the cost of standing (Table 2).

Discussion

The physiological components involved in the relationships between VO_2 and HR can be expressed by the following equation (Morhardt and Morhardt, 1971):

$$VO_2 \text{ (l·min}^{-1}) = HR \cdot SV \cdot (A-V)O_2 \text{ diff (2)},$$

where HR is in beats·min^{-1}, SV is the stroke volume (l blood·beat^{-1}), and (A-V) O_2 diff is the difference between the O_2 concentrations of arterial and venous blood (l O_2·l blood^{-1}). Equation 2 can be rearranged to show that the volume of O_2 consumed per beat, or O_2 pulse, is equal to the product of SV and (A-V) O_2 diff. If the O_2 pulse is constant, or varies systematically over a range of HR, errors in the prediction of VO_2 from HR will be small. This was the case in summer, when only slight increases in O_2 pulse with HR were observed for four of five caribou (Fig. 5); this indicated that variations in O_2 requirements within the range

of HR's observed were met primarily by changes in HR. Changes in stroke volume and (or) the arteriovenous O_2 differences were more pronounced in winter (Fig. 5). Because of seasonal differences in O_2 pulse, regression equations based on pooled data collected in summer and winter, such as those presented by Pauls *et al.* (1981), may be misleading.

Nilssen *et al.* (1984) measured VO_2 and HR of Norwegian reindeer (*R. t. tarandus*) and Svalbard reindeer (*R. t. platyrhynchus*) standing or running on a treadmill. The regression equations given by Nilssen *et al.* (1984) were recalculated for comparison with our results by assuming mean body weights of 89.1 and 76.0 kg for Norwegian and Svalbard reindeer, respectively (K. Nilssen, pers. comm.). The slopes of the regression lines for Norwegian reindeer (0.033 l $O_2 \cdot beat^{-1}$) and Svalbard reindeer (0.030 l $O_2 \cdot beat^{-1}$) in summer were within the range of those calculated for caribou (Figs. 1 - 3), but the intercepts calculated for Norwegian and Svalbard reindeer were lower than those for caribou. Conseqnently, the same HR would be associated with a lower VO_2 for reindeer when compared to caribou. The slope of the winter equation for Norwegian reindeer (0.035 l $O_2 \cdot beat^{-1}$) was also within the range of those calculated for caribou, but the slope for Svalbard reindeer (0.025 l $O_2 \cdot beat^{-1}$) was lower. Some of the differences noted above may be explained by the higher treadmill speeds used by Nilssen *et al.* (1984). Results of studies with humans (Rusher, 1965; Davies, 1968) and small mammals (Morhardt and Morhardt, 1971) indicate that as HR approaches a maximum, further increases in VO_2 are associated with only small changes in HR.

Pauls *et al.* (1981) and Renecker and Hudson (1983) used HR to predict energy costs of activites for wapiti (*Cervus elaphus*) and moose (*Alces alces*), respectively. The relationships between metabolic rates and HR they presented were curvilinear, probably because they included data for lying as well as active animals. Studies with dogs and humans have found that the mean O_2 pulse of inactive subjects is lower than that for the same individuals during exercise (Warnold and Avidsson Lenner, 1977), and that abrupt decreases in stroke volume can occur as a subject changes from a lying to standing position (Wang *et al.*, 1960; Rushmer, 1965). These findings suggest that when relationships
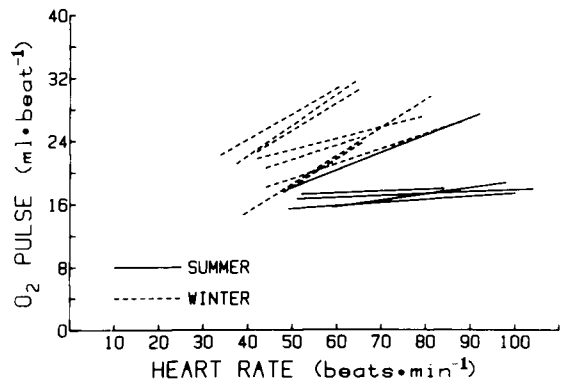

Fig. 5. Regressions of O_2 pulse on heart rate in summer and winter; values were calculated from data presented in Figures 1 - 3.

between VO_2 and HR are developed using only standing and active animals, as in this study, they will give unreliable estimates of lying costs. Indeed, the predicted 8.7% increase for caribou in the cost of standing relative to the cost of lying and ruminating, is only half of that determined from 22 paired VO_2 measurements of caribou lying and standing in a respiration chamber (16%; Fancy, 1986), and is much lower than the incremental cost of standing reported for other wild ruminants (Fancy and White, 1985b). Consequently, the costs of lying were overestimated and the values in Table 2 should not be used to calculate energy budgets.

Because ruminants spend a large portion of the day grazing and browsing, the costs of these activities are a major component of daily energy budgets. The estimated 17% increase in the energy cost of grazing above standing for caribou (Table 2) agrees closely with the mean difference of 16% between VO_2 of caribou standing and feeding in a respiration chamber or headstall (n=4; Fancy, 1986). Movements of the neck and mouth apparently account for most of the incremental cost, as VO_2 returned to standing values within 30 sec after the end of the feeding bout. The reported incremental costs of grazing by wapiti (6.0%; Pauls *et al.*, 1981) and moose (4.6%; Renecker and Hudson, 1983) are lower than those for caribou, possibly because standing costs for those two species are higher than those for caribou (Fancy and White, 1985b). The mean energy cost of browsing costs for moose and wapiti were also similar (2 - 4% higher) to grazing costs (Pauls *et al.*, 1981; Renecker and Hudson, 1983).

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The energy cost of walking, above that required for standing, increases linearly with walking speed for caribou and most other species (Fancy and White, 1985b). The energy cost of walking predicted from HR's of caribou M1, F1 and F2 was 46% higher than the standing metabolic rate. From VO_2 measurements for these three caribou while walking on a treadmill (n=407), we determined that the metabolic rate of these caribou would be 46% above the standing rate when they walked at 3.4 km·h⁻¹. We did not measure walking speeds of caribou in the enclosure, but the energetically-optimal walking speed (Fancy and White, 1985b) for caribou is approximately 3.5 km·h⁻¹, and a mean walking speed of 3.4 km·h⁻¹ during HR measurements appears reasonable.

The close relationships between VO_2 and HR suggest that HR telemetry could be extremely useful in describing the energetics of wild caribou, particularly in summer when variations in O_2 requirements are met primarily by changes in HR. The pulsed signals can be received several kilometers from the transmitter; therefore, it would be possible to monitor HR's without influencing the behaviour of the caribou. Reasonably accurate predictions of VO_2 from HR could be made using an equation combining data from several caribou. For example, the standard error of the estimate calculated from the combined summer data for caribou M2, F2, F3 and F4 (Y=—0.242 + 0.020 X; r^2=0.79; n=144) is within 10.6% of mean VO_2. Changes in stroke volume and O_2 extraction from the blood are of greater importance in winter than in summer for meeting varying O_2 requirements. Because these components differ substantially between individuals in winter (Fig. 5) it is unlikely that a general regression equation for accurately estimating activity costs from HR in winter could be developed.

References

Acheson, K. J., Campbell, I. T., Edholm, O. G., Miller, D. S., and Stock, M. J. 1980. The measurement of daily energy expenditure — an evaluation of some techniques. — Amer. J. Clin. Nutr. 33:1155-1164.

Bradfield, R. B., Huntzicker, P. B. and Fruehan, G. J. 1969. Simultaneous comparisons of respirometer and heart-rate telemetry techniques as measures of human energy expenditure. — Amer. J. Clin. Nutr. 22:696-700.

Brockway, J. M. and McEwan, E. H. 1969. Oxygen uptake and cardiac performance in the sheep. — J. Physiol. 202:661-669.

Brody, S. 1945. Bioenergetics and Growth. — New York: Hafner. 1023 p.

Davies, C. T. M. 1968. Limitations to the prediction of maximum oxygen intake from cardiac frequency measurements. — J. Appl. Physiol. 24:700-706.

Fancy, S. G. 1986. Daily energy budgets of caribou: a simulation approach. — Ph. D. thesis, Univ. Alaska, Fairbanks. 226 p.

Fancy, S. G. and White, R. G. 1985a. Energy expenditures by caribou while cratering in snow. — J. Wildl. Manage. 49:987-993.

Fancy, S. G. and White, R. G. 1985b. Incremental cost of activity. — In: Hudson, R. J. and White, R. G. (eds.). Bienergetics of wild herbivores. Boca Raton, Fl: CRC Press. 143-159.

Follmann, E. H., Manning, A. E. and Stuart, J. L. 1982. A long-range implantable heart rate transmitter for free-ranging animals. — Biotelem. and Patient Monitor. 9:205-212.

Holter, J. B., Urban, W. E., Jr., Hayes, H. H. and Silver, H. 1976. Predicting metabolic rate from telemetered heart rate in white-tailed deer. — J. Wildl. Manage. 40:626-629.

Holter, J. B., Urban, W. E., Jr., Hayes, H. H., Silver, H. and Skutt, H. R. 1975. Ambient temperature effects on physiological traits of white-tailed deer. — Can. J. Zool. 53:679-685.

Johnson, S. G. and Gessaman, J. A. 1973. An evaluation of heart rate as an indirect monitor of free-living energy metabolism. — In: Gessaman, J. A. (ed.). Ecological energetics of homeotherms, Monograph Series No. 20. Logan, Utah: Utah State University Press. 44-54.

Lifson, N., Gordon, G. B. and McClintock, R. 1955. Measurement of total carbon dioxide production by means of $D_2^{18}O$. — J. Appl. Physiol. 7:704-710.

Morhardt, J. E. and Morhardt, S. S. 1971. Correlations between heart rate and oxygen consumption in rodents. — Amer. J. Physiol. 221:1580-1586.

Neter, J. and Wasserman, W. 1974. Applied linear statistical models. — Homewood, Ill.: Irwin. 842 p.

Nilssen, K. J., Johnsen, H. K., Rognmo, A. and Blix, A. S. 1984. Heart rate and energy expenditure in resting and running Svalbard and Norwegian reindeer. — *Amer. J. Physiol. 246 (Reg. Integr. Comp. Physiol. 15):R963-R967.*

Osuji, P. O. 1974. The physiology of eating and the energy expenditure of the ruminant at pasture. — *J. Range Manage. 27:437-443.*

Pauls, R. W., Hudson, R. J. and Sylven, S. 1981. Energy expenditure of free-ranging wapiti. — *Univ. Alberta Feeders Day Report 60:87-91.*

Renecker, L. A. and Hudson, R. J. 1983. Winter activity budgets of free-ranging moose, using a calibrated heart rate index. — *Proc. 4th Intern. Conf. on Wildlife Biotelemetry, Halifax, Nova Scotia. 187-211.*

Richards, J. I. and Lawrence, P. R. 1984. The estimation of energy expenditure from heart rate measurements in working oxen and buffalo. — *J. Agric. Sci., Camb. 102:711-717.*

Robbins, C. T., Cohen, Y. and Davitt, B. B. 1979. Energy expenditure by elk calves. — *J. Wildl. Manage. 43:445-453.*

Rushmer, R. F. 1965. Control of cardiac output. — *In: Ruch, T. C., and Patton, H. D. (eds.). Physiology and biophysics. Philadelphia: Sauders. 644-659.*

Wang, Y., Marshall, R. J. and Shephard, J. T. 1960. The effect of changes in posture and of graded exercise on stroke volume in man. — *J. Clin. Invest. 39:1051-1061.*

Warnold, I. and Arvidsson Lenner, R. 1977. Evaluation of the heart rate method to determine the daily energy expenditure in disease: A study in juvenile diabetics. — *Amer. J. Clin. Nutr. 30:304-315.*

Webster, A. J. F. 1967. Continous measurement of heart rate as an indicator of the energy expenditure of sheep. — *Br. J. Nutr. 21:769-785.*

Yamamoto, S., McLean, J. A. and Downie, A. J. 1979. Estimation of heat production from heart-rate measurements in cattle. — *Br. J. Nutr. 42:507-513.*

Young, B. A., Leng, R. A., White, R. G., McClymont, C. L. and Corbett, J. L. 1969. Estimation of energy expenditure from measurements of carbon dioxide entry rate. — *In: Blaxter, K. L., Kielanowski, J. and Thorbek, G. (eds.). Energy metabolism of farm animals. Newcastle-upon Tyne: Oriel Press. 435-443.*

Zar, J. H. 1973. Using regression techniques for prediction in homeotherm bioenergetics. — *In: Gessaman, J. A. (ed.). Ecological energetics of homeotherms. Monograph Series, No. 20. Logan, Utah: Utah State University Press. 115-133.*