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Energy Costs of Locomotion in Wapiti

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Two ten month old wapiti, *Cervus canadensis* (Erxleben, 1777), heifers were trained to walk on a treadmill wearing a respiratory mask. Oxygen consumption was measured during lying, standing and exercise. The mean cost of walking for all belt speeds (2, 3 and 4 $km.h^{-1}$) was 0.43 $kcal.kg^{-1}.km^{-1}$ for one wapiti and 0.55 $kcal.kg^{-1}.km^{-1}$ for the other with an overall mean of 0.49 $kcal.kg^{-1}.km^{-1}$. The increment in energy expenditure due to walking on a per unit time basis increased linearly with velocity, whereas there was no consistent trend when energy expended was expressed on the basis of distance travelled.

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1. INTRODUCTION

A major component of the daily energy budget of free-ranging animals arises from such activities as standing, travelling, social interaction and feeding. Determination of the energy cost of an activity and of the amount of time an animal engages in it permits an estimation of the total energy required for that activity. Optimistically, simple summation of estimated energy costs of recognizable activities and of the basal requirement would give a reasonable estimate of the overall energy needs of the animal.

Such time-activity analyses have been used in a number of studies on wild ruminants which have sought to disclose the significance of social behavioral patterns (Moen, 1973) or the potential impact of harassment by man (Geist, 1971). However, only recently has information on the energy costs of locomotion become available (Mattfeld, 1974; Brockway & Gessaman, 1977). This paper deals with the energy requirements of low speed locomotion in wapiti (*Cervus canadensis*) and touches on energy expenditures associated with different postures.

2. MATERIALS AND METHODS

Two ten month old hand-reared wapiti heifers were trained to walk on a custom-designed treadmill while wearing a respiratory mask. Animal 1 weighed 153 kg and Animal 2 weighed 161 kg. The experimental period, extending from February to April, commenced after approximately two months of training. Oxygen consumption was measured in a thermoneutral environment (+10°C) with an open circuit respiratory pattern analyser (Young *et al.*, 1975). Rates of energy expenditure were calculated using a caloric equivalent for oxygen of 4.89 $kcal.l^{-1}$ (McLean, 1970). The rate of flow of air through the mask was 120 $l.min^{-1}$.

Standing oxygen consumption was measured before and after periods of enforced exercise on the treadmill. The exercise periods were up to 3 hours in length. At the low velocities used in this study, oxygen consumption rapidly dropped at the end of each trial, suggesting that oxygen debt was not an important consideration. Incidental measurements of oxygen consumption while lying were made when an animal assumed this posture.

Although belt speeds of 2 to 5 $km.h^{-1}$ were used initially, 5 $km.h^{-1}$ was evidently too rapid as the animals were obviously distressed at this speed. Consequently data were collected for speeds of 2, 3 and 4 $km.h^{-1}$.

3. RESULTS

The increment in energy expenditure due to walking increased linearly with velocity. For Animal 1 this relationship was found to be:

$$E \text{ walk} = 0.4165\ V + 0.0148\ (r^2 = 0.73,\ n = 40) \quad (1)$$

Table 1
Energy expenditure (Mean ± SD in $kcal.kg^{-1}.h^{-1}$) during lying, standing and walking.

Energy Cost	N	Animal 1	N	Animal 2
Standing	18	1.30±.11	17	1.27±.06
Lying	—	—	7	1.03±.10
Walking *				
2 $km.h^{-1}$	11	0.88±.08	15	1.29±.21
3 $km.h^{-1}$	20	1.23±21	17	1.53±.25
4 $km.h^{-1}$	9	1.71±.19	12	1.98±.14

* Difference from standing energy expenditure.

and for Animal 2:

$$E \text{ walk} = 0.3426\ V + 0.5697\ (r^2 = 0.62,\ n = 44) \quad (2)$$

where E walk is the increment in energy expenditure due to walking ($kcal.kg^{-1}.h^{-1}$) at velocity V ($km.h^{-1}$). By combining data from both individuals the relationship was found to be:

$$E \text{ walk} = 0.3714\ V + 0.3248\ (r^2 = 0.53,\ n = 84). \quad (3)$$

At each rate of speed, from 0 to 4 $km.h^{-1}$, the mean values of energy expenditure for the two animals (Table 1) differed significantly ($P < .05$). Mean walking values for Animal 2 consistently exceeded those for Animal 1 whereas the reverse was true for standing values.

Animal 2 frequently assumed a lying position at the end of exercise periods. This permitted a comparison of the energy cost of standing *vs* lying (Table 1). The mean difference between these two postures was 0.24 $kcal.kg^{-1}.h^{-1}$.

For Animal 1 the energy cost of walking per unit distance remained relatively constant with increasing velocity while values for the other individual decreased with speed (Table 2). The overall mean energy cost of walking was calculated to be 0.49 $kcal.kg^{-1}.km^{-1}$; individual mean values were 0.43 and 0.56 for Animals 1 and 2, respectively.

Stride frequencies were similar ($P > .05$) for both individuals at each walking speed (Table 3). Mean stride frequencies were 62, 77 and 92

Table 2
Energy expenditure ($kcal.kg^{-1}.km^{-1}$) per kilometer at different velocities.

Velocity of Walking ($km.h^{-1}$)	Energy cost of walking 1 km (Increment above standing)			
	Animal 1		Animal 2	
	N	Mean ± SD	N	Mean ± SD
2	11	.44±.05	15	.65±.11
3	20	.41±.07	17	.51±.08
4	9	.43±.05	12	.50±.04
Mean		.43±.02		.56±.08
Overall Mean	.49+.09 $kcal.kg^{-1}.km^{-1}$			

Table 3
Energy expenditure ($kcal.kg^{-1}.km^{-1}$) in the both wapiti heifers at different walking speed.

Velocity, $km.h^{-1}$	$Paces.min^{-1}$	$Paces.km^{-1}$	Energy Expenditure (Assuming 3×10^{-4} $kcal.kg^{-1}.pace^{-1}$)
2	62	1860	.558
3	77	1540	.462
4	92	1380	.414

paces per minute for belt speeds of 2, 3 and 4 $km.h^{-1}$ respectively. The relationship between walking velocity and stride frequency was described by the regression equation:

$$V = 0.064\, F - 1.901 \; (r^2 = 0.95,\ n = 59) \quad (4)$$

where V is walking velocity in $km.h^{-1}$ and F is stride frequency in paces • min^{-1}.

4. DISCUSSION

In the present study linear increases in energy expenditure per unit time were observed as speed of walking increased over the limited range of 2—4 $km.h^{-1}$. Results were in general agreement with studies on most other species. Clapperton (1961, 1964) found that the energy cost of walking in sheep increased with speed. Taylor *et al.* (1974) found a similar linear pattern in a series of divergent species including cheetahs, gazelles and goats. The relationship appeared to hold over a wide range of velocities and was expressed:

$$M = 8.46\ W^{-0.40}$$

where M is the slope of the relationship (O_2 consumption (ml).$g^{-1}.km^{-1}$) and W is body weight (g). Based upon this equation (with appropriate corrections for units) the slope of the relationship between energy expenditures and velocity for an animal approximately the size of the wapiti used in this study was predicted to be 0.339 $kcal.kg^{-1}.km^{-1}$. The observed value for the slope taken from Eqn. 3 (0.370 $kcal.kg^{-1}.km^{-1}$) was only slightly greater. A recent study by Brockway & Gessaman (1977) indicates that the red deer also conforms to this relationship.

In contrast to energy expenditure expressed as a function of time, total energy expended per unit distance usually declines with increasing velocity to a minimum cost which has been widely used in cross-species comparisons (Tucker, 1975). This is due largely to the changing proportional contributions of standard metabolism and the activity increment as velocity increases. At higher velocities both total and incremental costs per unit distance are relatively constant. Is this experiment the mean value for the increment of energy cost per unit distance was 0.49 $kcal.kg^{-1}.km^{-1}$. This value compares with 0.54 $kcal.kg^{-1}.km^{-1}$ for man (Smith, 1922), 0.58 for the dog (Lusk, 1931), 0.39 for the horse (Brody, 1945), 0.59 for sheep (Clapperton, 1961, 1964).

Estimates of the energy cost of standing over lying for sheep and cattle have ranged from 6% (Blaxter & Wainman, 1962; Osuji, 1973) to over 30% (Graham, 1964). A generally accepted value for domestic animals is 9% (Blaxter, 1969). Although there was considerable variance and a relatively small sample, data from the present study suggested a difference in energy expenditure of 18.6% between these two postures. The limited number of studies on other wild ruminants suggest similar high values. Increments of over 20% have been measured in pronghorn antelope (Wesley *et al.* 1973) and roe deer (Weiner, 1977).

Estimates of walking velocity can be obtained from observations of stride frequency (Eqn. 4). Gold (1973) hypothesized that all animals require the same quantity of energy to carry a unit of their body mass one step (3×10^{-4} $kcal.kg^{-1}$). Using this principle, the calculated energy expenditures for speeds of 2, 3 and 4 $km.h^{-1}$ were .558, .462 and .414 $kcal.kg^{-1}.km^{-1}$, respectively (Table 3). This compares closely with empirical observations of .54, .46 and .47 $kcal.kg^{-1}.km^{-1}$.

The data obtained in this experiment indicated that the energy costs of locomotion in wapiti, at least at low velocities, conforms to inter-species relationships described by other workers. However, it is important to consider the possibility of important physiological distinctions in other species, since several such as the African lion (Chassin *et al.*, 1976) have unexpectedly high costs of locomotion.

The utility of the type of data generated in this study can be demonstrated by considering the contribution of locomotion to the energetic requirements of a free ranging wapiti weighing 200 kg. Assuming that about 7% of a 24 hour period (1.7 hours) is spent travelling (Craighead *et al.*, 1973) at an average rate of travel of 3 $km.h^{-1}$ (a comfortable walking rate), the calculated total energy cost is 415 $kcal.d^{-1}$. This represents an 8.7% increase in daily energy expenditure. If movement during feeding periods were included this estimate would increase substantially. Similar values have been calculated for various domestic ruminants (Osuji, 1974).

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ENERGETYCZNY KOSZT PORUSZANIA SIĘ U WAPITI

U dwu 10-miesięcznych, oswojonych jałówek wapiti zbadano energetyczny koszt poruszania się w kieracie, przy szybkościach 2, 3 i 4 $km.h^{-1}$, porównując go z metabolizmem spoczynkowym podczas stania i leżenia (Tabela 1). Stwierdzono, że wydatki energetyczne, zużyte na chodzenie wzrastają średnio o 0.49 $kcal.kg^{-1}.km^{-1}$;, niezależnie od dystansu. Przyrastają one liniowo wraz z szybkością (Tabela 2), kiedy za podstawę odniesienia przyjęto jednostkę czasu. Nie zauważono natomiast podobnych trendów, gdy wydatki energetyczne zużywane na chodzenie odnoszono do przebytej odległości (Tabela 3).