

The energy costs of walking on the level and on negative and positive slopes in the Granadina goat (*Capra hircus*)

BY M. LACHICA, THE LATE C. PRIETO AND J. F. AGUILERA*

*Animal Nutrition Department, Estación Experimental del Zaidin (CSIC), Profesor Albareda, 1,
18008 Granada, Spain*

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The energy expenditure of six goats averaging 35 (SE 0.3) kg was measured when the animals were standing or walking on a treadmill enclosed in a confinement-type respiration chamber at different speeds (0.167, 0.333 and 0.500 m/s) and slopes (–10, –5, 0, +5 and +10%). The energy costs of locomotion, estimated from the coefficients of linear regressions of heat production (HP) per kg body weight *v.* distance travelled were 1.91, 2.33, 3.35, 4.68 and 6.44 J/kg BW per m for –10, –5, 0, +5 and +10% inclines respectively, indicating that the energy expenditure of walking over standing changes with slope according to a slightly curvilinear relationship. The energy cost of raising 1 kg body weight one vertical metre was found to be 31.7 J, giving an average efficiency for upslope locomotion of 30.9%. The energy recovered on vertical descent was estimated as 13.2 J/kg per m, indicating an efficiency of the energy recovered above the theoretical maximum.

Goat: Locomotion: Energy cost

The energy expenditure of locomotion contributes significantly to the energy requirement of animals in free-living conditions and must be included for accurate evaluation of the energy needs of the grazing animal. Past attempts to measure the energy expenditure of the animal at pasture have been reviewed by Whitelaw (1974) and Brockway (1978). In the main, data have been derived either from estimates of feed intake for constant live weight or by direct measurements on range. The usual and more reliable procedure for estimating free-living energy expenditure is the factorial method, whereby energy expenditure is calculated from calorimetric determination of the energy cost of various activities. Most of the increase in energy expenditure of physical activity results from grazing and locomotion costs, whereas the contribution of other activities is usually considered to be negligible. Although the energy cost of locomotion is relatively well defined in cattle (Ribeiro *et al.* 1977; Shibata *et al.* 1981; Lawrence & Stibbards, 1990), sheep (Clapperton, 1964; Farrell *et al.* 1972; Brockway & Boyne, 1980), equines (Yousef *et al.* 1972; Dijkman, 1992) and wild ungulates (Taylor *et al.* 1974; Brockway & Gessaman, 1977; Cohen *et al.* 1978; White & Yousef, 1978; Parker *et al.* 1984; Fancy & White, 1985; Dailey & Hobbs, 1989), no systematic studies, with the exception of the survey of Taylor *et al.* (1974), have been made with domestic goats. Published data suggest that there are interspecies differences in locomotory efficiency as a result of morphological, physiological and behavioural adaptations. Consequently, extrapolation of values derived from ruminant species other than the goat need further validation. While most of the studies have examined the energy cost of locomotion on the level, few studies have investigated the efficiencies associated with vertical ascent or descent. The present study was undertaken with the aim of determining the energy cost of

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walking on the level and on slopes in the Granadina goat (*Capra hircus*). A brief account of some preliminary results have been given elsewhere (Aguilera *et al.* 1991).

MATERIALS AND METHODS

Animals

Six adult female goats of the Granadina breed, of average body weights 29 (SE 0.2), 31 (SE 0.1), 34 (SE 0.6), 35 (SE 0.2), 39 (SE 0.1) and 42 (SE 0.3) kg were used. They were given lucerne (*Medicago sativa*) hay at about maintenance level. The estimated metabolizable energy content of the hay was 7.4 and 8.3 MJ/kg DM in the first and second experiment respectively. The energy requirement for maintenance was taken as 401 kJ/kg body weight (BW)^{0.75} per d (Aguilera *et al.* 1990).

Respiration chamber

The heat production (HP) of each animal while standing at rest and while walking on a treadmill enclosed in a confinement-type respiration chamber (Lachica *et al.* 1995) was calculated from measurements of CH₄ and CO₂ production and O₂ consumption (Brouwer, 1965). A confinement-type respiration chamber with fast response applications was used. The chamber was made of transparent acrylic plates and was provided with an internal ventilation system. When an animal was introduced into the chamber an aliquot sample of the air was continuously sucked from the chamber for analysis and then returned to the chamber. Before the CO₂ level increased to about 1%, the chamber was flushed out for a few minutes with a stream of fresh air. Shortly after the start and before the end of each confinement period the chamber air was sampled and its composition measured. The volume of the system multiplied by the concentrations of CO₂ and O₂ gave the volumes of these gases present at each measurement and, by difference, the amount produced and consumed. To calibrate the whole system pure CO₂ and O₂-free N₂ were injected into the chamber from cylinders and the amounts of gases delivered determined gravimetrically. Over the course of the present experiments two calibrations per week were performed.

Treadmill

The treadmill (model BETA BRB/P, Beta Bellarosa, Ilario D'enza, Italy) had a belt which was supported on rollers and provided with a non-slipping surface (1.32 m long by 0.48 m wide) made of rubber. It allowed selection of speeds and slopes in the range of 0–15 km/h and –5 to +15% respectively. The –10% slope was achieved by raising the rear part of the treadmill with an appropriate wedge. No changes in the composition of the air of the chamber were detected when the treadmill belt was rolling at its highest speed in a preliminary blank test.

The tethering system for the goat consisted of a neck collar attached to the front panel of the treadmill by a short light chain. Each goat was repeatedly trained to walk on the treadmill. Full experimental adaptation was assumed when the animals walked in a steady way without dragging against their tethers.

Experimental design

Two experiments were performed. In the first, two replicate observations were made on each animal while standing at rest (speed 0 m/s) on each of five different slopes (–10, –5, 0, 5 and 10%), giving a total of sixty (six animal × two replicate × five slope)

determinations. This group of measurements was made to test the hypothesis of the existence of a postural effect on the goat's energy expenditure. In the second set of measurements, three replicate observations were made on each animal at each treatment combination of speed (0.167, 0.333 and 0.500 m/s) and slope (-10, -5, 0, 5 and 10%), involving 270 (six animal \times three replicate \times three speed \times five slope) determinations. The experimental treatments were arranged sequentially according to travel speed, so that each series of gas exchange measurements at a given speed was preceded by a measurement while the goat was standing still on the level (speed 0 m/s; slope, 0%), therefore giving fifty-four (six animal \times three replicate \times three speed) additional measurements of the goats' energy expenditure.

The determinations began when the animals were well adapted to the experimental procedures and showed no signs of stress. The measurements of the energy expenditure took place 16–20 h after feeding. The goats were placed on the treadmill in the chamber at 09.00 hours. The experimental schedule consisted of 25–30 min standing followed by 20–25 min walking at each slope, the gas exchange being recorded after 5–10 min of adaptation of the animal to a new physical activity, to confirm that a steady state had been reached, and then for exactly 15 min. The HP of the animal, calculated from the measured gas exchange, was referred to body weight and extrapolated to 1 h (J/kg BW per h). The same pattern was repeated at each speed assayed. The length of the adaptation period was taken according to Shibata *et al.* (1981), who reported in heifers no significant differences in the energy expenditure of standing before and after 5–10 min walking at 0.5–1.0 m/s, a fact which indicates the lack of carry-over effects from preceding physical activities. They also found a significant decrease in O₂ consumption during the first minute of exercise. Furthermore, Yoshida *et al.* (1959) obtained steady-state O₂ consumption in cattle while pulling a load after 5 min of physical work.

The data from the first set of measurements were subjected to ANOVA (five treatments (slope) \times six animals, with two replicates (calorimetry runs per animal)) following a two-way ANOVA with replication, with thirty degrees of freedom for within-animal error. The Bonferroni test was used to ascertain the statistical significance of differences in the energy cost of maintaining posture according to the slope assayed.

The energy costs of locomotion within slopes were estimated from the coefficient of linear regressions of HP (J/kg BW per h) *v.* distance travelled (D_t , m). For that purpose regression equations were obtained for each goat and the mean and standard error of the regression slopes were calculated (n 6). A one-way ANOVA analysis was made to assess differences between means.

The energy cost of vertical ascent and the energy recovered on vertical descent were calculated by multiple regression equations of HP (J/kg BW per h) *v.* distance travelled horizontally (D_h , m) and vertically in ascent (D_u , m) or descent (D_d , m) respectively, using the following approach:

$$D_u = \text{distance upward; equals 0 otherwise,}$$

$$D_d = \text{distance downward; equals 0 otherwise.}$$

Equations were fitted for each goat and estimates were then summarized over the six animals.

RESULTS

In the first experiment, carried out on goats standing still at each slope, eight determinations were discarded due to anomalous RQ values which could not be attributed

Table 1. *The heat production (HP, J/kg body weight per h) and respiratory quotient (RQ) of goats (Capra hircus) walking on a treadmill belt at various speeds (m/s) and slopes (%)*
(Mean values with their standard errors)

	Body wt (kg)		HP		RQ		n
	Mean	SE	Mean	SE	Mean	SE	
Speed							
0*	35.3	0.73	6960	177	0.89	0.016	52
0.167	35.4	0.58	8988 ^a	182	0.91 ^a	0.009	89
0.333	35.1	0.51	11 531 ^b	308	0.85 ^b	0.010	86
0.500	34.5	0.54	13 835 ^c	392	0.84 ^b	0.012	87
Slope							
- 10	34.3	0.65	9354 ^a	270	0.93 ^a	0.012	53
- 5	35.4	0.73	9680 ^{ab}	278	0.85 ^b	0.016	51
0	35.0	0.70	10 914 ^b	333	0.86 ^b	0.014	54
+ 5	34.9	0.73	12 552 ^c	444	0.85 ^b	0.013	53
+ 10	35.4	0.75	14 732 ^d	579	0.85 ^b	0.013	51

^{a,b,c,d} Mean values within a column not sharing a common superscript letter were significantly different ($P < 0.05$).

*Standing at rest on the level.

Table 2. *The heat production (HP, J/kg body weight per h) of goats (Capra hircus) walking on a treadmill belt at various combinations of speed (m/s) and slope (%)*
(Mean values with their pooled standard error, for eighteen observations for each combination of speed and slope)

	Slope						Pooled SE
	0*	- 10	- 5	0	5	10	
Speed							
0.167	6660	8832	8306	8515	9404	10 465	172
0.333	7219	9103	9514	11 329	12 810	14 718	174
0.500	6987	10 613	11 289	12 897	15 613	19 011	173
Pooled SE	246	241	244	248	249	244	

* Standing at rest on the level.

to either the calorimetric technique or the animal's behaviour. The energy expenditure of the goats was the same ($P > 0.05$) irrespective of the slope assayed. Average values for HP (n 6) were 6343(SE 221), 6367(SE 355), 6431(SE 242), 6047(SE 241) and 6471(SE 410) J/kg BW per h, for - 10, - 5, 0, 5 and 10 % slopes respectively, giving an overall mean value of 6332(SE 67) J/kg BW per h (369(SE 3.9) J/kg^{0.75} per d). An average value of 0.89(SE 0.018) (n 52) for RQ was observed. As no postural effect on HP was detected, in the second set of experiments the energy expenditure of the goats while standing at rest was always measured with the treadmill belt horizontal.

In this second set of trials one animal showed signs of disease and was removed from the experiment until it achieved complete recovery. For that reason only 262 individual measurements of the energy expenditure of goats travelling on various gradients at different speeds, plus fifty-two additional HP determinations on animals standing at rest on the level, were performed. Tables 1 and 2 show the average results of the HP and RQ of goats walking at different speeds on the level and on positive and negative slopes. The factors 'speed' and 'slope' were highly significant ($P < 0.001$), as well as the interaction speed \times slope ($P < 0.05$). The mean values of the energy cost of walking, estimated within

Table 3. Average values (*n* 6) of the energy cost of walking (EC_w , J/kg BW per m) for goats (*Capra hircus*) estimated by individual regressions of heat production (HP, J/kg BW per h) *v.* distance travelled (D_t , m)

(Mean values with their standard errors)

	Slope (%)									
	- 10		- 5		0		+ 5		+ 10	
	Mean	SE								
EC_w	1.91 ^a	0.129	2.33 ^a	0.130	3.35 ^b	0.127	4.68 ^c	0.148	6.44 ^d	0.245
HP at rest	6960	365	6910	366	6883	342	6841	333	6838	329

^{a,b,c,d} Mean values within a row bearing unlike superscript letters were significantly different ($P < 0.05$).

slope from linear regression of HP (J/kg BW per h) *v.* distance travelled (D_t , m) for each animal, appear in Table 3. The intercepts of the regression equations are estimates of the goats' metabolic rate while standing at rest (J/kg BW per h). These were not statistically different and were similar to the mean value of 6960(SE 177) J/kg BW per h (see Table 1) found in direct measurements of the goats while standing. This average value is equivalent to 405 kJ/kg^{0.75} per d. The mean RQ value for all observations was 0.87(SE 0.0006) (*n* 314). The mean slopes of these regression equations indicate that in the goat the energy cost of locomotion increases from 1.91 to 6.44 J/kg BW per m (or from 0.09 to 0.32 ml O₂/kg BW per m) on increasing the slope of the treadmill belt from - 10 to +10%. From these estimates exponential relationships were derived which allow the calculation of the energy cost of locomotion (EC_w , J/kg BW per m) as a function of slope (SI, %):

$$EC_w = 3.39 (SE 1.022)e^{0.063 (SE 0.0031) SI}, r 0.996; \text{residual SD } 0.049; n 5. \quad (1)$$

The mean values (*n* 6) of the energy cost of walking, calculated for each goat by separation of the horizontal (D_h) and vertical (D_u and D_d) components by multiple regression of HP (J/kg BW per h) *v.* the horizontal and vertical distances travelled (m) in ascent or descent, were those given by the average equation:

$$HP = 6724 (SE 301) + 3.31 (SE 0.148) D_h + 31.7 (SE 1.59) D_u - 13.2 (SE 1.33) D_d, \quad (2)$$

where the regression coefficients of D_h , D_u and D_d indicate values for the net energy cost (J/kg BW per m) for horizontal (EC_h) and vertical locomotion on ascent (EC_u) and on descent (EC_d) respectively.

The energy equivalent of the O₂ consumed by the goats while walking, above that observed while standing at rest on the treadmill belt, was calculated by regressing the net energy expenditure due to locomotion ($HP_{\text{walking}} - HP_{\text{standing}}$, J/h) *v.* the increase in O₂ consumption above standing ($O_{2\text{walking}} - O_{2\text{standing}}$, ml/h) and was found to be 20.3(SE 0.03) (*n* 262).

DISCUSSION

The specific objectives of the present study were to assess the net energetic costs of horizontal and vertical locomotion of the Granadina goat by means of indirect calorimetry and to evaluate its additional energy expenditure due to physical activity in order to provide estimates of the overall energy expenditure of the grazing goat. The aim was to obtain more accurate estimations of its energy requirements on which to base patterns of management according to the availability of herbage. We are aware of the limitations of

data derived from experiments with treadmills when extrapolating to free-living situations, particularly when the animal has to walk on soft, uneven or wet surfaces instead of on the firm, even surface of a treadmill (Fancy & White, 1985). The experimental values assigned to the variables were selected to give rise only to moderate physical efforts, as is expected to happen in the grazing goat. During the present trials the animals travelled daily distances which ranged from 1500 to 4500 m, while their metabolic rate was measured throughout 2.5 h. Prieto *et al.* (1991) reported that goats grazing on semi-arid lands travelled, on average, daily distances of 3482–6432 m in autumn and summer respectively, depending on the seasonal availability of the pasture.

In the present study the speeds assayed were lower than those used in earlier trials (i.e. Taylor *et al.* 1974; Brockway & Gessaman, 1977; Cohen *et al.* 1978; White & Yousef, 1978; Boyne *et al.* 1981; Dailey & Hobbs, 1989). The use of high speeds might improve the accuracy of the estimates of the locomotion costs, since in this case the energy expenditure of the animal while standing still is proportionately a minor fraction of total energy expenditure when exercising. However, the degrees of exercise and slope used in the present study did produce elevated HP up to 2.5 times that associated with rest.

Throughout the second set of experiments the goats kept a fairly constant body weight (35.03 (SE 0.29) kg) and their energy expenditure when standing at rest was close to 405 kJ/kg^{0.75} per d. These results suggest that the goats were well adapted to the experimental procedures, as previous results from this laboratory (Aguilera *et al.* 1990) indicate that the energy requirement for maintenance of the Granadina goat is 401 kJ/kg^{0.75} per d. However, it should be pointed out that measurements were made 16–20 h after feeding. The energy expenditure over this period is unlikely to reflect accurately the mean daily heat production as many of the digestive, absorptive and metabolic processes will be 'post-peak'. Care needs to be exercised, therefore, in using the value obtained in the present experiment for comparative purposes.

We did not find statistical significance between the intercepts of the linear regression equations relating HP and distance travelled (Table 3), a fact which corroborates previous results from Brockway & Gessaman (1977), suggesting that the energy cost of maintaining posture does not differ during walking and standing.

The net energy cost of locomotion, on the level, of a Granadina goat with an average body weight of 34.95 kg was 3.35 J/kg BW per m, a value somewhat lower than that of 3.63 J/kg BW per m which can be calculated from data reported by Taylor *et al.* (1974) for another breed of domestic goat (*Capra hircus*), whereas it is close to that of 3.23 J/kg BW per m, published by the same authors, for the desert gazelle (*Gazella gazella*). For other farm ruminant species the data lie well below the value found here. In sheep, Clapperton (1964), Farrell *et al.* (1972) and Brockway & Boyne (1980) reported values of 2.47, 2.83 and 2.30 J/kg BW per m respectively; Ribeiro *et al.* (1977), Shibata *et al.* (1981) and Lawrence & Stibbards (1990) obtained, in cattle, net energy expenditures of 2.09, 1.54 and 1.91 J/kg BW per m respectively. In wild ungulates, specifically in the mountain goat (*Oreamnos americanus*) and the bighorn sheep (*Ovis canadensis*), Dailey & Hobbs (1989) calculated, from the slopes of linear regressions, net energy costs of horizontal locomotion which ranged from 0.24 to 0.28 ml O₂/kg BW per m, with little variation between goats and sheep of similar body weight. When using our experimental value of 20.3 J/ml O₂ the net energy cost of horizontal locomotion obtained in these trials was, on average, about 35% lower than the values reported in the American survey.

It is well documented that the energy cost of horizontal locomotion decreases with increasing body weight. However, the allometric equations proposed to estimate this cost as a function of body size (Taylor *et al.* 1970; Cohen *et al.* 1978) seem to be of

questionable value because of interspecies differences in morphology, physiology and behaviour, causing great variations between predicted and observed locomotion costs.

It is generally recognised that the net energy cost of upslope locomotion is higher than that for moving on the level due to the energy expended to work against gravity, whereas during downslope travel potential energy is recovered as kinetic energy, leading to a decrease in energy expenditure relative to horizontal costs. Equation (1) states that the change in energy cost of locomotion with slope is slightly curvilinear.

The validity of the estimation of the energetic efficiency of locomotion by separation of the vertical and horizontal components (Stainsby *et al.* 1980), as made by equation (2) has been questioned, because with this method of calculation some work is done by raising the body's centre of gravity at each step, while travelling on the level is ascribed to the vertical component. Consequently, this procedure would overestimate the energy cost of vertical movement at the expense of the horizontal component. Our results seem to be free of this bias, as shown by comparing the estimate given by the mean slope of the linear regressions for locomotion on the level (Table 3) with the average coefficient of the horizontal component of the multiple regression equations mentioned above (3.35(SE 0.127) v 3.31(SE 0.148)).

The net energy cost of lifting was calculated according to equation (2) at 31.7(SE 1.59) J/kg BW per m (n 6). The efficiency of upslope locomotion, calculated as the ratio of work done to the energy cost of doing it and expressed as a percentage, averaged 30.9%. Published data for the energy cost of vertical locomotion are 25.4–27.0 (Clapperton, 1964), 32.0 (Farrell *et al.* 1972) and 27.7–37.7 J/kg BW per m (Brockway & Boyne, 1980) for sheep; and 26.0 (Ribeiro *et al.* 1977) and 24.0–30.3 (Shibata *et al.* 1981) for cattle. From these costs apparent energetic efficiencies ranging from 40.9 to 26.0% can be calculated. The Agricultural Research Council (1980) gives a preferred value of 28 J/kg BW per m for the energy cost of the vertical movement for both sheep and cattle, equivalent to an energetic efficiency of 35%.

The information available on the energy cost of downslope locomotion seems to be controversial. The Agricultural Research Council (1980) states that there is a lack of available data on this cost of descent in ruminant animals and thus assumes that it is similar to that of walking on the level. It is believed that downslope movements are less expensive because gravitational energy is recovered as kinetic energy during descent and it has also been reported (Fancy & White, 1985) that the amount of potential energy recovered decreases with body weight and increasing angle of descent. It is doubtful whether this energy can be recovered by the body. The term 'negative work' although unacceptable according to thermodynamic laws, has been extensively used by physiologists to define the work done in activities such as lowering a weight or going downhill, when antagonist muscles lengthen under tension while others shorten. Data on the energy recovered during downslope locomotion are extremely variable (18.2–19.9, Margaria *et al.* 1963; 5.8–7.0, White & Yousef, 1978; 2.8–7.4, Parker *et al.* 1984; –0.2–0.2, Dailey & Hobbs, 1989; and 2.0–4.2 J/kg BW per m, Dijkman, 1992). We observed that the average amount of energy recovered when moving downslope, calculated by equation (2), was 13.2(SE 1.33) J/kg BW per m (n 6). The energetic efficiency of this activity, calculated as the energy recovered: energy stored ratio and expressed as a percentage, was found to be 134.6%. Our results indicate that, as reported by other authors (Margaria *et al.* 1963 and Boyne *et al.* 1981, in human subjects; Raab *et al.* 1976, in dogs), the amount of energy recovered during downslope locomotion exceeds the maximum transfer in potential energy per metre vertical movement, being impossible to conceive a satisfactory explanation in terms of saving of negative work. As stated by G. Cavagna (personal communication), efficiency in

a physical sense can only be measured during positive work, but not during negative work when both chemical and mechanical energies enter the muscle and nothing is produced except heat. Similarly, K.L. Parker (personal communication) points out that the classic method of calculation of efficiency, based on the recovery of potential energy, is meaningless. Consequently, we think that the coefficient of the vertical component (D_d) in the regression equation (2) is only an index of the likely energy-saving effect of negative work and has no other meaning, such as the recovery of gravitational potential energy.

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