

Estimation of the energy costs of locomotion in the Iberian pig (*Sus mediterraneus*)

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The energy cost of locomotion of four Iberian pigs was measured in two experiments conducted when the animals averaged 41.3 (SE 0.1) kg (first experiment) and 84.1 (SE 0.1) kg (second experiment). The heat production of the pigs was determined when standing or walking at a speed of 0.555 m/s on a treadmill enclosed in a confinement-type respiration chamber, on different slopes (−10.5, 0, and +10.5% in the first experiment, and −5.25, 0 and +10.5% in the second experiment). The energy costs of locomotion, estimated from the coefficients of linear regressions of heat production per kg body weight (BW) on distance travelled, were in the first experiment 2.99, 3.31 and 5.88 J/kg BW per m for −10.5, 0, and +10.5% inclines respectively, and 2.56, 2.84 and 7.13 J/kg BW per m for −5.25, 0 and +10.5% inclines respectively, in the second experiment. The net energy cost of locomotion on the level appeared to be independent of live weight, attaining a value of 2.98 J/kg BW per m. Also, it was found that within experiments the net energy cost of walking on negative slopes was similar to that for locomotion on the level, indicating that no energy was recovered on vertical descent. Mean values were 3.11 and 2.72 kJ/kg BW per m for the light and heavy pigs respectively. The energy cost of raising 1 kg BW one vertical metre was found to be 27.1 J/kg BW per m in the first experiment and 40.0 J/kg BW per m in the second experiment. Correspondingly, the calculated efficiency for upslope locomotion appeared to decline with increasing BW, resulting in average values of 36.2 and 24.5%.

Locomotion: Energy cost

At present there is considerable interest in Europe for the diversification of the pig industry towards more extensive and sustainable production forms. This interest stems partly from the present surplus production of standard quality pork meat, but also from the growing concern of society about matters of animal welfare, pollution and environmental degradation caused by intensive farming. With extensification the production of native pig breeds and the use of local feed resources are both encouraged. This helps to maintain genetic diversity and facilitates the provision of high-organoleptic-quality niche products to consumers. Therefore, it is believed that extensive pig farming will expand in the near future at the expense of intensive systems of pig production. However, some potential constraints for further development of extensive pig production must be overcome to ensure optimal productivity. The provision of adequate nutrition is of utmost importance and must be based on a sound knowledge of nutrient and energy requirements at all stages of production. Physical activity of the free-living pig, and specifically the energy expenditure of

locomotion, may considerably increase the energy requirement for maintenance compared with the restrained animal and must be taken into account for an accurate assessment of its total energy needs. Although the energy cost of locomotion is relatively well defined in some farm animals (Lachica *et al.* 1997), with the exception of the surveys of Petley & Bayley (1988) and Jakobsen *et al.* (1994), no systematic studies have been carried out in the pig, to our knowledge. Also, there is no available information concerning efficiencies associated with vertical ascent or descent. Interspecies differences in locomotory efficiency exist as a result of morphological, physiological and behavioural adaptations (Taylor & Heglund, 1982), and may invalidate extrapolation of values derived from other species to the pig.

The present work was undertaken with the aim of determining the energy cost of walking on the level and on slopes in the Iberian pig (*Sus mediterraneus*), a native breed whose extensive production is strongly linked to the use of the area of the Mediterranean woodland prairie and has a long tradition in the south-west of Spain.

Abbreviations: BW, body weight; HP, heat production; ME, metabolizable energy.

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Materials and methods

Animals

Four growing castrated male pigs of the Iberian breed, with average body weights (BW) 43 (SE 0.1), 42 (SE 0.2), 41 (SE 0.3) and 39 (SE 0.1) kg in Expt 1, and 85 (SE 0.1), 84 (SE 0.2), 82 (SE 0.2) and 84 (SE 0.5) kg in Expt 2, were used. The same animals were used in both trials. They were 5 and 8 months old in Expt 1 and Expt 2 respectively, being called 'marranos' and 'primales', in each case. Throughout the two experiments they were given a commercial diet whose metabolizable energy (ME) content was estimated as 12.2 MJ/kg DM, at approximately 1.6 × maintenance intake. The ME requirement for maintenance was taken as 458 kJ/kg BW^{0.75} per d (Agricultural Research Council, 1981). These pigs were selected from a group of eight (34 (SE 0.3) kg BW) because they responded readily to a locomotory training programme in a motor-driven treadmill (Lachica *et al.* 1997). During 2 weeks each pig was repeatedly trained to walk on the belt of the treadmill moving at 0.555 m/s for several periods of 10–15 min daily. Full experimental adaptation was assumed when the animals walked in a steady way. Four animals failed to walk or maintained inadequate postures on the treadmill and were not used for the experiments.

Respiration chamber

The heat production (HP) of each animal while standing at rest or walking on the treadmill enclosed in a confinement-type respiration chamber (Lachica *et al.* 1995) was calculated from measurements of CO₂ production and O₂ consumption (Brouwer, 1965). The confinement-type respiration chamber was chosen because it is best suited for fast highly accurate response applications. The chamber is made of transparent acrylic plates and is provided with an internal ventilation system. An aliquot sample of the air was continuously sucked from the chamber for analysis and then returned to the chamber. To prevent increases of CO₂ level above 1% as a result of the animal's gas exchange, the chamber was flushed out for a few minutes with a stream of fresh air before each confinement period. 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 amounts 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. One calibration per week was performed over the course of the present experiments.

Experimental design

Two experiments were performed. In Expt 1, two set of measurements were made. The first set consisted of three replicates per pig while standing at rest (speed 0 m/s) on each of three different slopes (−10.5, 0 and +10.5%), giving a total of thirty-six (4 (animal) × 3 (replicate) × 3 (slope)) observations. This group of measurements was made to test

the hypothesis of the existence of a postural effect on the pig's energy expenditure. In the second set of measurements, three replicate observations were made per animal walking at a constant speed of 0.555 m/s on each slope (−10.5, 0 and +10.5%), involving thirty-six (4 (animal) × 3 (replicate) × 3 (slope)) determinations. The experimental treatments of these sets were combined and arranged sequentially according to slope, so that each gas exchange measurement on locomotion was preceded by a measurement while the pig was standing still at the same slope. Each pig performed a single replicate of slope treatments per day. Therefore, in one day a total of six calorimetry runs (three while the animal was standing at rest and three with the pig walking on the belt) were made per pig. The sequence of slope treatments was randomly established within days. In Expt 2, the procedure was similar except that the gas exchange measurements standing at rest were made only on the level (speed 0 m/s; slope, 0%), therefore giving a total of twelve (4 (animal) × 3 (replicate)) gas exchange determinations, which were combined with a set of thirty-six (4 (animal) × 3 (replicate) × 3 (slope)) measurements of the animals' energy expenditure on locomotion. In this experiment, two animals refused to walk on the −10.5% incline and a slope of −5.25% was used for all pigs instead. Consequently, slope treatments were set at −5.25, 0 and +10.5% when the pigs were walking.

The experimental procedure was as described by Lachica *et al.* (1997) with small variations. The determinations began when the animals were well adapted to the experimental treatments and showed no signs of stress. The measurements of gas exchange took place 16–20 h after feeding. The pigs were placed on the treadmill in the chamber at 09.00 hours. The environmental temperature in the chamber was 20 ± 0.5° with a relative humidity of 60 ± 3%. The experimental schedule consisted of 25–30 min standing followed by 20–25 min walking at each slope, the gas exchange being recorded after approximately 5 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 treatments imposed took place one after the other, except for brief pauses required between them for flushing the chamber with fresh air. It took 2 weeks for each animal to complete all treatments designed at each body weight. The HP of the animal was referred to BW and extrapolated to 1 h (J/kg BW per h). The data from the first set of measurements of Expt 1 were subjected to ANOVA (3 treatments (slope) × 4 animals, with 3 replicates (calorimetry runs per animal)) following a two-way ANOVA with replication, with 24 d.f. 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.

Two different procedures were used to estimate the energy cost of locomotion. (a) By subtracting the energy expenditure of the pig while standing at rest from that measured during walking (subtraction approach):

$$EC_w = (HP_w - HP_{st}) / (BW \times D_t), \quad (1)$$

where EC_w is the energy cost of walking (J/kg BW per m), HP_w and HP_{st} are the heat production (J) of the pig while

walking and standing respectively, BW is the animal body weight (kg) and D_t is the distance travelled (m).

The net energy cost of vertical movement on ascent, i.e. the energy expended in raising 1 kg BW one vertical metre (EC_{up} , J/kg BW per m) was calculated as:

$$EC_{up} = (EC_{sl} - EC_1) / \sin \alpha, \quad (2)$$

where EC_{sl} and EC_1 are the energy cost of walking (J/kg BW per m) on slope and on the level respectively, and $\sin \alpha$ is the fraction of a metre ascended per metre travelled.

The efficiency with which the pig performed the work of walking on positive slopes was calculated as the ratio 9.81 (J potential energy per kg BW raised 1 m) : EC_{up} and expressed as a percentage.

The net energy expenditure of vertical movement on descent, i.e. the energy recovered on lowering 1 kg BW 1 m (EC_{down} , J/kg BW per m) was estimated as:

$$EC_{down} = (EC_1 - EC_{sl}) / \sin \alpha, \quad (3)$$

where EC_1 and EC_{sl} have the same meaning as in equation 2 and $\sin \alpha$ is the fraction of a metre descended per metre travelled.

The efficiency of the recovery of potential energy while walking on negative slopes was calculated by dividing EC_{down} by 9.81, and expressed as a percentage.

(b) The energy cost of locomotion within slopes was also estimated from the coefficient of linear regressions of HP (J/kg BW per h) *v.* distance travelled (D_t , m; $m \geq 0$) (regression approach). For that purpose regression equations were obtained for each pig. The regression coefficients with their standard errors were used to test whether they were homogeneous (Steel & Torrie, 1981). Differences between individual regression slopes were not significant and a pooled regression equation using the data from the four pigs was calculated for each slope.

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) on 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 = distance upward; equals 0 otherwise,

D_d = distance downward; equals 0 otherwise.

Equations were fitted for each pig and estimates were then summarized over the four animals.

Results

Five and four determinations were discarded in Expts 1 and 2 respectively, due to anomalous RQ values, which could not be attributed to either the calorimetric technique or the animal's behaviour.

Table 1 shows the average results for HP and RQ of pigs standing at rest or walking on different slopes. In the first set of measurements within Expt 1, carried out on the lighter pigs standing still at each slope, it was found that the energy expenditure of the pigs was the same ($P > 0.05$) irrespective of the slope assayed. The overall mean value for the standing HP (n 33) was 11.99 (SE 0.47) kJ/kg BW per h. As no postural effect on HP was detected, in Expt 2 the energy expenditure of the pigs while standing at rest was always measured with the treadmill belt on the level and a mean value (n 10) of 11.54 (SE 0.49) kJ/kg BW per h was obtained. Average values of 0.86 (SE 0.02) and 0.78 (SE 0.02) were observed for RQ of the animals when standing at rest in Expts 1 and 2 respectively.

The exercise load had a significant effect on HP ($P < 0.001$) and RQ ($P < 0.01$). However, no significant differences were found between the HP of the pigs walking on the level *v.* downslope. Within experiments the standing HP was significantly lower ($P < 0.05$) than that observed on locomotion. In the light pigs the highest increases in energy

Table 1. The heat production (HP, kJ/kg body weight per h) and RQ of pigs standing at rest or walking at 0.555 m/s on a treadmill belt at various slopes

	Physical activity	Body weight (kg)		Slope (%)			Statistical analysis		
		Mean	SE	-10.5	0	+10.5	SEM	<i>P</i>	
Exp 1	Standing at rest	41.3	0.1	HP	12.57	12.37	11.19	0.476	NS
				RQ	0.85	0.84	0.87	0.012	NS
				<i>n</i>	10	11	12		
	Locomotion	41.3	0.1	HP	18.01 ^a	18.70 ^a	23.78 ^b	0.377	***
				RQ	0.82	0.79	0.79	0.010	NS
				<i>n</i>	12	10	12		
Expt 2	Standing at rest	84.1	0.1	HP	–	11.54 (SE 0.491)	–		
				RQ	–	0.78 (SE 0.015)	–		
				<i>n</i>		10			
	Locomotion	84.1	0.1	HP	16.70 ^a	17.28 ^a	25.69 ^b	0.307	***
				RQ	0.83 ^a	0.81 ^{ab}	0.77 ^b	0.012	*
				<i>n</i>	12	10	12		

^{a,b,c} Mean values within a row not sharing a common superscript letter were significantly different: $P < 0.05$.

* $P < 0.05$; *** $P < 0.001$.

Table 2. The energy cost of walking in pigs, estimated from linear regression of heat production (HP, J/kg BW per h) v. distance travelled (D_t , m)

Body wt (kg)		Slope (%)	Linear regression equation	r	RSD	n
Mean	SE					
41.3	0.1	-10.5	HP = 11998(SE 445) + 2.99(SE 0.429) D_t	0.728	2559	45
		0	HP = 11993(SE 458) + 3.31(SE 0.469) D_t	0.741	2631	43
		+10.5	HP = 11993(SE 434) + 5.88(SE 0.420) D_t	0.906	2496	45
84.1	0.1	-5.25	HP = 11531(SE 708) + 2.56(SE 0.496) D_t	0.773	2239	20
		0	HP = 11538(SE 400) + 2.84(SE 0.267) D_t	0.921	1265	22
		+10.5	HP = 11539(SE 451) + 7.13(SE 0.308) D_t	0.982	1428	22

RSD, residual standard deviation.

expenditure due to exercise load were accompanied by detectable decreases in RQ values, but this was not the case in the heavier animals.

Subtraction and regression approaches gave results for the energy cost of locomotion which were within 1.5% of difference. Thus, both calculation approaches were mutually corroborative. Only the results derived from the regression approach are reported here. The mean values of the energy cost of walking, estimated from linear regression of HP (J/kg BW per h) on distance travelled (D_t , m) for each slope, appear in Table 2. The intercepts of the regression equations are estimates of the pigs' metabolic rate while standing at rest (J/kg BW per h). No statistically significant differences between them were found. Moreover, these values did not differ statistically from the mean values of 11.99 (SE 0.47) and 11.54 (SE 0.49) kJ/kg BW per h (see Table 1) found in direct measurements of the pigs while standing, in Expt 1 and Expt 2 respectively. The mean slopes of these regression equations indicate that in the pig the energy cost of locomotion increases from 2.99 to 3.31 and from 3.31 to 5.88 J/kg BW per m on increasing the slope of the treadmill belt from -10.5 to 0 and from 0 to +10.5% at an average BW of 41.3 kg. At live weight averaging 84.1 kg it increased from 2.56 to 2.84 and from 2.84 to 7.13 J/kg BW per m on increasing the slope from -5.25 to 0 and from 0 to +10.5%. The analysis of covariance indicated that the regression coefficients of the equations that estimate the energy cost of locomotion on the level for pigs at 41.3 and 84.1 kg BW on average were not significantly different (3.31 (SE 0.47) and 2.84 (SE 0.27) respectively) and a pooled equation was calculated:

$$\text{HP} = 11887(\text{SE } 348) + 2.98D_t(\text{SE } 0.296), \quad (4)$$

r 0.786, residual SD 2283; n 65.

Similarly, the covariance analysis indicated that within experiments the regression coefficients of the lines calculated for the horizontal and downward slopes were homogeneous, and a pooled equation for each experiment was calculated accordingly:

$$\text{Expt 1: HP} = 11994(\text{SE } 418) + 3.11D_t(\text{SE } 0.330), \quad (5)$$

r 0.802; residual SD 2399; n 55,

$$\text{Expt 2: HP} = 11536(\text{SE } 587) + 2.72D_t(\text{SE } 0.354), \quad (6)$$

r 0.817; residual SD 1855; n 32.

The regression coefficients of these equations are not statistically significantly different and a pooled regression was obtained:

$$\text{HP} = 11887(\text{SE } 344) + 2.91D_t(\text{SE } 0.242), \quad (7)$$

r 0.796; residual SD 2253; n 87.

The mean values of the energy cost of walking were calculated by separating the horizontal (D_h) and vertical (D_u and D_d) components by a multiple regression equation of HP (J/kg BW per h) on the horizontal and vertical distances travelled (m) in ascent or descent, 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. It was found that the coefficient of the D_d term was not significantly different from zero. Thus, these equations were recalculated as follows:

$$\text{HP}_{\text{marranos}} = 11993(\text{SE } 435) + 3.31(\text{SE } 0.445)D_h + 24.7(\text{SE } 2.06)D_u, \quad (8)$$

r^2 0.796; residual SD 2497; n 55

$$\text{HP}_{\text{primales}} = 11540(\text{SE } 406) + 2.84(\text{SE } 0.271)D_h + 41.2(\text{SE } 2.49)D_u, \quad (9)$$

r^2 0.954; residual SD 1284; n 34.

As indicated earlier, the analysis of covariance demonstrated that the coefficients of the D_h term were not significantly different. For that reason, the coefficients of the D_u term in equations (8) and (9) were recalculated using the value of 2.98 J/kg BW per m as the energy cost of walking on the level irrespective of live-weight stage. These coefficients, expressing the net energy cost of lifting 1 kg BW, were 27.1 (SE 3.7; n 55) and 40.0 (SE 2.2; n 34) J/kg BW per m for Expts 1 and 2 respectively, and differed significantly ($P < 0.05$). Accordingly, the net energetic efficiency of upslope locomotion (vertical movement on ascent), calculated as the ratio work done: energy cost of doing it and expressed as a percentage, averaged 36.2 and 24.5%.

The energy equivalent of the O_2 consumed and of the CO_2 produced by the pigs while walking above that observed while standing at rest on the treadmill belt was calculated by regression of the net energy expenditure due

to locomotion ($HP_w - HP_{st}$, J per h) v. the increase in O_2 consumption or CO_2 production above standing ($(O_{2w} - O_{2st})$ or $(CO_{2w} - CO_{2st})$, ml per h) and was found to be 20.2 (SE 0.03) and 25.2 (SE 0.15) respectively (n 111). These values or the corresponding RQ could be used to calculate HP from O_2 or CO_2 measurements using a dilution technique (doubly-labelled water or CO_2 entry rate techniques).

Discussion

The specific objectives of the present study were to assess the net energetic costs of horizontal and vertical locomotion of the Iberian pig by means of indirect calorimetry, and to evaluate its additional energy expenditure due to physical activity. The final aim was to provide estimates of the overall energy expenditure of the grazing pig by applying the factorial approach. As stated previously (Lachica *et al.* 1997), we are aware of the limitations of extrapolating to free-living situations data derived from experiments with treadmills, particularly when the animal has to walk on soft, uneven or wet surfaces instead of the firm even surface of a treadmill (Fancy & White, 1985). The experimental values assigned to the variables were selected to give rise only to mild or moderate work loads, as are expected to occur in the grazing pig. During the present trials the animals travelled a distance of 2500 m daily, while their metabolic rate was measured throughout 75–90 min. The physical activities imposed on the animals required at most 50% of maximal O_2 consumption, calculated from values reported by Petley & Bayley (1988) for young growing pigs. The use of a higher speed might have improved the accuracy of the estimates of the locomotion costs, since in this case the energy expenditure of the animal while standing still would have been proportionately a minor fraction of total energy expenditure during exercise. Nevertheless, the work loads used in the present study increased the animals' HP to values up to 2.0–2.2 times those associated with standing at rest.

In a separate group of measurements we failed to find significant differences in HP of standing before and after 10 min of travelling at 0.555 m/s on different slopes. The mean value of differences between pre- and post-exercise HP (J/kg BW per h) was 0.25 (SE 1.04) (n 8). This would suggest that the work loads assayed did not produce a detectable O_2 debt and that there was a lack of carry-over effects from preceding physical activities.

During the 3-month interval that elapsed between Expts 1 and 2 the weight of the pigs increased from 41.3 to 84.1 kg. However, a non-significant decline in standing HP was observed (12.0 (SE 0.5) v. 11.5 (SE 0.5) kJ/kg BW per h). When expressed relative to metabolic BW these values were equivalent to 730 and 838 kJ/kg BW^{0.75}. One would expect lower metabolic rates and a comparatively lower value in the heavier pigs. However, experiments encompassed a 2–3 h period 16–20 h after feeding. Energy expenditure over this period of measurements is unlikely to reflect accurately the mean daily HP as many of the digestive, absorptive and metabolic processes will be 'post-peak'. Care therefore needs to be exercised in using this value for comparative purposes. Different factors may have contributed to the high values observed for the standing HP: energy cost of

standing, residual effect of feeding intake, etc. Even a certain degree of excitement of the animals when placed in the chamber should not be disregarded. The values for energy expenditure due to standing were estimated to be 6.46 and 5.41 kJ/kg BW per h on the basis of data reported by Noblet *et al.* (1993), who observed an average increase of 0.273 kJ/min per kg BW^{0.75} in the HP of adult sows when standing over resting. Therefore this cost represented about 50% of the total HP measured when the pigs were standing at rest. Accordingly, in our experiments the HP not accounted for by standing attained values equivalent to 337 and 443 kJ/kg BW^{0.75} per d respectively for lighter and heavier pigs, which are reasonably close to literature values for fasting growing pigs.

The pattern of RQ indicates a preferential oxidation, in muscles, of fatty acids as energy yielding nutrients. This was expected to be so as the animals were in a postabsorptive state at the time when measurements were made. In the light pigs the exercise caused a further increase in O_2 consumption relative to CO_2 production, therefore showing an enhanced use of fat as the substrate being oxidized. It is likely that in the lighter pigs liver glycogen or glucogenic amino acids could have contributed significantly to providing glucose as the energy source for the mild physical activity of maintaining the standing position.

We did not find significant differences between the intercepts of the linear regression equations relating HP and distance travelled (Table 2). This agrees with previous observations of Brockway & Gessaman (1977) in red deer (*Cervus elaphus*) and earlier results from our laboratory obtained with Granadina goats (*Capra hircus*) (Lachica *et al.* 1997) suggesting that the energy costs of maintaining posture did not differ between walking and standing.

The net energy costs of locomotion on the level of Iberian pigs with average BW of 41.3 (SE 0.1) and 84.1 (SE 0.1) kg were 3.31 and 2.84 J/kg BW per m respectively. These values were not significantly different and, therefore, the pooled value of 2.98 J/kg BW per m was calculated. However, our values would suggest a lowering effect of BW on the net energy cost of horizontal locomotion, a fact well documented (Taylor *et al.* 1970; Cohen *et al.* 1978), although of limited practical value for interspecies comparisons. There is a paucity of information about the energy cost of locomotion in pigs. Only two papers, those by Petley & Bayley (1988) and Jakobsen *et al.* (1994), have been found in which the increases in HP of pigs moving on the level over that of standing were measured. However, neither in the paper by Petley & Bayley (1988) nor in the work of Jakobsen *et al.* (1994) are the energy costs of walking reported. Net energy costs in the range of 5.59–6.43 J/kg BW per m can be calculated from data for energy expenditure (kJ/kg BW per h) measured by Petley & Bayley (1988) while the pigs were walking on the level on a treadmill belt at speeds varying from 0 to 1.94 m/s. The measurements were made in pigs of 9.5 kg live weight subjected to submaximal and maximal O_2 consumption tests, beginning the exercise load at 0.833 m/s and increasing the speed stepwise every 5–10 min. From the study of Jakobsen *et al.* (1994) made on pigs of 88.6 and 78.7 kg average BW we have calculated mean values of 5.00 and 4.78 J/kg BW per m for the net cost of horizontal locomotion. In the

work of Jakobsen *et al.* (1994), the HP of the animals was measured before, during and after walking on a horizontal moving belt. The energy costs for horizontal locomotion calculated from both trials are higher than those reported in the present experiments. The small size of the pigs used in the survey of Petley & Bayley (1988) may, to some extent, explain the high costs of locomotion observed there. Moreover, it should be mentioned that in both experiments the gas exchange of the pigs was measured over short periods of time by means of open-circuit respiration chambers. Except with new equipment a lag time may be necessary for response to changes in O₂ and CO₂ content in the air within the chamber, a fact which could have a deep influence on the accuracy of the estimates. Nienaber *et al.* (1985) reported on difficulties encountered for accurate partition of energy expenditure into fasting HP and HP relative to physical activity in experiments on fasted calves, sheep and pigs designed to measure the increase in HP due to physical activity by means of open-circuit respiration chambers. The confinement-type respiration chamber used in our experiment relies almost exclusively on the accuracy of the analytical equipment being particularly appropriate for gas exchange measurements over short periods of time.

Most of the available data on energy cost of locomotion of farm animals refer to ruminants. Concerning the net energy cost of horizontal locomotion, Taylor *et al.* (1974) obtained a value of 3.63 J/kg BW per m in the domestic goat, a value somewhat higher than that of 3.35 J/kg BW per m which we found in the Granadina goat (Lachica *et al.* 1997); Clapperton (1964), Farrell *et al.* (1972) and Brockway & Boyne (1980) reported, in sheep, values of 2.47, 2.83 and 2.30 J/kg BW per m respectively; and 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 BW. Assuming a factor of 20.3 J/ml O₂ consumed (Lachica *et al.* 1997) net energy expenditures in the range of 4.87 to 5.68 J/kg BW per m are obtained. In the desert gazelle (*Gazella gazella*) Taylor *et al.* (1974) found a value of 3.23 J/kg BW per m. The lowest energy costs of locomotion on the level have been reported in equines (0.97 J/kg BW per m in donkeys (Dijkman, 1992); 1.02 J/kg BW per m in ponies (Booth *et al.* 1992); 1.54 J/kg BW per m in horses (Brody, 1945)). Boyne *et al.* (1981) obtained, in human subjects, values of 2.10 and 2.27 J/kg BW per m for the net energy cost of locomotion on the level.

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 the horizontal costs. However a survey of the data for HP shown in Tables 1 and 2 demonstrates that the pig seems to have a low ability to move downslope, which results in energy expenditures and net energetic costs close to those found when moving on the level. This helps to explain some particular difficulties

we observed in fully adapting the animals to walk on negative slopes during the training stage. Although the regression coefficients of equations 5 and 6 are not statistically significantly different, they were derived from data obtained in experiments in which different negative gradients were assayed. Therefore, an overall value for the net energy cost of locomotion on the level and on negative slopes irrespective of the BW, derived from a pooled single equation (7), should be taken with caution.

In the present experiments the values for net energetic efficiency of upslope locomotion (vertical movement on ascent) were found to average 36.2 and 24.5 % for light and heavy pigs. Published data on energy cost of vertical locomotion are in the range 25.4–37.7 J/kg BW per m for sheep (Clapperton, 1964; Farrell *et al.* 1972; Brockway & Boyne, 1980); and 26.0–30.3 J/kg BW per m for cattle (Ribeiro *et al.* 1977; Shibata *et al.* 1981). From these costs apparent energetic efficiencies ranging from 40.9 to 26.0 % can be calculated. In Granadina goats we found an average value of 31.7 J/kg BW per m for the energy cost of upslope locomotion corresponding to an apparent net efficiency of 30.9 %. The apparent efficiency of the performance of muscular work in raising body mass vertically for human subjects obtained by Boyne *et al.* (1981) was 31.2 %. It is generally assumed that the energetic efficiency of upslope locomotion is independent of live weight (Farrell *et al.* 1972; White & Yousef, 1978; Shibata *et al.* 1981; Dailey & Hobbs, 1989). 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 %. Contrary to this assumption our results show that in the pig the efficiency of physical work declines on increasing BW.

Controversial results have been reported concerning the energy cost of downslope locomotion. For this reason, and given the dearth of data available, the Agricultural Research Council (1980) assumes that for ruminants this cost of descent is similar to that of walking on the level. Theoretically, downslope locomotion is less expensive because gravitational energy is recovered as kinetic energy during descent. It is doubtful whether this energy can be recovered by the body. Data on the net energy recovered during downslope locomotion are extremely variable (J/kg BW per m: 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, Dijkman, 1992), giving values of recovery efficiencies in the range of 20.4 to 202.9 %. Therefore some of them exceed the maximum transfer in potential energy per metre of vertical movement. The average amount of energy recovered while the pigs were moving on negative slopes was found to be not significantly different from zero, and so it should be assumed that no recovery of potential energy can be obtained by the pig when moving on negative slopes. For that reason, no statistical differences in the HP of the pigs were found between walking on the level and downslope (Table 1) which resulted in similar energy costs. It should be mentioned that when the animal moves downslope, antagonist muscles lengthen under tension while others shorten, performing what has been defined as ‘negative work’. Under these circumstances, the calculation of the efficiency of

recovery of potential energy would have no meaning, and the coefficient of D_d would be only an index of the likely energetic saving effect of negative work (Lachica *et al.* 1997).

The production of the Iberian pig is strongly linked to the use of the Mediterranean woodland prairie, which spreads over 2.4 million hectares, most of them in the regions of Extremadura and Western Andalusia, in south-western Spain. No data are available on distances walked by Iberian pigs on grazing conditions, but our estimates are in the range of 1.5–3 km/d. According to our results the energy expenditure of a pig of 80 kg BW walking 2 km and ascending 200 m daily would be $80 \times (2000 \times 2.84 + 200 \times 41.2) \text{ J} = 1.11 \text{ MJ}$. Assuming a net efficiency of utilization of ME for maintenance of 0.8 this increase would require an additional 1.39 MJ ME/d.

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