Published December 4, 2014

Energy cost of activities and locomotion of grazing cows: A repeated study in larger plots[1]

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ABSTRACT: We determined the energy costs associated with the activities of beef cows grazing on Mediterranean foothill rangeland covered with herbaceous vegetation. Our central aim was to compare the energy cost coefficients obtained in this study, using relatively large plots, with those obtained in a previous study conducted on smaller plots. Measurements were performed in 3 seasons: in March on nursing cows grazing a 135-ha plot of high quality herbage (11.4 MJ/kg of ME), and in May and September on nonlactating cows grazing a 78-ha plot of low quality herbage (6.2 MJ/kg of ME). Poultry litter manure was given as a supplement in September. Stocking rates on the respective plots were 2.25 and 1.95 ha/cow; 5, 5, and 7 cows were monitored in the respective months. Heat production was determined by continuous monitoring of the heart rate and measurement of the oxygen consumption per heartbeat. Animal location was tracked with global positioning system (GPS) collars equipped with motion sensors. Activity was determined for 5-min intervals using suitable calibration equations. Horizontal and vertical distances traveled were computed by integrating GPS data and plot maps in a geographic information system. Three models were used to estimate the energy cost coefficients of engaging in a given activity and locomotion. Total daily heat production ranged from 644 (September) to 1,014 kJ·kg of $BW^{-0.75}·d^{-1}$ (March; $P = 0.04$). Estimates of the energy cost coefficients for activity states (kJ·kg of $BW^{-0.75}·d^{-1}$) ranged from 42.7 to 46.2 for standing, from 84.5 to 92.4 for walking idle, and from 89.4 to 103.2 for grazing; those for locomotion (kJ·kg of $BW^{-0.75}·d^{-1}·km^{-1}$) ranged from 2.8 to 2.9 for horizontal locomotion and from 21.4 to 27.9 for vertical locomotion. Estimated cost coefficients of standing, grazing, and horizontal locomotion derived in the present study from animals on relatively larger plots were similar to those of the previous study based on data from smaller plots, but the energy costs of walking idle and of vertical locomotion were greater in the present study than in the previous one. The differences found are associated with the fact that cows in the present study walked for longer periods of time and traveled longer distances in single uninterrupted bouts of locomotion than those in the previous study.

Key words: cattle, energy cost, global positioning system, grazing, heart rate, heat production

J. Anim. Sci. 2010. 88:315–323
doi:10.2527/jas.2009-2108

INTRODUCTION

The energy expenditure or, equivalently, heat production (**HP**) of cattle on rangelands is influenced by the interrelated factors of forage supply and quality, environmental conditions, and behavior. A mechanistic approach to deriving daily HP should integrate rates that change according to the diverse repertoire of actions that make up daily behavior. This requires continuous and simultaneous monitoring of behavior and HP. Such an approach was developed by Brosh et al. (2006), who used the heart rate (**HR**) method to measure HP and global positioning system (**GPS**) collars to determine behavior. Behavior was defined in terms of activity and locomotion. Activity comprised 4 states: resting while lying down, resting while standing, grazing, and walking idle (i.e., without grazing). Locomotion was considered separately because the rate of HP during grazing and walking idle depends on how fast

[1]Contribution from the Agricultural Research Organization, Bet Dagan, Israel, No. 499/07. Partly supported by grant US-3694-05 from BARD, the United States-Israel Binational Agricultural Research and Development Fund. The authors thank Zadok Cohen, manager of Karei Deshe Experimental Farm, for his extraordinary assistance and support during this project.

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Received May 5, 2009.
Accepted August 27, 2009.

the animal moves and on the breakdown of that movement into its horizontal and vertical vectors. This approach can yield cost coefficients to evaluate the energy expended on activities and locomotion by cows grazed under different conditions, when these behavioral components are recorded.

To develop confidence in the estimates generated by a new methodology, it is important to expand the range of conditions under which the data are gathered. The study of Brosh et al. (2006) was conducted in relatively small plots of 28 ha. Plot size may affect animal behavior (Hunt et al., 2007); in larger plots (**LP**) each individual has a larger area to explore for herbage selection, and this exploration may affect the time spent and distances covered in various activities.

The objective of the present study was to obtain estimates of the energy cost coefficients from animals foraging in larger plots, and compare them with the estimates obtained previously in smaller plots. The study hypothesis is that the energy cost coefficients can be regarded as constants that are little affected by plot size.

MATERIALS AND METHODS

All procedures involving animals were approved by the Israeli committee for animal care and experimentation.

Experimental Site

The present study was conducted in 2004 on the Karei Deshe Experimental Farm, the same site used in the previous study of Brosh et al. (2006). It is situated in the Lower Galilee, Israel, near the Jordan River's entry into the Sea of Galilee; latitude 32° 55′ N, longitude 35° 35′ E, altitude 60 to 250 m above sea level (Gutman et al., 1999). The topography is hilly, with slopes generally less than 20° (Seligman et al., 1989). The site has a Mediterranean climate, characterized by wet, mild winters with mean minimum and maximum temperatures of 7 and 14°C, respectively; the average annual precipitation is 570 mm, mostly from November to March. The summer is dry and hot, with mean minimum and maximum temperatures of 19 and 32°C, respectively. There are at least 6 mo (May to October) of dry weather, with very little or no rain (Sternberg et al., 2003). Throughout the days of measurement, average minimum and maximum temperatures were 11.4 and 27.4°C in March, 15.4 and 26.9°C in May, and 14.6 and 35.1°C in September. Average minimum and maximum relative humidity, respectively, were 27 and 83 in March, 32 and 78 in May, and 25 and 86% in September. There were 31 mm of rain in March, and none in May and September.

The soils in the experimental area are brown basaltic protogrumusols of variable depth, seldom deeper than 40 cm, with a rock cover of about 30% (Gutman and Seligman, 1979). The vegetation is characterized by species richness: a total of 166 herbaceous plant species were identified in the experimental plots from 1994 to 1997 (Sternberg et al., 2000).

Experimental Plots, Stocking Rates, and Measurement Months

Topographic maps of the 2 LP, A and B, used in the present study are shown in Figure 1. The small plot (**SP**), C, used in the previous study (Brosh et al., 2006) is also shown for comparison. The area of plot A was 135 ha; its maximum length and width were 1.7 and 0.8 km, respectively; and the maximum distance from a water trough was 1.2 km. Plot B was 78 ha in size, its maximum length and width were 1.1 and 0.75 km, respectively, and the maximum distance to water was 1.1 km. The maximal vertical ranges within both plots were 75 m. Measurements in plot A were conducted in March 2004 (early spring), on cows stocked at a rate of 2.25 ha/cow-calf pair (60 cows/plot). Measurements in plot B were conducted in May and September 2004 (early summer and late summer, respectively), at a stocking rate of 1.95 ha/cow (40 cows/plot). In September, a sole supplemental feed of broiler poultry manure (**PL**) was offered freely to the cows from a wagon that served as a mobile feed trough; PL was available to the cows throughout the day. Poultry manure consumption was 1.31 kg of DM/d per cow. The quality of PL in the present study was better than that used by Brosh et al. (2006), and this was reflected in greater CP (23.6 vs. 20.3%) and lesser NDF (27.6 vs. 33.7%). In each plot there was a water trough and a PL feeding trough located within 100 m.

Animals and Measurements

Mature, medium frame Simford (Simmental × Hereford) crossbred cows, with about 20% blood from local eastern Mediterranean breeds, were used. Simultaneous measurements of HP and behavior (activity and locomotion distance) were conducted on 17 animals: 5 in March, 5 in May, and 7 in September. These animals were designated as the **ActY** group. The availability of equipment enabled us to measure HP on 12 additional animals (designated the **ActN** group): 4 in March, 6 in May, and 2 in September. The database of HP measurements was extended this way to provide some indication of the representativeness of the ActY group. Different individuals were monitored in each month because the experiments were carried out in a commercial herd, and we did not want to disturb the cow hierarchy and behavior.

In each month, HP and behavior were monitored continuously over 4 consecutive days. On the following day we measured BW and BCS on a 1 to 5 scale (Edmonson et al., 1989) and oxygen consumption. The ages (years; mean ± SE) of the cows in groups ActY and ActN were, respectively, 8 ± 0.3 and 9 ± 1.5 in March, 9 ± 1.5 and 8 ± 0.5 in May, and 8 ± 0.6 and

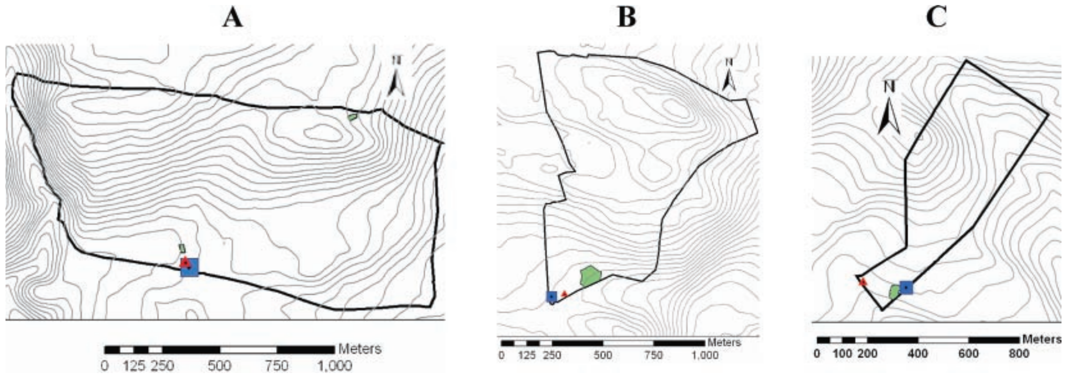

Figure 1. Contour maps of the plots used in the present study (A: 135 ha; B: 76 ha) and in the previous study (C: 28 ha; Brosh et al., 2006); ▲ = place of supplement feed trough; ■ = place of water trough; small patch represents tree-shaded area. The vertical distance between contour lines is 10 m.

10 ± 1.5 in September. The BW (kg; mean ± SE) of the cows in groups ActY and ActN were, respectively, 426 ± 12 and 420 ± 21 in March, 449 ± 41 and 492 ± 26 in May, and 479 ± 28 and 460 ± 25 in September. The BCS of the cows (mean ± SE) in groups ActY and ActN were, respectively, 3.0 ± 0.03 and 3.2 ± 0.13 in March, 3.0 ± 0.07 and 3.2 ± 0.13 in May, and 3.3 ± 0.10 and 3.0 ± 0.10 in September.

Reproductive state was deduced from the calving date, assuming a 280-d pregnancy. In March, cows were nonpregnant and nursed calves 53 ± 13 d old. In May, cows were nonlactating and in early pregnancy, with an average fetus age of 32 ± 18 d. In September, cows were nonlactating and in mid to late pregnancy, with a fetus age of 197 ± 22 d.

Cow Measurements

HP. The measurement procedures were identical to those described by Brosh et al. (2006). Heat production was calculated by multiplying the recorded HR by the oxygen consumption per heart beat (the O_2 pulse) and by the constant value of 20.47 kJ/L of O_2 consumed (Nicol and Young, 1990). The O_2 pulse was determined once for each cow, 1 d after the 4th day of HR and activity measurements. Measurements from each cow were taken over 10 to 15 min (Aharoni et al., 2003; Brosh, 2007). Measurements of oxygen consumption were taken in the shade when the cows were standing in a cow squeeze. The measurements were started in the morning, at about 0700 h, and taken for about 3 to 4 h in each month. Heart rate was measured with 2 electrocardiogram electrodes and recorded with a Polar instrument set comprising a model T51H HR RF transmitter and a Watch Model S610 data logger (Polar Electro Oy, Kempele, Finland). The devices were attached to the thorax, behind the forelegs, by means of a specifically designed elastic belt (Pegasus, Eli-ad, Israel). The logger (Polar watch) was programmed to record HR at 1-min intervals; series of 5 HR records were averaged to represent each 5-min interval.

Activity and Locomotion Distance. Animal activity and locomotion distance were determined from data recorded by Lotek GPS collars of the 2200 Series (Lotek Engineering Inc., Newmarket, Ontario, Canada). The collars were configured to record GPS positions at 5-min intervals, as well as the number of vertical and horizontal movements of the collar detected by the built-in motion sensors during 4 of the intervening minutes. Four activities: lying, standing, grazing, and walking idle (i.e., walking without grazing), were determined from the collar data using the calibration equations developed by Ungar et al. (2005). Horizontal and vertical locomotion distances during each 5-min interval were computed with the ArcView 9.1 geographic information systems software from layers containing the GPS and topographic data. The time devoted to each activity and the horizontal and vertical distances covered were also calculated on a daily basis.

Herbage Analyses

The biomass and chemical composition of herbage in the plots were determined for the weeks during which animal measurements were conducted. Herbage was sampled by clipping to ground level 10 quadrates (0.25 × 0.25 m) along each of the four 100-m transects (i.e., 40 samples per plot). The samples were dried at 60°C for 48 h. Samples for chemical analysis were prepared by pooling the 10 herbage samples from each transect, yielding 4 representative samples for each combination of plot and measurement month. Chemical analyses of the herbage were carried out for DM (105°C), CP (Kjeldahl), and ash (550°C) according to the AOAC (1980). The NDF content was determined with the Ankom Fiber Analyzer (Fairport, NY) according to Van Soest et al. (1991); in this modification of the Ankom system, the sample is enclosed in a filter bag in which it remains throughout the process. Metabolizable energy concentration of the samples was determined separately from the NDF analysis. In vitro DM and OM disappearance were determined with the Ankom Daisy system

(Ankom). In this analysis we used the 2-stage system of 48 h of microbial digestion, followed by 48 h of pepsin-HCl; therefore, digestible microbial material was removed. Organic matters of the herbage samples and of the herbage undigested material were determined, and OM digestibility was calculated from the DM digestibility. The DE content of the digestible OM fraction of the herbage was calculated from the in vitro OM disappearance on a basis of 18.7 MJ/kg. Metabolizable energy of the herbage was calculated as ME = 1.01 × (DE − 1.88; NRC 1989; transformed from Mcal to MJ units).

Data Analysis

The data are presented as means ± SE. The differences among months in terms of herbage chemical composition and biomass were tested by 1-way ANOVA, in which each month (plot) was represented by 4 samples, 1 for each transect in the plot.

The effect of month on the total daily heat production of a cow (**THP**; kJ·kg of $BW^{-0.75}\cdot d^{-1}$) was tested by ANOVA. Separate 1-way ANOVA were conducted for the THP data collected for: a) all 29 cows used in the study; b) the 17 cows in group ActY; and c) the 12 cows in group ActN. The difference in THP between groups ActY and ActN was tested by 2-way ANOVA.

The differences among months in daily duration of activities (h/d) of each cow and the daily horizontal and positive vertical distances traveled (m/d) while cows grazed and walked idle (together and separately) were tested by 1-way ANOVA.

Derivation of the Energy Cost Coefficients

The energy cost coefficients were derived from data on 17 cows throughout 4 d of measurement at 5-min intervals. Each record in the data set included the following variables: cow identification (17 levels); month (3 levels: March, May, and September); hour of the day (24 levels); activity (4 levels: lying down, standing, walking idle, and grazing); horizontal and positive vertical locomotion distances; and HP. Even though locomotion energy cost per movement of 1 m was directly measured per 5 min (i.e., at a speed of 1 m/5 min), they were expressed as kilometers per day by multiplying the m/5 min by 1,000/288.

Analysis Models

HP. Total daily HP is strongly affected by level of energy intake (Brosh et al., 2004; Brosh, 2007), and this, in turn, depends on herbage quality and availability and on the reproductive state of the cow (Aharoni et al., 2004). In addition, the pattern of HP changes in cows during the day is affected by factors such as weather, day length, and pasture conditions (Brosh et al., 2004), many of which are interrelated. The usual approach to estimating the effects of possibly interrelated variables is using step-down multiple regressions (the stepwise model), which for the first time includes all the assumed effects together. In this procedure, every variable that is not found to be significant in a full model is excluded from the final best model; however, a model that takes into consideration the contributions of all these factors together to form a baseline HP, and attributes additional HP to an activity, is still expected to yield estimates that are biased because of confounding effects among the remaining factors and variables. On the other hand, if some of these factors are not taken into account by the model, the estimations of energy costs of the activity of the cow may also be biased, but differently so; therefore, we constructed 3 partial models to receive a range of estimates of activity cost across these models. All 3 models were used as a stepwise model (i.e., variables whose effect was found insignificant were excluded from the model).

Three models were used in the study: 1) the full model; 2) as model 1, but without month and the month × hour interaction; 3) as model 2, but without time of day.

The models were defined as follows:

$$1)\ HP_{ijkm} = K + A_i + AC_m + DH + DV + M_j + (M_j \times H_k) + e,$$

$$2)\ HP_{ikm} = K + A_i + AC_m + DH + DV + H_k + e,$$

$$3)\ HP_{im} = K + A_i + AC_m + DH + DV + e,$$

where HP = measured heat production (kJ·kg of $BW^{-0.75}\cdot d^{-1}$); K = constant; A_i = random effect of cow i, i = 1 to 17; AC_m = fixed effect of activity m, m = 1 to 4; DH = horizontal velocity ($km\cdot d^{-1}$); DV = positive vertical velocity ($km\cdot d^{-1}$); M_j = fixed effect of month j, j = 1 to 3; H_k = fixed effect of hour of day k, k = 0 to 23; and e = random residual effect.

With respect to activity, the analysis yielded the energy cost coefficients in terms of the expected increase in HP above the lying-down state generated by standing, grazing, and walking idle, and by horizontal and positive vertical locomotion costs.

Herbage chemical composition, calculated ME, biomass, and animal BW, BCS, and reproductive state were not included in the statistical analysis of the energy expended on activities and locomotion to avoid confounding between measurement month and these variables and factors, but part of their effects can be interpreted from comparing coefficients and locomotion costs of the models, as will be explained in the next section. High herbage ME and nursing calves are the most dominant variables that cause increase in HP of grazing cows (Brosh et al., 2004) and affect the duration of the daily activities of the cows (Brosh et al., 2006). The meaning of the similarity between model 1 and model

Table 1. Standing biomass, chemical composition, and ME content of the herbage samples (DM basis) taken in March (early spring), May (early summer), and September (late summer) and chemical composition of the poultry litter (PL)[1] samples

Item	March	May	September	PL	SE
Biomass, kg/ha	1,084[a]	2,415[b]	1,104[a]	—	149
Ash, g/kg	171[c]	116[a]	135[b]	180	8.6
NDF, g/kg	364[a]	673[b]	655[b]	276	17.9
CP, g/kg	195[b]	54[a]	46[a]	236	15.9
ME, MJ/kg	11.36[b]	6.18[a]	6.20[a]	—[2]	0.53

[a–c]Within a row, means without a common superscript differ ($P < 0.05$).

[1]Poultry litter chemical composition is not included in the statistics and superscripts.

[2]The ME concentration of PL is not presented because in vitro digestibility of this supplement could not be used for the ME calculation (Brosh et al., 2004).

2 in a specific coefficient of activity, and of locomotion costs, is that the month of measurement did not affect the specific coefficient and specific estimated locomotion cost; consequently, the logical interpretation of the similarity between the estimated costs of model 1 and model 2 is that variables like reproductive state (lactating vs. nonlactating cow) and herbage nutritional quality do not affect the specific energy cost of each of the defined activity and locomotion costs.

Daily Energy Expenditure on Activities and Locomotion. For each activity state of standing, grazing, and walking idle, the daily energy expended by an animal (exclusive of the locomotion component for grazing and walking) was calculated by multiplying the total amount of time allocated to it in the course of a day by its cost coefficient. The daily energy expended on horizontal locomotion was calculated by multiplying the total horizontal distance covered by an animal in the course of a day by its cost coefficient. The energy expended on positive vertical locomotion was calculated similarly. The total amount of energy expended on grazing was calculated by summing the energy expended by being in the state of grazing, and the energy expended on locomotion while grazing. The total amount of energy expended on walking was calculated similarly. The total daily increment in energy expenditure above the lying-down state (**EAC**) was equal to the sum of energy expended on standing, grazing, and walking. All the above calculations used the energy cost coefficients estimated by model 1.

All analyses were performed with Genstat software, seventh edition (Lawes Agricultural Trust, 2003). Effects on HP were analyzed by the REML procedure, with fixed effects of month, time of day, activity, and all their interactions.

RESULTS

Herbage sampled in early spring (March) was of significantly better quality than that sampled later in the year (May and September), as reflected by the lesser NDF and greater CP and ME concentrations in March (Table 1).

HP

The oxygen pulse (mL·beat^{-1}·kg of BW$^{-0.75}$) of all cows used was 0.362 ± 0.014 in March, tended to decrease (0.325 ± 0.012) in May ($P < 0.1$) and to decrease further (0.306 ± 0.013) in September ($P < 0.1$). Total daily heat production was significantly affected by measurement month. Values measured in March, May, and September for all 29 cows that wore HR monitors were, respectively, 950 ± 43, 650 ± 26, and 645 ± 22 kJ·kg of BW$^{-0.75}$·d^{-1} ($P < 0.001$); those of group ActY were, respectively, 1,014 ± 50, 679 ± 47, and 644 ± 25 kJ·kg of BW$^{-0.75}$·d^{-1} ($P < 0.05$), and those of group ActN were, respectively, 870 ± 47, 627 ± 31, and 646 ± 28 kJ·kg of BW$^{-0.75}$·d^{-1} ($P < 0.05$). Neither THP nor basic physiological status (BW, BCS, and reproductive state) differed significantly between animals in groups ActY and ActN within each month. The similarity in THP between the 2 groups suggests that the animals in group ActY can be regarded as a representing a larger sample of the herd. The THP of the lactating cows grazing in March (on lush, green, high quality herbage) was greater ($P < 0.05$) than that measured in the other months. This is consistent with common knowledge of the dependency of THP on ME intake and with earlier work (Brosh, 2007) on grazing cows, showing that THP is strongly influenced by ME intake, which, in turn, depends on herbage ME and animal reproductive state.

Energy Cost Coefficients

The 3 statistical models examined yielded highly significant ($P < 0.001$) estimates of the energy cost coefficients associated with an activity state and locomotion over and above the energy expended while lying down (Table 2). The coefficients of determination (R^2) of the 3 models ranged from 0.55 to 0.60. The energy cost coefficient associated with an activity state was 44 kJ·kg of BW$^{-0.75}$·d^{-1} for standing (average estimate for the 3 models), and double that amount for walking idle (88 kJ·kg of BW$^{-0.75}$·d^{-1}). The energy cost coefficient for grazing (94 kJ·kg of BW$^{-0.75}$·d^{-1}) was about 7% greater than that for walking idle. The energy cost coefficient of vertical locomotion was approximately 8 times that

Table 2. Coefficients of energy increment above lying-down state of activity (kJ·kg of $BW^{-0.75}·d^{-1}$) and locomotion (kJ·kg of $BW^{-0.75}·d^{-1}·km^{-1}$), as determined by 3 statistical models

	Activity state					Locomotion						Entire model
Item[1]	Standing	Walking	Grazing	SEM	$P^2 <$	Horizontal	SEM	$P^3 <$	Vertical	SEM	$P^4 <$	R^2
Model												
1	43.2	86.1	89.4	4.2	0.001	2.80	0.135	0.001	21.42	1.36	0.001	0.60
2	42.7	84.5	90.8	4.3	0.001	2.80	0.138	0.001	22.22	1.39	0.001	0.58
3	46.2	92.4	103.2	4.3	0.001	2.92	0.142	0.001	27.92	1.40	0.001	0.55
Average	44.03	87.67	94.47	—	—	2.84	—	—	23.85	—		
CV%	2.48	2.75	4.64	—	—	1.45	—	—	8.58	—		

[1]The models are defined in the Materials and Methods.
[2]P-value of activity term in the model (AC_m).
[3]P-value of horizontal distance term in the model (DH).
[4]P-value of positive vertical term in the model (DV).

of horizontal locomotion. The calculated coefficients of models 1 and 2 were almost identical. This means that measurement month, which includes differences in reproductive state and herbage quality, did not affect the coefficient estimations. Model 3, which did not take into account the effect of the time of the day, differed somewhat from models 1 and 2; for activity states the greatest estimate (generated by model 3) was greater than the lesser estimate by 8% for standing, 9% for walking, and 15% for grazing. For locomotion cost, the largest estimate (model 3) was 4 and 30% greater than the smallest estimate (models 1 and 2) for horizontal and vertical movement, respectively.

Time Spent and Distance Covered in Each Activity

The time spent lying down ranged from 5.4 to 7.1 h/d and did not differ significantly among months (Table 3). Standing accounted for 6.6 to 9.0 h/d and was less in March than in May and September ($P < 0.05$). In contrast, grazing time was longer ($P < 0.05$) in March (11.7 h/d) than in May and September. The time spent walking idle increased ($P < 0.05$) from March to May and increased further ($P < 0.001$) to 1.1 h/d in September.

The horizontal distances covered by an animal in the course of a day while grazing or walking varied in direct proportion to the time allocated to these activities. The distance covered was, for grazing, longest in March and shortest in September, whereas for walking idle the distance covered was shortest in March and longest in September (Table 3). The total horizontal locomotion distance reached a maximum of 3,550 m/d in September. The mean horizontal locomotion speed was 208 m/h for grazing and 1,813 m/h for walking idle. Despite the hilly topography of the study site, the positive vertical distances covered by an animal in the course of a day were short, ranging from 85 to 124 m. In March and May, about 93% of vertical travel occurred during grazing. On the average, the ratio of vertical to horizontal locomotion distance was 4.6% when grazing and 2.3% when walking idle; however, because of the much greater locomotion speed when walking idle, the mean vertical locomotion speed was 36.4 m/h when walking idle vs. 9.5 m/h when grazing.

Table 3. Time devoted to various activity states and locomotion distances traveled by free-ranging cows, according to month of measurement

Behavior	March	May	September	SEM
Activity state, h/d				
Lying down	5.43	6.23	7.07	1.22
Standing	6.63^a	9.03^b	8.42^b	0.77
Grazing	11.68^b	8.32^a	7.43^a	0.90
Walking idle	0.18^a	0.40^b	1.07^c	0.10
Locomotion distance, m/d				
Horizontal while grazing	$2,327^b$	$1,832^a$	$1,551^a$	198
Horizontal while walking	315^a	677^a	$1,999^b$	199
Horizontal total	$2,642^a$	$2,509^a$	$3,550^b$	277
Positive vertical while grazing	112^b	80^a	68^a	11
Positive vertical while walking	8^a	5^a	56^b	4
Positive vertical total	120^b	85^a	124^b	12

[a–c]Within a row, means without a common superscript differ ($P < 0.05$).

Table 4. Daily energy (kJ·kg of $BW^{-0.75}$·d^{-1}) expended on activity states and locomotion, the sum of these (EAC), and total daily heat production (THP) of free grazing cows according to month of measurement

Item[1]	March	May	September
a. Standing state	11.96	16.28	15.15
b. Grazing state	43.56	31.04	27.73
c. Walking state	0.71	1.46	3.84
d. Horizontal locomotion	7.41	7.04	9.96
e. Vertical locomotion	2.56	1.82	2.66
f. Horizontal and vertical locomotion while grazing	8.91	6.86	5.81
g. Horizontal and vertical locomotion while walking	1.06	2.00	6.81
h. Total grazing (b + f)	52.47	37.90	33.53
i. Total walking idle (c + g)	1.77	3.46	10.65
j. EAC (a + h + i)	66.2	57.63	59.33
k. Contribution of standing state to EAC, % (a/j)	18.1	28.2	25.5
l. Contribution of grazing to EAC, % (h/j)	79.3	65.8	56.5
m. Contribution of walking to EAC, % (i/j)	2.7	6.0	18.0
n. THP	1,014	679	644
o. Contribution of EAC to THP, % (j/n)	6.5	8.5	9.2

[1]Full description of the variables is presented in Materials and Methods.

Energy Expenditure on Activities and Locomotion

The total amount of energy expended by an animal for activities and locomotion in the course of a day over and above EAC ranged from 66 kJ·kg of $BW^{-0.75}$·d^{-1} in March to 58 to 59 kJ·kg of $BW^{-0.75}$·d^{-1} in May and September, and constituted between 6.5 and 9.2% of THP (Table 4). Although EAC was fairly stable among months, there were considerable changes in its constituent components. Most notably, the amount of energy expended on grazing (inclusive of locomotion) was almost 20 kJ·kg of $BW^{-0.75}$·d^{-1} greater in March than it was in September. Walking made its largest contribution to energy expenditure in September, when it accounted for 18% of EAC.

DISCUSSION

Coefficients of Activities and Locomotion Costs

This study reports the direct field estimation of the energy cost coefficients associated with the activities and movements of free-ranging cows, using the methodology of the previous study by Brosh et al. (2006). The main hypothesis of the study was that the coefficient of activity costs and locomotion are not affected by measurement conditions. This hypothesis is strongly supported by the very similar estimations of models 1 and 2 of the coefficients of cost of activity and locomotion.

How do the estimates of the energy cost coefficients obtained in this study compare with those of Brosh et al. (2006)? In the previous study the energy cost coefficient for being in the standing activity state was between 40.2 and 48.5 kJ·kg of $BW^{-0.75}$·d^{-1}, depending on the statistical model used. The SEM of the energy cost coefficients for the standing, walking idle, and grazing activity states ranged from 5.1 to 7.7 kJ·kg of $BW^{-0.75}$·d^{-1}. The estimates for standing obtained in the present study ranged from 42.7 to 46.2 kJ·kg of $BW^{-0.75}$·d^{-1}, depending on the statistical model, and the SEM of the energy cost coefficients for the 3 activity states ranged from 4.2 to 4.3 kJ·kg of $BW^{-0.75}$·d^{-1}. Thus the estimates from the 2 studies for the cost coefficient of the standing state are clearly similar; a 1 SE range from the smallest estimate of one study overlaps with a 1 SE range from the greatest estimate of the other study.

For the grazing activity state, the mean of the energy cost coefficients generated by the various statistical models examined in the 2 studies were very similar: 91.0 kJ·kg of $BW^{-0.75}$·d^{-1} in the previous study vs. 94.5 kJ·kg of $BW^{-0.75}$·d^{-1} in the present one.

For the walking idle activity state, the present study yielded energy cost coefficients in a wider range (84.5 to 92.4 kJ·kg of $BW^{-0.75}$·d^{-1}) than those obtained in the previous study (52.8 to 73.9 kJ·kg of $BW^{-0.75}$·d^{-1}), as reflected in the quite different average estimates of 87.7 vs. 62.2 kJ·kg of $BW^{-0.75}$·d^{-1} for the present and previous studies, respectively. This difference is discussed below.

The energy cost coefficient of horizontal locomotion ranged from 2.43 to 3.19 kJ·kg of $BW^{-0.75}$·km^{-1}·d^{-1} in the previous study, and the 3 estimates obtained in the present study (2.80, 2.80, and 2.92 kJ·kg of $BW^{-0.75}$·km^{-1}·d^{-1}) fell within this range. The average estimates were 2.92 and 2.84 kJ·kg of $BW^{-0.75}$·km^{-1}·d^{-1} for the previous and present studies, respectively.

The energy cost coefficients for positive vertical locomotion were much greater in the present than in the previous study and more in line with expected values. The previous estimates were recognized as being gross underestimates, and this was attributed to short vertical travel distances traveled by cows coupled with GPS constraints in detecting small altitude changes.

The reason why the present study might have yielded better estimates will be discussed below. The energy cost coefficient for positive vertical locomotion in the present study was, on the average, 23.85 kJ·kg of $BW^{-0.75}$·km^{-1}·d^{-1}, or 8.4 times the average coefficient for horizontal locomotion, and close to the treadmill measured ratio of 9 given by Lachica et al. (1997).

The previous and present studies were conducted at the same research station, on similar animals, and at similar times of the year from the point of view of the production cycles of both animals and plants. So what could explain the quite different energy cost coefficients that were obtained for walking idle and positive vertical locomotion between the 2 studies? We suggest that the answer lies in an important difference that existed between the studies, plot size, its effect on animal behavior, and a time lag in the response of HR to behavioral changes. In the relatively large plots of the present study animals tended to engage in longer walking bouts (i.e., number of consecutive 5-min periods classified as walking) than they did in the relatively small plots of the previous study. The mean duration of a walking bout was longer ($P < 0.0001$) in LP (10.0 min) than in SP (7.6 min; SEM = 0.57); the mean horizontal distance covered in a walking bout was longer ($P = 0.05$) in LP (305 m) than in SP (263 m; SEM = 21.2); and the mean positive vertical distance covered in a walking bout was greater ($P = 0.003$) in LP (6.72 m) than in SP (3.56 m; SEM = 1.06). It is known from exercise studies (Loeppky et al., 1981) that whereas HR starts to respond immediately to changes in effort, there is a time lag until it stabilizes at a different rate. In the field, if interludes of walking idle are short, a significant proportion of the time over which the heart operates at a rate characteristic of walking idle may be registered after the animal has switched to a different activity (the classification of which is based on data from the GPS collar only). The longer the walking bout, the greater the proportion of it that will be associated correctly with its characteristic HR. If the lag concept can be substantiated and quantified in further study, it may be possible to incorporate it into the statistical models.

Activity Duration and Total Daily Energy Expended on Activities and Locomotion

Measurement conditions, such as plot size, reproductive state, herbage ME, can affect daily activity durations and locomotion distances; consequently, they may affect the total daily energy expended on a certain activity and the entire daily HP.

To compare the results of the present study with Brosh et al. (2006) we used the low stocking rate treatment of Brosh et al. (2006) because its stocking rate was almost identical to that used in the present study (approximately 2 ha/cow). In terms of measurement months, February, June, and August of the present study are most comparable with March, May, and September of the previous study, respectively.

The partitioning of time among the 4 activity states was similar in the 2 studies. Of the 12 combinations of activity state and measurement month, the difference between the studies in the time devoted to an activity was less than 1, 2, and 3 h in 7, 3, and 2 comparisons, respectively. In the spring season, this difference was less than 1 h for all 4 activities.

As was found by Brosh et al. (2006), THP, total energy expenditure on grazing, and EAC are greatest when cows graze on herbage with the greatest ME; however, under these conditions, EAC constitutes the smallest proportion of THP, suggesting that the rate of energy retention is greatest, as would be expected. We do note, however, that in early spring, EAC, both in absolute terms and in relation to THP (represented in %), was slightly less in LP (66.2 kJ·kg of $BW^{-0.75}$·d^{-1}; 6.5%, respectively) than in SP (72.6 kJ·kg of $BW^{-0.75}$·d^{-1}; 7.6%, respectively). This raises the question of whether, at the same animal density, a larger plot size can confer some short-term advantage in the energy balance of the animal. Concurrent measurement in plots of different sizes will be required to test this rigorously. We have noted that since conducting the present study, high resolution pedometers have been incorporated into the methodology (Aharoni et al., 2009). This is expected to improve the classification of activities and the estimation of distances traveled, compared with the use of GPS collars alone, and may be important in future tests of plot size effects.

In conclusion, time spent on activities was mainly affected by season (i.e., by grazed ME level and by being in the lactation state when grazed on high quality herbage). Cows in the present study in larger plots walked for longer periods of time and traveled longer distances in single uninterrupted bouts of locomotion than those measured by Brosh et al. (2006) in smaller plots. Consequently, the estimated energy cost coefficients of being in a walking idle state and of vertical locomotion were greater, and more realistic, in the present study, in larger than in smaller plots.

LITERATURE CITED

Aharoni, Y., A. Brosh, P. Kurilov, and A. Arieli. 2003. The variability of the ratio of oxygen consumption to heart rate in cattle and sheep at different hours of the day and under different heat load conditions. Livest. Prod. Sci. 79:107–117.

Aharoni, Y., A. Brosh, A. Orlov, E. Shargal, and M. Gutman. 2004. Measurements of energy balance of grazing beef cows on Mediterranean pasture, the effects of stocking rate and season: 1. Digesta kinetics, faecal output and digestible dry matter intake. Livest. Prod. Sci. 90:89–100.

Aharoni, Y., Z. Henkin, A. Ezra, A. Dolev, A. Shabtay, A. Orlov, Y. Yehuda, and A. Brosh. 2009. Grazing behavior and energy costs of activity: A comparison between 2 types of cattle. J. Anim. Sci. 87:2719–2731.

AOAC. 1980. Official Methods of Analysis. 13th ed. Assoc. Off. Anal. Chem., Washington, DC.

Brosh, A. 2007. Heart rate measurements as an index of energy expenditure and energy balance in ruminants: A review. J. Anim. Sci. 85:1213–1227.

Brosh, A., Y. Aharoni, E. Shargal, I. Choshniak, B. Sharir, and M. Gutman. 2004. Measurements of energy balance of grazing beef cows in Mediterranean pasture, the effects of stocking rate and season: 2. Energy expenditure estimation from heart rate and oxygen consumption, and the energy balance. Livest. Prod. Sci. 90:101–115.

Brosh, A., Z. Henkin, E. D. Ungar, A. Dolev, A. Orlov, Y. Yehuda, and Y. Aharoni. 2006. Energy cost of cows' grazing activity: The use of heart rate GPS methods for direct field estimation. J. Anim. Sci. 84:1951–1967.

Edmonson, A. J., I. J. Lean, L. D. Weaver, T. Farver, and G. Webster. 1989. A body condition scoring chart for Holstein dairy cows. J. Dairy Sci. 72:68–78.

Gutman, M., Z. Holzer, H. Baram, I. Noy-Meir, and N. G. Seligman. 1999. Heavy stocking of beef cattle and early season deferment of grazing on Mediterranean-type grassland. J. Range Manage. 52:590–599.

Gutman, M., and N. G. Seligman. 1979. Grazing management of herbaceous Mediterranean foothill range in the upper Jordan Valley and its effect on cattle and vegetation. J. Range Manage. 32:86–92.

Hunt, L. P., S. Petty, R. Cowley, A. Fisher, A. J. Ash, and N. MacDonald. 2007. Factors affecting the management of cattle grazing distribution in northern Australia: Preliminary observations on the effect of paddock size and water points. Rangeland J. 29:169–179.

Lachica, M., C. Prieto, and J. F. Aguilera. 1997. The energy cost of walking on the level and on negative and positive slopes in the Granadina goat (*Capra hircus*). Br. J. Nutr. 77:73–81.

Lawes Agricultural Trust (Rothamsted Experimental Station). 2003. Genstat for Windows. 7th ed. VSN International, Oxford, UK.

Loeppky, J. A., R. Green, D. E. Hoekenga, A. Caprihan, and U. C. Luft. 1981. Beat-by-beat stroke volume assessment by pulsed Doppler in upright and supine exercise. J. Appl. Physiol. Respir. Environ. Exerc. Physiol. 50:1173–1182.

Nicol, A. M., and B. A. Young. 1990. Short-term thermal and metabolic responses of sheep to ruminal cooling: Effects of level of cooling and physiological state. Can. J. Anim. Sci. 70:833–843.

NRC. 1989. Nutrient Requirements of Dairy Cattle. 6th rev. ed. Natl. Acad. Press, Washington, DC.

Seligman, N. G., M. Gutman, Z. Holzer, I. Noy-Meir, and H. Baram. 1989. Stocking density of cattle and herbage production on Mediterranean grassland. J. Agric. Sci. 113:51–58.

Sternberg, M., M. Gutman, A. Perevolotsky, D. Ungar, and J. Kigel. 2003. Effects of grazing on soil seed bank dynamics: An approach with functional groups. J. Veg. Sci. 14:375–386.

Sternberg, M., M. Gutman, A. Perevolotsky, E. D. Ungar, and J. Kigel. 2000. Vegetation response to grazing management in a Mediterranean herbaceous community: A functional group approach. J. Appl. Ecol. 37:224–237.

Ungar, E. D., Z. Henkin, M. Gutman, A. Dolev, A. Genizi, and D. Ganskopp. 2005. Inference of animal activity from GPS collar data on free-ranging cattle. Rangel. Ecol. Manag. 58:256–266.

Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods of dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. J. Dairy Sci. 74:3583–3597.