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## ORIGINAL ARTICLE

## Physical activity energy expenditure has not declined since the 1980s and matches energy expenditures of wild mammals

KR Westerterp<sup>1</sup> and JR Speakman<sup>2</sup><sup>1</sup>Department of Human Biology, Maastricht University, Maastricht, The Netherlands and <sup>2</sup>School of Biological Sciences, Aberdeen Centre for Energy Regulation and Obesity, University of Aberdeen, Aberdeen, Scotland**Objective:** Obesity results from protracted energy imbalance. Whether this comprises excessive energy intake, lowered physical activity or both, remains disputed.**Design:** Physical activity energy expenditure, evaluated in three different ways from daily energy expenditure (DEE) measured using doubly labelled water, was examined for trends over time. Data included subjects in Europe (Maastricht, the Netherlands) and North America extending back to the 1980s. These data were compared with measures from the third world, and measures made on wild terrestrial mammals.**Results:** Physical activity expenditure in Europe (residual of the regression of DEE on basal energy expenditure (BEE)) has slightly but significantly increased since the 1980s. There was no trend over time in physical activity level (PAL = DEE/BEE), or in the residual variance in DEE once mass, sex and age were accounted for. This latter index of physical activity expenditure also significantly increased over time in North America. DEE of individuals in Europe and North America was not significantly different from individuals measured in the third world. In wild terrestrial mammals, DEE mostly depended on body mass and ambient temperature. Predicted DEE for a 78 kg mammal living at 20 °C was 9.2 MJ per day (95% CI: 7.9–12.9 MJ per day), not significantly different from the measured DEE of modern humans (around 10.2–12.6 MJ per day).**Conclusion:** As physical activity expenditure has not declined over the same period that obesity rates have increased dramatically, and daily energy expenditure of modern man is in line with energy expenditure in wild mammals, it is unlikely that decreased expenditure has fuelled the obesity epidemic.*International Journal of Obesity* (2008) 32, 1256–1263; doi:10.1038/ijo.2008.74; published online 27 May 2008**Keywords:** doubly labelled water method; healthy adults; body size; time trend; wild mammals; physical activity level

## Introduction

In the early 1980s 8% of adults in the United States were obese (body mass index (BMI) > 30). By 2005 this prevalence had increased to 22%.<sup>1</sup> Similar increases were evident throughout the Western world,<sup>2,3</sup> and more recent data indicate that the epidemic has spread globally.<sup>4</sup> Because obesity increases the risk of developing diabetes,<sup>5</sup> cardiovascular disease<sup>6</sup> and cancer,<sup>7</sup> the implications of increases in obesity prevalence are enormous. Estimates of economic costs amount to 5% of all healthcare spending in most Western societies.<sup>8</sup> Costs to

the wider economy indicate a problem that exceeds tens of billions of dollars in its global impact.<sup>9</sup> Most researchers agree that obesity is caused by protracted energy imbalance where intake exceeds expenditure.<sup>10,11</sup> Whether this imbalance is caused by excessive energy consumption, perhaps related to passive over-consumption of foods high in fat that have high energy density and may be less satiating,<sup>12,13</sup> or due to reduced energy expenditure correlated with our increasingly sedentary lifestyle<sup>14,15</sup> is unclear. In the past few years, evidence has suggested that the primary problem lies not with increased energy intake<sup>15–18</sup> but with reduced expenditure, that is reduced physical activity.<sup>15,19–21</sup>

With respect to dietary intake, surveys between the 1970s and 2000s do not indicate that total energy consumption has increased.<sup>15,16</sup> Moreover, fat consumption seems to have decreased.<sup>17,18</sup> Unfortunately, most of this evidence is based on self-reported food intakes. Food intake data derived from

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food balance sheets, as used as an indication of national food consumption trends, showed a considerable increase in total energy availability and energy from lipids over the past 40 years.<sup>22</sup> Differences in trends of total energy supply per capita between countries explained 41% of the variation of trends in mean BMI.<sup>23</sup> However, daily energy demands can be measured directly using a method called the doubly labelled water (DLW) technique.<sup>24,25</sup> When this method was used to compare self-reported energy intakes with energy expenditure, it became clear that energy intake was often considerably underestimated, due to a combination of underrecording and temporary under-eating.<sup>26,27</sup> Importantly, the degree of underestimation of intake was positively related to the BMI of the subjects. Consequently, dietary surveys cannot be used for drawing conclusions on dietary intake over time, or for comparing lean to obese subjects. With respect to physical activity, it became evident that the energy expended on physical activity level (PAL) had also generally been underestimated. Direct observations of the obese suggest they move less than non-obese individuals, however, DLW measurements show that this does not necessarily mean that they spend less energy on physical activity than lean people do,<sup>20,21,28</sup> because the costs of moving around in the obese are greater, in part because they also have greater lean body mass in addition to greater fat mass.

By measuring daily energy expenditure (DEE) with DLW in combination with basal energy expenditure (BEE) using indirect calorimetry, it is possible to obtain estimates of physical activity energy expenditure in several different ways. One popular index of physical activity is  $PAL = DEE/BEE$ .<sup>29</sup> The PAL normally varies between 1.5 and 2.0.<sup>30,31</sup> The PAL of modern humans has been previously compared with that of wild mammals,<sup>32</sup> and on that basis it was suggested that modern humans have lower than expected energy expenditure on activity and hence that low-activity energy expenditure has fuelled the obesity epidemic. However, this latter study failed to adequately account for body size effects and the effects of ambient temperature on energy demands, a point we shall address in the current paper.

Here we test the hypothesis that reduced levels of physical activity energy expenditure have driven the obesity epidemic. Three separate tests were executed. We compiled data on levels of DEE measured by the DLW method and BEE by respirometry over time in contemporary Western society (Europe and North America) and searched for an effect of year of measurement on indices of activity energy expenditure. Then, we compared the levels of expenditure in modern Western societies with those from the third world countries generally mirroring the physical activity in Western societies in the past. Finally, we compared the levels of expenditure and PAL of modern humans with those of wild terrestrial mammals taking into account both body size and temperature effects.

## Methods

We collected data from four sources for this study. Although the DLW method was first invented in the 1950s, it was not applied to humans until 1982,<sup>24</sup> because the precision and accuracy of mass spectrometry devices prior to that time made the technique too expensive to apply to anything but small animals. We therefore have no direct measures of human energy demands that predate the 1980s. Relatively few sites have continuously studied free-living individuals between the 1980s and the present day, to permit an evaluation of how levels of energy expenditure have changed over the same period that rates of obesity have increased. One such site is the town of Maastricht and surroundings in the Netherlands. The Maastricht protocol for the measurement of DEE in adult subjects with DLW<sup>33,34</sup> usually covers an interval of 2 weeks. The isotopes are administered as a mixture of <sup>2</sup>H<sub>2</sub>O (99.9 at%) and H<sub>2</sub><sup>18</sup>O (10 at%) resulting in an initial excess body water enrichment of 150 p.p.m. for deuterium and 300 p.p.m. for oxygen-18, leaving a sufficient excess enrichment at the end of the observation period. The dose volume is typically 80–160 ml for adults. The isotopes are administered as a last consumption before the night. Subjects provide a background body water sample (blood or urine) immediately before isotope consumption. Then, equilibration takes place overnight and the first post-dosing sample is collected in the early morning, in case of urine from the second voiding. For an observation period of 2 weeks, samples from the second and another voiding on the first, mid and last day of the observation period are sufficient. There are three criteria to judge the validity of the results of isotope analyses for energy expenditure measurements. First, duplicate analyses should not differ more than 1 p.p.m. Typically, the s.d. for replicate samples averages 0.2 and 0.3 p.p.m. for deuterium and oxygen-18, respectively. Secondly, the ratio between the deuterium dilution space and oxygen-18 dilution space is expected to be close to 1.03. As a third criterion, the fit of the isotope elimination curves should be high, or results based on morning and evening samples over corresponding intervals should be close. Carbon dioxide production, as calculated from the isotope elimination rates, is converted to energy expenditure using an energy equivalent based on the substrate mixture oxidized. The protocol allows comparisons of calculated energy expenditure within the first and second week of a 14-day observation period to check for sampling errors. Typically, the difference is smaller than 10% and samples are re-analyzed when the difference is larger. Validation studies in human subjects reviewed in<sup>25</sup> reveal the average discrepancy of DLW estimates to simultaneous indirect calorimetry estimates is less than 3%. Between 1983 and 2005, 366 subjects were measured in Maastricht (first publication 1988) using both the DLW method and direct estimates of their BEE. This sample excludes individuals aged under 18 years, or those involved in interventions in energy intake, physical activity including athletic performance, or

those that were pregnant, lactating or diseased (Table 1). For studies involving dietary or exercise interventions, only the pre-intervention data or that for control groups was used.

There are three different ways of assessing the physical activity energy expenditure using data on DEE and BEE. The first method is to regress DEE on BEE. The residual variation to the fitted regression directly reflects individual variability in activity energy expenditure. A second popular approach is to calculate the ratio of DEE to BEE called the PAL. Finally, if data on BEE was not available one might make the assumption that most of the variation in DEE once the effects of body mass and sex had been accounted for would be due to differences in physical activity. This is not strictly correct because some of this variation would also reflect differences in BEE that had not been accounted for by body mass or sex. Nevertheless, this provides a third approach for measuring levels of activity energy demands.

Because the Maastricht data were collected from a single site these data are well controlled, but the extent of increase in obesity in the Netherlands over the period that the measurements were made is relatively modest compared to the expansion of obesity elsewhere—such as in the United States. The absence of any trends in DEE in the Maastricht data might therefore be attributed to the measurements being made only in the early phase of an obesity epidemic at this site. As a second source of information therefore we systematically reviewed the literature for data on energy demands in North America. We surveyed all published applications of the method between 1982 and 2005 using databases that include peer-reviewed publications (Medline, PubMed and ISI Web of Science). We searched for papers in these databases using the search terms: doubly labelled water, doubly labeled water, double labelled water and double labeled water to cover both English and American spellings of the term labelled and labeled, respectively. We only searched for articles written in English. We collated copies of the original papers to extract the relevant data for analysis. We excluded any measurements that concerned subjects that were not healthy, and studies where subjects were part of a dietary or physical activity intervention. We also restricted the data to subjects aged between 18 and 50 years. In total we obtained estimates of DEE for 393 subjects across 13 studies, although in many studies the individual data were unavailable and we had access only to means and sample sizes for sub-populations (Table 2). Moreover, a second problem with these data was that BEE data were available for only a small subset of the total sample. Accordingly, we analysed these data using only the third method described above (residual analysis of DEE over time with the effects of body mass, sex and age removed).

Although the data we have analysed for human energy demands stretch back over 20 years and include two sites, one at an early, and the other at an advanced, stage of the obesity epidemic, it might be argued that none of these direct measures of energy expenditure have been made early enough, and that the predisposing change in energy

**Table 1** Subject characteristics of Maastricht

	Mean	s.d.	Range
<i>Women (n = 167)</i>			
Age (years)	30	9	18–50
Height (m)	1.68	0.06	1.52–1.86
Body mass (kg)	73	18	47–164
BMI (kg/m <sup>2</sup> )	26.3	6.5	16.6–55.3
DEE (MJ per day)	10.9	1.8	7.0–18.4
<i>Men (n = 199)</i>			
Age (years)	33	9	18–50
Height (m)	1.80	0.07	1.64–1.97
Body mass (kg)	83	21	50–216
BMI (kg/m <sup>2</sup> )	25.7	6.0	15.6–61.7
DEE (MJ per day)	14.0	2.6	9.5–22.6

Abbreviations: BMI, body mass index; DEE, daily energy expenditure.

**Table 2** Subject characteristics of studies in North America and the third world

Reference	Subjects (women/men)	Age (years)	Body mass (kg)	DEE (MJ per day)
<i>North America</i>				
<sup>35</sup>	13/0	31	49	8.9
	70/0	31	58	10.1
	33/0	31	81	11.5
<sup>36</sup>	2/2	29	63	12.0
<sup>37</sup>	12/0	36	107	12.8
	10/0	40	134	14.7
	8/0	35	162	16.1
<sup>38</sup>	0/17	22	68	12.0
<sup>39</sup>	9/0	23	58	7.0
	8/0	22	60	9.5
<sup>40</sup>	13/0	28	58	10.8
	16/0	28	58	10.4
	19/0	28	64	10.8
<sup>41</sup>	14/0	40	91	10.8
<sup>42</sup>	0/14	22	73	14.6
<sup>24</sup>	1/3	26	78	13.6
<sup>43</sup>	9/0	40	64	10.3
	15/0	38	68	9.2
	8/0	38	68	8.2
<sup>44</sup>	0/24	23	72	14.1
	10/0	25	55	9.9
<sup>45</sup>	8/0	23	57	11.1
	8/0	25	84	12.0
<sup>46</sup>	27/0	32	62	9.3
	20/0	38	67	8.2
<i>Third world</i>				
<sup>47</sup>	0/8	34	61	20.3
	0/8	36	62	17.0
<sup>48</sup>	0/8	25	61	16.2
<sup>49</sup>	7/0	26	50	9.5
<sup>50</sup>	14/0	21	54	7.2
<sup>51</sup>	0/6	27	55	11.4
<sup>52</sup>	10/0	32	49	10.1
<sup>53</sup>	15/0	36	54	8.7
<sup>54</sup>	40/0	43	65	9.5
	0/33	43	73	12.1

Abbreviation: DEE, daily energy expenditure.

demands preceded any available direct measurements. It is impossible to test this directly. However, an indirect assessment can be made by comparing the energy demands of

individuals in Western society with the energy demands of individuals living in non-Westernized rural societies in the third world (Table 2). Several studies of such populations have been made using the DLW method and we compiled data from the literature on their levels of expenditure and compared them to the data from Maastricht and North America using standard general linear modelling with gender as a factor and age and body mass as covariates.

It might be argued that whatever community is chosen in the modern world their levels of activity may be lower than levels historically in pre-Westernized societies. If modifications to our environment that reduced our energy demands precede the 1980s, and are not well reflected by the third world populations then we should be able to pick this up by reductions in our demands relative to that expected for equivalent-sized wild mammals as suggested previously.<sup>32</sup> The fourth source of information we analysed therefore was for all the published data on wild terrestrial mammals using the DLW method. Although the DLW method was invented during the 1950s work on wild mammals did not start until the 1970s. We surveyed the literature between 1970 and 2005 for measurements of energy demands using the DLW method on free-living wild mammals. We searched the same databases as used for the human literature search including only studies on wild free-living terrestrial mammals. We included only peer-reviewed publications and excluded data on domesticated mammals and those involved in unusual activity (for example dogs in sled dog races). We did not exclude data pertaining to mammals in reproduction because often these were not separated in the original papers from data on non-reproductive animals. None of the data refer to mammals in hibernation states. Many studies of wild mammals report data collected in different seasons, under different environmental conditions. Moreover, for some species there are multiple studies by different authors pertaining to populations at different field sites. Because ambient temperature varies both seasonally and with different study locations, and because ambient temperature is a key variable driving energy demands,<sup>55</sup> we collated the data for different seasons and study sites separately. In total we obtained 207 measurements of 90 different terrestrial mammal species and we obtained estimated ambient temperature measurements at the study sites for 167 of them. Many studies of wild mammal DEE include estimates of BEE in the thermoneutral zone for the same mammals studied using DLW. We supplemented these direct estimates using data on BEE for eight species from the review of White and Seymour<sup>56</sup> yielding a total of 163 BEE estimates from which we could calculate the PAL.

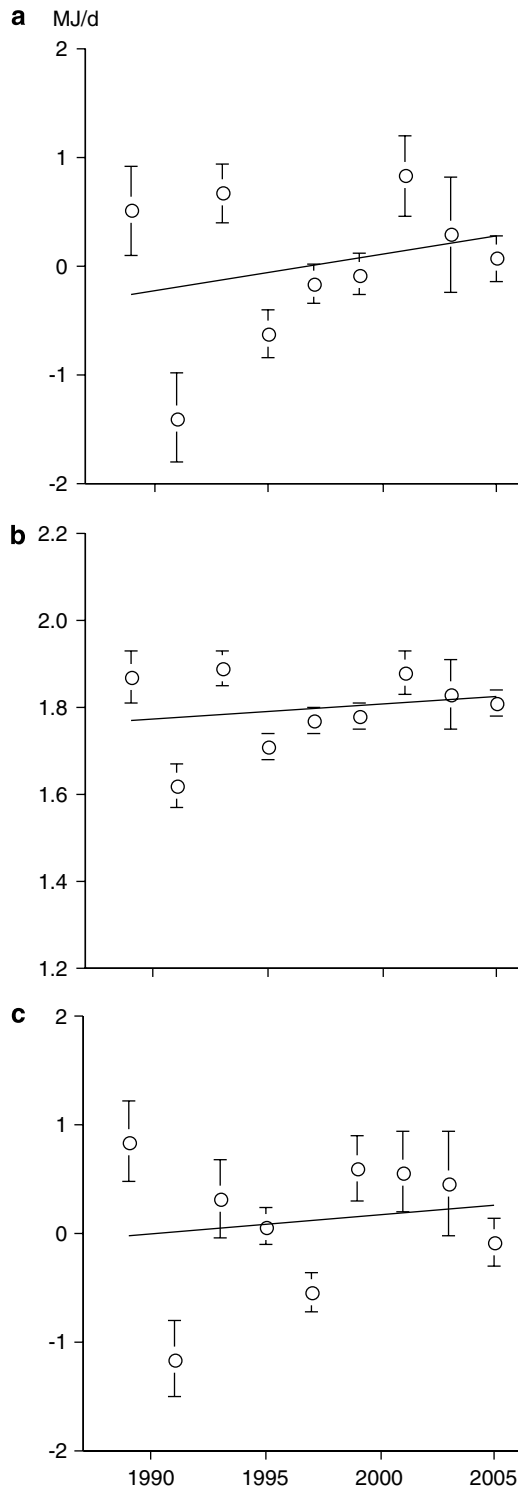
Two factors are likely to make our prediction of the energy demands of modern humans from the relationships derived in wild mammals slightly overestimates. First, we did not exclude measurements of wild mammals engaged in reproductive activities that are likely to elevate energy requirements. We did this because data reported for reproductive and non-reproductive animals were often not separated in

the original papers. Second, as we have previously highlighted,<sup>57</sup> the routine methods for calculating energy demands by DLW have been differently applied by workers studying wild mammals compared with humans. The reasons for this difference are historical and reflect the fact that validation studies for small mammals, suggest a single-pool model is most appropriate, whereas in humans a two-pool model seems to work best.<sup>24</sup> A comprehensive review<sup>25</sup> of validation studies of different-sized mammals concluded that the two-pool model is probably most appropriate for mammals weighing more than 4 kg. Yet workers on mammals weighing more than 4 kg have routinely used the single-pool model calculation. The single-pool model gives a higher estimate of DEE than the two-pool model (by between 4 and 10%) but re-calculating the data for mammals over 4 kg is not possible because the required data to make these recalculations are generally not provided in the original publications. These two factors mean that there will be a tendency for the predicted energy demands for mammals > 4 kg to be slightly overestimated.

## Results

Using the Maastricht database ( $n = 366$  subjects; Table 1) we evaluated the trends in time of physical activity energy expenditure calculated in three different ways. There was a highly significant positive relationship between DEE and BEE with an  $r^2$  of 53%. We calculated the residuals to the fitted regression on this relationship and then explored the trends of these residuals with date of study. There was a slight but significant ( $F = 3.89$ ,  $P = 0.049$ ) trend for the residual of DEE on BEE to increase between 1988 and 2006 (Figure 1a) suggesting activity energy expenditure has slightly increased over the past two decades. Second, we calculated PAL, and explored trends of PAL over time (Figure 1b). There was no significant increase in PAL between 1988 and 2006 ( $F = 2.91$ ,  $P = 0.089$ ). Finally, we included DEE in a generalized linear model with body mass, age, gender and the date of publication and their interactions as predictors. None of the two-way and higher interaction terms were significant. The major effect on DEE was body mass, explaining 32% of the variance. There were additional significant effects of age (lower DEE as get older) and gender (women lower independent of body mass and age). Together these factors and body mass explained 54% of the variation in DEE. However, there was no significant effect of the date of measurement ( $F = 0.40$ ,  $P = 0.529$ ; Figure 1c). Over the same time period that these measurements were made, rates of obesity in the Netherlands doubled from 5 to 10%.<sup>58</sup>

Rates of obesity in North America increased over the same period, from 8 to 22%.<sup>1</sup> The second set of DEE data for 393 subjects from North America were measured using DLW over approximately the same interval. The dominant factors influencing energy expenditure were body mass and gender.



**Figure 1** Trends in physical activity energy expenditure (MJ per day, mean  $\pm$  s.e.) over time (year of publication) for a population in Northern Europe (Maastricht). (a) The residual of the regression of daily energy expenditure (DEE) on basal energy expenditure (BEE); (b) physical activity level (PAL) which is the ratio of DEE to BEE; (c) the residual of the regression of DEE on body mass, sex and age.

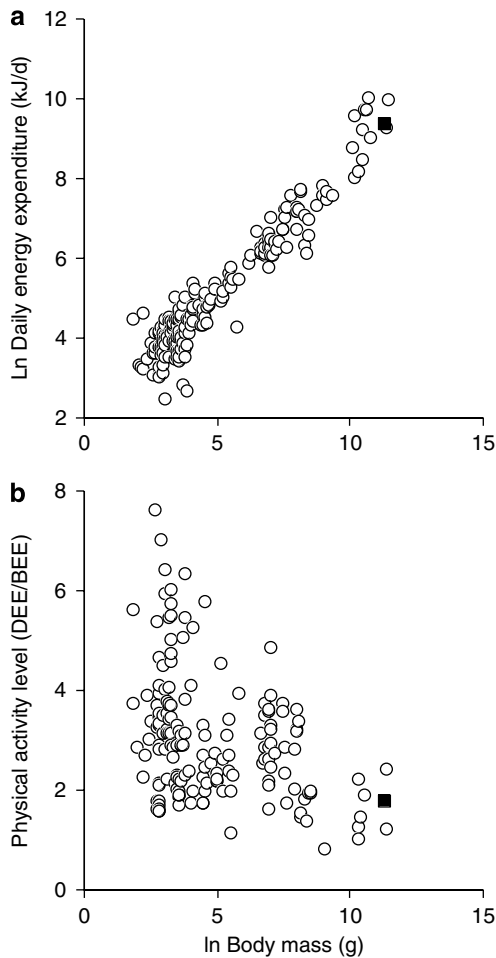
In these data there was a significant positive effect ( $F = 4.89$ ,  $P = 0.028$ ) of the date of measurement on levels of DEE adjusted for body mass, gender and age, again suggesting activity expenditure has increased over the past two decades.

The third set of DEE data, consisting of compiled DLW data from the third world countries, was compared with those from Maastricht and North America. In this combined data set there were significant effects of body mass ( $F = 35.43$ ,  $P < 0.001$ ) and gender ( $F = 116.07$ ,  $P < 0.001$ ). Although there were some groups of subjects that had high rates of expenditure in the third world, for example a small group of male subjects studied in the Gambia, overall across all studies the impact of whether the measurements were from Maastricht, North America or the third world was not significant ( $F = 1.10$ ,  $P = 0.297$ ). Thus, the DEEs of individuals from the most rural third world communities lie on the expected line determined by gender, age and body mass for individuals in Western societies.

To compare modern humans with wild mammals, literature data on DEE of wild mammals determined with the DLW method were compiled. The major factors influencing DEE were body mass (Figure 2a), and ambient temperature. The best-fit regression equation was  $\text{Ln DEE (kJ per day)} = 2.353 + 0.649 \text{ Ln (body mass, g)} - 0.0256 \text{ Temp (}^\circ\text{C)}$  that explained 92.0% of the variation in DEE ( $n = 167$ ). Knowing the body mass and ambient temperature at which a wild animal lives, allows a prediction of its expected daily energy demands. We used this equation to predict the energy demands expected for modern humans (averaging a body mass of 78.6 kg—the mean mass of the subjects measured at Maastricht) and living at typical room temperatures of 20  $^\circ\text{C}$ , which yielded 9.16 MJ per day (95%CI = 7.9–2.9 MJ per day). The actual expenditure across all the Maastricht data was 12.6 MJ per day. A review of 574 measurements made using the DLW method on subjects worldwide published in 1996 gave an average value (for adults excluding athletes) of 11.2 MJ per day<sup>30</sup> and our own summary for data in the United States gives a weighted average of 10.9 MJ per day (lower body weight (70.5 kg) because of 85% women in the sample). None of these values is lower than the prediction based upon average body mass and room temperatures. Moreover, all the suggested potential biases indicate that the prediction from wild mammals would likely if anything be an overestimate.

## Discussion

Using a variety of different techniques to analyse the data on DEE and BEE, we evaluated how levels of activity energy expenditure have changed over time since the first uses of the DLW method in the 1980s. Independent of the method used, there was no indication that energy expenditure on physical activity or total expenditure has declined over the past two decades in Northern Europe (Maastricht). Indeed



**Figure 2** (a) Effect of body mass on daily energy expenditure (DEE) in wild terrestrial mammals; (b) effect of body mass on the ratio of DEE to basal energy expenditure (BEE) for terrestrial mammals. In both plots the value for humans is indicated as a closed square.

the trends when significant were actually in the opposite direction—suggesting levels of activity energy expenditure may have actually increased over this time interval. Similar data trends were apparent in data compiled from across North America using the only analysis method that was possible to apply to this data set. Over the same period that we have data for DEE, obesity has increased from 8 to 11% in the Netherlands and from 14 to 22% in North America. The trend for an increase in activity energy expenditure in time possibly resulted from an increase in body weight, with a consequent increase in the cost of moving around.<sup>26</sup>

Given that the data from Maastricht were collected from a relatively small population around a single city, by a single research group, and included subjects that were measured either as controls, pre-intervention or non-intervention groups the sample is probably a representative sample of the population. This is important because the absence of a trend in energy expenditure with time in this analysis is

founded on the assumption that the sample included in the analysis is unbiased. The same cannot be said for the sample from North America that included mostly women (85%) and was drawn from an ethnically diverse background across an enormous geographic range. The positive trend of expenditure with time in this sample may thus be a sampling artefact. Nevertheless, it is reassuring that the data from North America did not contradict the much better controlled sample from Europe. Unfortunately, these data are the best data we have. Accepting the potential caveats in the American data we suggest it is unlikely that decreased activity energy expenditure is responsible for these phases of the obesity epidemic in the respective continents. Surprisingly, DEE of modern humans in Westernized societies was also completely in line with estimates for people measured in the third world countries, and the predicted DEE from an equation derived from measurements of wild terrestrial mammals. These latter data suggest that even earlier phases of the epidemic were probably also not triggered by lowered levels of activity energy expenditure due to reduced PALs.

These data would seem to be at odds with anecdotal suggestions that levels of physical activity have declined over time<sup>15</sup> and direct observations that the obese are less physically active than their lean counterparts. This phenomenon has caused an obvious misunderstanding. Ekelund *et al.*<sup>28</sup> compared the energy expended on activity as well as direct observations of body movement in obese (BMI > 30) and matched non-obese adolescents. Although the obese subjects performed less physical activity than the non-obese, there was no difference in their expenditure of energy on activity. Obese subjects move less, but this does not necessarily mean they have a lower energy expenditure on activity, because energy expenditure while they are active is higher. Very few longitudinal data exist but our analysis and conclusions are consistent with observations that weight gain by individual Pima Indians over a 4-year interval was not correlated to their initial levels of physical activity energy expenditure, but rather positively linked to their total energy intake.<sup>59</sup>

Our analysis of human energy demands relative to those of wild mammals is discrepant with a previous comparison that concluded humans have lower energy demands than expected.<sup>32</sup> The reason for this discrepancy is because the previous study compared PAL values between humans and other species, but did not account for the effects of body mass on PAL. PAL values are calculated using the resting energy at thermoneutral conditions (BEE) under the assumption that the remaining energy demand predominantly fuels activity. This is only correct, however, when the DEE is also measured at thermoneutrality, as it is in humans. For many wild mammals measures of DEE are made at ambient temperatures below the relevant thermoneutral zone, hence PAL for these mammals reflects the combination of activity metabolism and the energy spent on thermoregulation. In fact PAL calculated as (DEE/BEE) is negatively related to body

mass (Figure 2b) reflecting the increasing thermoregulatory load as body size declines. Hence, PAL for contemporary humans is at the lower end of the distribution of PAL values when the effects of body mass are ignored, in line with the previous findings,<sup>30</sup> but they are at exactly the expected level, once the effect of body mass on PAL is taken into account (Figure 2b).

In conclusion, energy expenditure in Europe and North America has not declined between the 1980s and 2005, a period during which obesity rates have increased. Neither is energy expenditure in Western society lower than in the third world, nor than expected from measures of wild terrestrial mammals. Of course, obesity can only result from an imbalance between intake and expenditure. On the basis of these analyses, the data indicate that reduced energy expenditure due to lowered physical activity expenditure is unlikely to have fuelled the obesity epidemic.

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