

# Intraspecies Variation in BMR Does Not Affect Estimates of Early Hominin Total Daily Energy Expenditure

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**ABSTRACT** We conducted a meta-analysis of 45 studies reporting basal metabolic rate (BMR) data for *Homo sapiens* and *Pan troglodytes* to determine the effects of sex, age, and latitude (a proxy for climate, in humans only). BMR was normalized for body size using fat-free mass in humans and body mass in chimpanzees. We found no effect of sex in either species and no age effect in chimpanzees. In humans, juveniles differed significantly from adults (ANCOVA:  $P < 0.001$ ), and senescent adults differed significantly from adults younger than 50 years ( $P < 0.001$ ). Europeans differed significantly from tropical populations ( $P < 0.001$ ). On the basis of these observations,

we derived new equations describing the relationship between BMR and body size, and used them to predict total daily energy expenditure (TEE) in four early hominin species. Our predictions concur with previous TEE estimates (i.e. Leonard and Robertson: *Am J Phys Anthropol* 102 (1997) 265–281), and support the conclusion that TEE increased greatly with *H. erectus*. Our results show that *intraspecific* variation in BMR does not affect TEE estimates for *interspecific* comparisons. Comparisons of more closely related groups such as humans and Neandertals, however, may benefit from consideration of this variation. *Am J Phys Anthropol* 131:552–559, 2006. ©2006 Wiley-Liss, Inc.

The field of energetics has grown as an approach in biological anthropology recently (Leonard and Ulijaszek, 2002), with studies using energy to address a number of topics, including hominin foraging strategies and diet quality (Leonard and Robertson, 1997) and sex differences in primate reproductive effort (Key and Ross, 1999). Rather than making new energy measurements, researchers often employ methods that utilize existing data or published equations to estimate quantities such as basal metabolic rate (BMR) and total daily energy expenditure (TEE). This is due to the difficulty of directly measuring these values in the field in nonhuman primates and human foragers. BMR is the energy expended at rest and in a fasted state (i.e. the “maintenance” cost of the body), and is the largest contributor to daily energy expenditure, or TEE. TEE is the sum of all energy costs for an individual during any particular 24-h period, including energy spent in activity and during sleep and rest.

Because BMR constitutes such a large portion of daily energy expenditure, activity costs can be calculated as multiples of BMR using established constants (Coelho, 1974; Coelho et al., 1976, 1979; FAO/WHO/UNU, 1985). This is known as the factorial method. For example, the constant for feeding is 1.38, meaning that this activity incurs a metabolic cost 1.38 times as large as BMR over a given time period. In contrast, the constant for rest is 1.25, while energy spent during sleep is considered to be equivalent to BMR. Locomotor costs, because they depend also on speed of movement, are generally calculated using published equations rather than constants (Taylor et al., 1970; Taylor and Rowntree, 1973). All such costs for a single day are then summed to arrive at TEE.

The accuracy of TEE estimates obtained using the factorial method thus depends heavily on the accuracy of the initial BMR estimates. Some evidence calls into question the validity of BMR values some recent studies use to esti-

mate TEE by the factorial method. This is because available equations and data for predicting BMR in human and nonhuman primates fail to consider at least one of several variables that are thought to affect BMR intraspecifically; namely age, climate, and sex. If these variables exert a large effect, TEE estimated from BMR values that fail to consider them could be inaccurate, affecting the overall conclusions of such studies.

To examine this possibility, we conducted a meta-analysis of 45 human BMR studies and a sample of chimpanzees much expanded over those used in past studies. Using analysis of covariance (ANCOVA), we tested for the effects of age and sex within each species, and climate in humans alone. The use of ANCOVA allows the comparison of discreet classes of data after removing the effects of a major confounding variable, in this case, body size. For humans, we used fat-free mass (FFM) as a measure of body size, to control for population level variation in body fat. Adipose tissue has little to no metabolism, and varies in humans with sex, age, and climate, among other variables. Thus, the use of whole body mass (which incorporates fat mass) to normalize BMR masks population level differences in body fat, potentially biasing results. Nonetheless, for chimpanzees we used whole body mass instead of FFM, since that was the only data available. On the basis of our results, we derived new equations for estimating BMR in humans and chimpanzees taking into considera-

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tion any significant effects we found for the aforementioned variables. We then used these equations to reevaluate the data and conclusions of two previous studies that used the factorial method to estimate primate TEE: Leonard and Robertson (1997) and Key and Ross (1999).

Leonard and Robertson (1997) estimated BMR from body mass in chimpanzees, extant human foragers (!Kung, Ache), and fossil hominins. Body mass data came from field data on foragers and wild chimpanzees (Wrangham, 1977; Lee, 1979; Hill et al., 1984, 1985; Hurtado et al., 1985), and laboratory estimates for fossil species (McHenry, 1992; Ruff and Walker, 1993). Chimpanzee BMR data came from three captive subjects, all classified as adult males (Bruhn, 1934), precluding any consideration of age or sex. Tropical forager BMR was estimated with an equation derived largely from Europeans (Schofield et al., 1985), meaning that if climate affects BMR, these estimates are likely inaccurate. Finally, BMR was estimated for *Australopithecus afarensis*, *A. africanus*, *Homo erectus* and early *H. sapiens* using Kleiber's (1961) equation for mammals, which does not account for any variable other than body mass.

Leonard and Robertson (1997) used these BMR data to calculate TEE in chimpanzees and extant foragers, with activity budgets drawn from published data (chimpanzees: Wrangham, 1977; Rodman and McHenry, 1980; Rodman, 1984; humans: Lee, 1968, 1979; Hill et al., 1984, 1985; Hurtado et al., 1985). These estimates were compared to a general regression equation relating TEE to body mass in anthropoid primates, derived from data on 18 species (Leonard and Robertson, 1997). The extent to which chimpanzees and humans diverged from this general pattern was assessed from  $z$ -scores ( $z = -0.45$  and  $1.54$  respectively), and these deviations were used to estimate TEE in the fossil hominin species; australopithecines based on the chimpanzee  $z$ -score, and the two *Homo* species based on the human forager  $z$ -score. Their results indicated that an increase in TEE of 80–85% over that of australopithecines accompanied the emergence of *H. erectus*. This conclusion could require revision, however, if biased BMR data led to inaccurate estimates of fossil hominin TEE.

Key and Ross (1999) also used the factorial method to estimate TEE in nonhuman primates, to address the question of sex differences in reproductive energy investment. They used the same activity budget data as did Leonard and Robertson (1997) to estimate TEE in chimpanzees, but used different body weights (Rodman, 1984) and the Kleiber (1961) equation for BMR. The fact that this equation does not account for BMR variation because of sex is potentially very important given that Key and Ross (1999) focused on sex differences in energy expenditure.

Key and Ross (1999) used their TEE estimates to calculate the energy cost per birth event for both sexes of individual primate species, using published coefficients (Portman, 1970) to estimate the costs of gestation and lactation as multiples of TEE in females. They concluded that no sex differences exist in reproductive costs outside of the effects of body size dimorphism, and that in highly dimorphic species, males may actually have higher absolute energy costs per birth event than females due to the necessity of maintaining large body size. They state that for species with less sexual dimorphism, such as chimpanzees, reproductive costs are higher in females than in males. If a sex difference in BMR does exist in chimpanzees, though, this might make the TEE estimates of Key and Ross (1999) inaccurate, at least regarding the degree

to which male and female values diverge. Any such errors would also be carried through to the calculation of sex-specific reproductive costs, possibly affecting their conclusions. Though Key and Ross (1999) examined 19 primate species, we limited our analysis to chimpanzees.

We based our choice to focus on age, climate, and sex as relevant factors on previous research, since many studies have examined these variables' effects on BMR in humans with mixed overall results. For example, while juvenile and adolescent humans consistently exhibit higher BMR<sub>adj</sub> (BMR normalized, or "adjusted," for differences in FFM) than adults (Butte et al., 1995; Kashiwazaki et al., 1995; Spurr et al., 1996), most likely because of growth costs (Holliday, 1971, 1986), the effects of age on BMR later in life are less clear. Many studies find a significant decrease in BMR<sub>adj</sub> with age in adults, most prominently at the transition from reproductive adulthood to senescence (Vaughan et al., 1991; Benedek et al., 1995; Visser et al., 1995; Klausen et al., 1997; Piers et al., 1998; Hunter et al., 2001). Others, however, find this result only in women (Galloway et al., 2000) or find no age influence at all (Keys et al., 1973; Callo-way and Zanni, 1980; Sathyaprabha, 2000).

Climate also affects BMR in a complex manner. Several independent studies show that circumpolar populations have higher BMR<sub>adj</sub> than those living in temperate areas (Katzmarzyk, 1994; Rode and Shephard, 1995; Shephard and Rode, 1996; Sorensen et al., 1999; Galloway et al., 2000). In addition, European temperate populations have higher BMR<sub>adj</sub> than tropical populations (Henry and Rees, 1991), while other temperate populations, such as North Americans and Australians, do not (Soares et al., 1993; Valencia et al., 1994; Piers et al., 1997; Van der Ploeg et al., 2001). Ethnic or population level genetic differences appear to have little effect on this variation, since individuals who become habituated to a new (nonnative) climate zone (e.g. South Asians who have moved to Britain) exhibit BMR<sub>adj</sub> statistically equivalent to that of the native population (Henry et al., 1987; Ulijaszek and Strickland, 1991; Hayter and Henry, 1993; Galloway et al., 2000). Although numerous studies have compared BMR between two climate groups, none have made broader climate comparisons on a more global level.

Finally, sex appears not to affect BMR<sub>adj</sub> in either juvenile or adult humans (Owen, 1988; Spurr and Reina, 1988; Mifflin et al., 1990; Ferraro et al., 1992; Spurr et al., 1992; Klausen et al., 1997; McCrory et al., 1998; Piers et al., 1998; Bucholz et al., 2001), though there is some disagreement. Arciero et al. (1993) report a small (3%), but significant, difference between men and women. There are reasons to question the veracity of this finding (see report by The Office of Research Integrity, US Justice Department, March 17, 2005), but we nevertheless tested for sex effects across studies to determine whether our results corroborated those of the individual studies.

The volume of research into factors affecting chimpanzee BMR is considerably smaller, consisting of a single study (Bruhn and Benedict, 1936) that found no effect of either age or sex on BMR, per kg body mass, in chimpanzees. This assessment, however, included no statistical tests, and, more important, employed "per-weight" methods to control for body size that have been shown to produce misleading results (Tanner, 1949; Poehlman and Toth, 1995). Both problems can be resolved by testing with ANCOVA. All wild chimpanzees live in tropical regions and are thus unlikely to exhibit BMR variation due to climate.

The goals of this study were threefold. First, to further investigate the influence of age, sex, and climate on BMR

TABLE 1. Raw mean body size and BMR data

Variable	N	FFM (kg)	Mass (kg)	BMR (kcal/d)
<i>Homo sapiens</i>				
Sex 1 (age < 18 yr)				
Male	15	26.8 ± 11.2		1166 ± 288
Female	16	24.8 ± 9.1		1111 ± 221
Sex 2 (age > 18 yr)				
Male	47	55.3 ± 7.6		1628 ± 198
Female	51	42.9 ± 4.2		1356 ± 140
Age				
<18 yr	31	25.8 ± 10.1		1138 ± 253
18–50 yr	70	48.3 ± 8.8		1497 ± 228
>50 yr	16	50.0 ± 8.3		1393 ± 156
Climate				
Tropical	35	33.3 ± 13.7		1180 ± 256
North American/ Australian	51	48.4 ± 11.9		1469 ± 214
European	26	43.2 ± 11.5		1442 ± 243
Circumpolar	17	48.6 ± 7.5		1605 ± 211
<i>Pan troglodytes</i>				
Sex				
Male	11		14.2 ± 12.1	511 ± 307
Female	14		25.9 ± 14.3	848 ± 359
Age				
Juvenile	12		7.5 ± 4.0	353 ± 99
Adult	13		33.0 ± 7.8	1020 ± 190

Values given are mean ± SD in the last 3 columns.

in humans by conducting a meta-analysis of published data. Second, to conduct the first statistical analysis of sex and age effects on BMR in chimpanzees using ANCOVA, and to provide some comparison to humans. Finally, to derive regression equations based on our analysis to test whether consideration of intraspecific variation due to age, climate, or sex would provide different BMR estimates than other methods, and, if so, how this would affect the conclusions of two recent studies in energetics, those of Leonard and Robertson (1997) and Key and Ross (1999).

## METHODS

### Humans

Our meta-analysis included 45 studies of BMR in subjects of varying age and climate, and of both sexes. We performed two tests for sex differences, one within juveniles and one within adults. Adults and juveniles were tested separately because of hormonal differences that begin with puberty and may affect BMR. We also tested for age differences, using three categories, or classes: 1) <18 years, 2) 18–50 years, 3) >50 years. The ages 18 and 50 years correspond roughly to the cessation of growth and the onset of senescence, respectively. For our climate test we used the following classes based on latitude: 1) circumpolar, 2) temperate, 3) tropical, with the temperate group further divided into a) Europeans, b) North Americans and Australians. We compared four distinct climate groups in all. In all, we gathered data for 11 distinct classes for four tests: Test 1, Juvenile Sex – juvenile males and juvenile females; Test 2, Adult Sex – Adult Males and Adult Females; Test 3, Age – <18, 18–50, and >50 years; Test 4, Climate – Tropical, North American/Australian, European, and Circumpolar. Descriptive data for each class are in Table 1.

Our overall sample size ( $n = 129$ ) was relatively small when compared with other meta-analyses (e.g. Schofield et al., 1985) because others used data on individual subjects. Instead, we chose to use group means, allowing us to

include many more studies since most report only group means rather than data on individuals. Here, we define a group as a set of data containing members of a single class of subjects pertaining to the variable of interest. In testing for sex differences, for example, the classes of interest are “male” and “female”. Thus, a group from which we could draw useful mean data would have to contain only males or only females, but could not include both. In this way, we ensured that the classes we compared for the variables of interest (sex, age and climate) were indeed distinct from one another with respect to the variable being tested. In a few cases where studies did report data for individuals, rather than mix these individual data with the group means from other studies, we calculated means for distinct groups defined according to the above criteria.

The use of group means as data points presents the potential problem that the variance ( $\sigma^2$ ) of each sample may be artificially decreased in comparison to a sample consisting of individual data points. To determine whether or not this might affect our study, we compared standard error of the mean (SEM) for our own samples composed of group means, to those of studies reporting means and standard errors for samples made up of individuals. SEM is calculated as:

$$\sigma/n^{0.5}$$

where  $\sigma$  is standard deviation (the square root of variance) and  $n$  is sample size. Thus, SEM increases or decreases with variance and can indicate what effect using group means had on our data.

For all 11 of our distinct samples, we made comparisons between groups of similar composition (in terms of the relevant variable) and sample size. Within the samples grouped by age, for instance, we compared our reproductive adult (18–50 years) sample ( $n = 70$ ) to published statistics for adults within the same age range, and a sample size between 65 and 75. In all but one case, the SEM calculated for each of our samples either fell within the range of published values or was higher, indicating more variance rather than less. This suggests that for the most part, reduced variance due to the use of group means rather than individual data is not a problem for this study. Our adult female group's SEM fell below the range of published values, the only one to do so. This does indicate a decrease in variance in this sample, and may affect our results. Decreased variance increases the likelihood of our finding a significant difference between this group and the adult male group. If such a difference is found, it must be interpreted with caution. For the other tests, though, this does not appear to be an issue.

We used Internet databases (ISI Web of Science, BIOSIS/Ovid) to locate data. Search criteria included year >1985; keywords – BMR, basal metabolic rate, RMR, resting metabolic rate, REE, resting energy expenditure. We limited our sample to studies that followed the standard measurement protocol for BMR (see Silverthorn et al., 2004) regardless of whether the study called the variable BMR, RMR (resting metabolic rate), or REE (resting energy expenditure). Therefore, to be included here, a study had to explicitly state that subjects had fasted for at least 12 h prior to measurement, and that data were collected under thermoneutral conditions (20–25°C), while subjects were at rest and free from anxiety. Strict exclusion criteria were observed in order to ensure that, whatever term individual studies used for their data, the data

were collected according to the standard protocol for BMR measurement.

Other steps ensured comparability between studies. We used only studies that used a respirometer validated against other such devices (Orsini and Passmore, 1951; McNeill et al., 1987; Segal, 1987; Soares et al., 1989). We also chose only studies that measured RQ, the ratio of CO<sub>2</sub> production to O<sub>2</sub> consumption, and used one of two comparable caloric conversion methods (Peters and Van Slyke, 1946; Weir, 1949), to control for differences in the relative proportion of fat and carbohydrate metabolized at rest. Where reported, data from women in the luteal phase of menstruation or taking oral contraceptive pills were excluded, since these elevate BMR (Anantharaman-Barr et al., 1990; Ferraro et al., 1992; Piers et al., 1995, 1997; Curtis et al., 1996; Diffey et al., 1997). We only included studies that reported FFM data so that the effects of the other variables could be determined independent of between group differences in body fat. A list of data sources for this study is available upon request from the first author.

### Chimpanzees

Only four publications of original BMR data exist for chimpanzees, two of which report no data on body size (Dale et al., 1967, 1970). The other two studies (Bruhn, 1934; Bruhn and Benedict, 1936) report whole body mass and BMR for a set of captive individuals. These subjects were measured during sleep to minimize muscular activity, and were not fed for at least 12 h prior to testing. Measurements were made within a temperature range of 25–29°C in one of two differently sized respiration chambers. Thus, these data were collected following standard BMR measurement protocol as closely as possible. The only substantial departure is that subjects were measured during sleep rather than while awake. Humans show lowered BMR values during sleep (Garby et al., 1987; Goldberg et al., 1988; Seale and Conway, 1999), which could also apply to chimpanzees; but, the differences are so small as to be unlikely to affect our study.

The three subjects from the study of Bruhn (1934), classified as adult males based on sexual maturity, had body masses lower than most of the adult females in the study of Bruhn and Benedict (1936). Because sexual maturity occurred before males, “attained . . . maximum physical development” (Bruhn and Benedict, 1936:267), it is possible that Bruhn’s (1934) subjects were still growing, making them juveniles in terms of BMR. We compared the body mass of Bruhn’s (1934) subjects with that of the 12 adults in the study of Bruhn and Benedict (1936), finding that body mass *z*-scores for two of the three subjects in the former study fall outside the 95% confidence interval for adults in the latter. We therefore reclassified these two as juveniles for our study.

Taken together, these two studies provide data on 25 individual chimpanzees of both sexes and a range of ages (Bruhn, 1934: *n* = 3; Bruhn and Benedict, 1936: *n* = 22). There are no FFM data for any of the chimpanzees in these studies, and none available elsewhere; so we used whole body mass instead to normalize BMR. This could result in artificially low estimates of BMR in wild chimpanzees if, because of inactivity, these captive subjects carried more body fat than their wild counterparts. We do not, however, expect this to be important here. The subjects were “housed in large outdoor living quarters,” (Bruhn and Benedict, 1936:263) providing them the

TABLE 2. 95% Confidence estimates for adjusted BMR

Variable	<i>P</i> -value <sup>1</sup>	Adjusted mean BMR (kcal/d) <sup>2</sup>	95% CI (kcal/d) <sup>3</sup>
<i>Homo sapiens</i>			
Sex 1 (age < 18 yr)			
Boys	0.800 (NS)	1142	1093–1191
Girls		1135	1089–1189
Sex 2 (age > 18 yr)			
Men	0.473 (NS)	1499	1357–1641
Women		1473	1316–1630
Age			
<18 yr	<0.001*	1513	1470–1557***
18–50 yr		1368	1345–1392***
>50 yr		1228	1182–1273***
Climate			
Tropical	<0.001*	1353	1315–1390**
North American/ Australian		1381	1351–1410**
European		1442	1402–1482**
Circumpolar		1514	1464–1564**
<i>Pan troglodytes</i>			
Sex			
Males	0.119 (NS)	672	633–711
Females		719	685–754
Age			
Juveniles	0.390 (NS)	648	583–713
Adults		750	690–810

<sup>1</sup>Results of ANCOVA. NS indicates no significant difference between groups, while \* Indicates significance.

<sup>2</sup>Mean BMR for each group after adjusting for between group differences in FFM (humans) or body mass (chimpanzees).

<sup>3</sup>95% Confidence interval of the adjusted mean BMR for each group.

\*\* Indicates that the group’s interval does not overlap with at least one other group.

\*\*\* Indicates that the group’s interval does not overlap with any other group for that test.

opportunity for more physical activity than if always caged. Also, the adults were weight stable (Bruhn and Benedict, 1936), indicating a good balance between dietary caloric intake and activity-based energy expenditure, and therefore a lack of excess fat deposition. These two factors suggest that the body composition of these captive chimpanzees resembles that of wild individuals within a level that should not affect BMR.

All subjects were housed near Jacksonville, Florida, rather than on the equator, but we do not expect this difference in latitude to affect BMR. Although temperatures in wild chimpanzee habitats (see Matsumoto-Oda, 2002; Takemoto, 2004) are somewhat hotter and cover a narrower range than in Florida, Jacksonville’s climate is subtropical, not temperate. Climate is thus unlikely to greatly affect BMR in the captive chimpanzee population when compared to wild conspecifics. Descriptive data are in Table 1.

### Statistical methods

We employed ANCOVA to test for differences between groups in BMR, using as the covariate FFM in humans, and body mass in chimpanzees. ANCOVA is a regression-based technique for assessing differences between discreet classes of data, where data are normalized for between-class-differences due to the effects of a major confounding variable, or covariate. It assumes homogeneity of slopes between the different classes (this assumption was met for all tests), thereby removing the effect of the covariate on the data. The adjusted regression data are then tested

TABLE 3. Human and chimpanzee equations compared<sup>1</sup>

Species	Y-intercept	Slope	BMR (kcal/d) <sup>2</sup>
<i>Pan troglodytes</i>	172 (121–223)*	25.45 (23.41–27.49)*	1445
<i>Homo sapiens</i>	744 (355–1133)*	10.56 (3.24–17.87)*	1272

<sup>1</sup> Regression statistics for BMR/body mass equations in humans and chimpanzees. Numbers in parentheses are 95% confidence intervals.

<sup>2</sup> BMR for a 50-kg individual as estimated using each equation.

\* Indicates significantly different.

for differences in Y-intercepts. Where three or more classes are compared (e.g. with the human age and climate tests here) group means, adjusted for differences in the covariate, are calculated post hoc using the test parameters (including Y-intercepts) generated by the analysis. For these adjusted group means, 95% confidence intervals are calculated for comparison with the other classes. Where no overlap occurs, a significant difference exists.

Calculations were made with SPSS Version 11.5 for Windows. We calculated 95% confidence intervals for each group's mean (adjusted for between-group differences in FFM), according to the protocol of Gabriel (1978), to determine the source of any significant differences found using ANCOVA. Once differences between groups were determined, we then used the results to derive group specific regression equations to predict BMR from FFM in humans and from body mass in chimpanzees.

## RESULTS

### Intraspecies variation in BMR

Table 2 contains mean BMR<sub>adj</sub> and 95% confidence intervals for between-group comparisons. Concurrent with the majority of other studies (e.g. Piers et al., 1998; Bucholz et al., 2001), our data show no significant effect of sex on BMR in humans younger than 18 years ( $P = 0.800$ ) or in adults ( $P = 0.473$ ). The latter finding is not affected by the decreased variance in the adult female sample (see earlier), since this biased the test toward finding a sex difference. In contrast to our results on sex, we find that BMR varies significantly with age ( $P < 0.001$ ) with no overlap of the 95% confidence intervals of the three groups. Children and adolescents have the highest BMR<sub>adj</sub>, followed in descending order by adults aged 18–50 years and adults older than 50 years. Climate groups also exhibit significant differences in BMR ( $P < 0.001$ ). The tropical group has the lowest BMR<sub>adj</sub>, followed in ascending order by the North Americans/Australians, Europeans, and finally the circumpolar group. There is some overlap at the margins of each group's 95% confidence intervals such that the North American/Australian group shares part of its range with both the tropical and European groups, while European and circumpolar subjects also overlap slightly. These overlaps probably reflect the use of latitude as a gross estimate of climate.

Our chimpanzee sample shows no significant sex ( $P = 0.119$ ) or age ( $P = 0.390$ ) differences in BMR<sub>adj</sub>, although females are 7% higher than males, and adults are 16% higher than juveniles. The lack of significance of these strong trends may result from the small sample size; a larger sample is needed to determine whether or not such trends are truly significant.

We calculated a regression equation for BMR vs. FFM in adult (18–50-year-old) tropical humans, combining males and females:

$$\text{BMR (kcal/d)} = 17.27 \times \text{FFM (kg)} + 605 \quad (1)$$

Given the lack of significant age and sex differences, we derived a single equation for all chimpanzees predicting BMR from whole body mass:

$$\text{BMR (kcal/d)} = 25.45 \times \text{Body Mass (kg)} + 172 \quad (2)$$

For comparison with chimpanzees, we also derived an equation predicting BMR from whole body mass in adult tropical humans:

$$\text{BMR (kcal/d)} = 10.56 \times \text{Body Mass (kg)} + 744 \quad (3)$$

The slopes and Y-intercepts of the chimpanzee and human equations using body mass differ significantly (Table 3), indicating that two separate, species-specific equations are indeed necessary. This result could be misleading, however, because of the use of whole body mass to normalize BMR. Body mass does not account for differences in body composition that may exist between humans and chimpanzees, thus potentially confounding the BMR comparison. The use of FFM would be preferable, as it would control for any body composition differences that may exist between the two species.

### Estimated BMR

To estimate BMR in free-ranging chimpanzees, we used the same published data on body mass as did Leonard and Robertson (1997). In contrast, estimating BMR in human foragers presented a challenge, since our human equation predicts BMR from FFM instead of body mass. No FFM or body composition data exist for the !Kung and, published body fat percentages for the Ache (men = 17.9%; women = 33.3%) come from individuals who have discontinued foraging and have subsisted chiefly through farming for the past 25 years (Bribiescas, 2001). Thus, we estimated percent body fat in active foragers, the Hadza, using published skinfold data (Hiernaux and Hartono, 1980) and a commonly used reference table (Durnin and Womersley, 1974; see Table 4). The Hadza body fat percentages were then applied to the calculation of FFM in the !Kung and the Ache, and also in fossil species (Table 4) from published body mass estimates (McHenry, 1992; Ruff and Walker, 1993).

We compared our BMR values to those of Leonard and Robertson (1997) (Table 5), finding values lower by 6% in the Ache and by 5% in the !Kung. This is expected based on the lower BMR in tropical people relative to European temperate populations. Our equation also gives BMR estimates 2% lower for *H. erectus* and early *H. sapiens* than what Leonard and Robertson (1997) reported. Here, the smaller difference results from Leonard and Robertson's use of Kleiber (1961) to calculate fossil BMR. Though Kleiber (1961) used European humans to calculate his general equation, his use of a wide range of mammalian taxa may have prevented his regression from being biased toward higher values despite including only Europeans.

TABLE 4. Estimates of FFM

Group/species	Sex	Body mass <sup>1</sup>	FFM <sup>2</sup>
Hadza	M	54.3	48.2
	F	48.3	37.1
Ache	M	59.6	52.9
	F	51.3	39.8
!Kung	M	46.0	40.8
	F	41.0	31.5
<i>H. erectus</i>	M	63.0	55.9
	F	52.3	40.2
Early <i>H. sapiens</i>	M	65.0	57.7
	F	54.0	41.5

<sup>1</sup>Hadza: Hiernaux and Hartono (1980); Ache: Hill et al. (1984, 1985), Hurtado et al. (1985); !Kung: Lee (1979); *H. erectus*: McHenry (1992), Ruff and Walker (1993); early *H. sapiens*: McHenry (1992).

<sup>2</sup>Estimated from Hadza skinfold data (Hiernaux and Hartono, 1980), and corresponding body fat percentages from the study of Durnin and Womersley (1974): men = 11.3%; women = 23.1%.

Thus, it appears that tropical dwelling humans have BMR values more similar to what is expected from mammals overall, whereas some temperate people (and circumpolar people) diverge from the mammalian pattern to a greater degree.

For chimpanzees, our new equation estimates BMR values 12% higher than the ones Leonard and Robertson (1997) obtained from the study of Bruhn (1934). Using our chimpanzee equation, we estimate that *A. afarensis* and *A. africanus* had BMR 6% higher than Leonard and Robertson's (1997) values obtained using Kleiber's (1961) general mammalian equation. Here, the divergence from Kleiber (1961) probably results from the fact that we used species-specific chimpanzee data to predict BMR in these australopithecine species. This remains consistent when our results are compared with those of Key and Ross (1999), who also used Kleiber's (1961) equation to estimate chimpanzee BMR: our equation produces BMR values 6–7% higher. In Kleiber's (1961) regression plot, the chimpanzee data point lies slightly above the regression line, indicating that chimpanzees have a marginally higher measured BMR than expected for mammals, but still within the 95% confidence limits. This may explain why our species-specific values diverge from the previous studies' results.

In combination, our estimates suggest that BMR in *H. erectus* and early *H. sapiens* exceeded that of australopithecines by 32%, due mainly to the larger body size of the former two species. This contrasts slightly with previous estimates of a 40% difference between these taxa (Leonard and Robertson, 1997). Per kg body mass, BMR in *H. erectus* and early *H. sapiens* is 82% of the australopithecine value, which is expected from allometry. With regard to Key and Ross (1999), we find that both sexes of chimpanzee have higher BMR than Kleiber (1961) predicts, but this does not affect the difference in BMR between males and females. Key and Ross (1999) show males to have absolute BMR ~20% higher than females, due mainly to body size dimorphism, and we find the same result using our new equation.

### Estimated TEE

We calculated TEE in extant chimpanzees and human foragers following the methods of Leonard and Robertson (1997) and Key and Ross (1999), but using our new BMR values. We found slightly higher TEE values for chimpan-

TABLE 5. Comparison with the study of Leonard and Robertson (1997)

Group/species	BMR (kcal/d)		TEE (kcal/d)	
	Leonard and Robertson (1997)	This study	Leonard and Robertson (1997)	This study
<i>P. troglodytes</i>	938	1054 <sup>1</sup>	1327	1409 <sup>2</sup>
Ache	1493	1406 <sup>3</sup>	2636	2592 <sup>2</sup>
!Kung	1291	1230 <sup>3</sup>	2016	1994 <sup>2</sup>
<i>A. afarensis</i>	1045	1113 <sup>1</sup>	1395	1478 <sup>4</sup>
<i>A. africanus</i>	1016	1076 <sup>1</sup>	1342	1434 <sup>4</sup>
<i>H. erectus</i>	1463	1435 <sup>3</sup>	2626	2574 <sup>5</sup>
Early <i>H. sapiens</i>	1493	1462 <sup>3</sup>	2692	2640 <sup>5</sup>

<sup>1</sup>Calculated using our new chimpanzee equation.

<sup>2</sup>Calculated from published activity budgets, and BMR from this study.

<sup>3</sup>Calculated using our new human equation and FFM estimates.

<sup>4</sup>Estimated based on chimpanzee divergence from general primate TEE equation.

<sup>5</sup>Estimated based on human foragers divergence from general primate TEE equation.

zees, and slightly lower values for Ache and !Kung foragers (Tables 5 and 6). When compared with values expected from Leonard and Robertson's (1997) general primate equation, our TEE estimates deviate with *z*-scores of -0.09 and +1.49, respectively. In contrast, Leonard and Robertson (1997) find *z*-scores of -0.45 for chimpanzees and +1.54 for humans. Our *z*-scores produce TEE values 6–7% higher for *A. afarensis* (1478 kcal/day) and *A. africanus* (1434 kcal/day), and 2% lower for *H. erectus* (2574 kcal/day) and early *H. sapiens* (2640 kcal/day), compared with the values that Leonard and Robertson (1997) report (Table 5). We find *H. erectus* TEE to be 175–180% of the value for australopithecines, virtually identical to the results of Leonard and Robertson (1997).

Key and Ross (1999) also present a general primate equation for TEE, which we used to calculate expected values for chimpanzees (Table 6). For male chimpanzees, the expected value falls midway between our species-specific TEE estimate and that of Key and Ross (1999). In contrast, for females, the expected value is higher than the species-specific value Key and Ross (1999) report, but was almost identical to our own prediction (difference of 2 kcal/d). We also followed the methods of Key and Ross (1999) to estimate reproductive costs in male and female chimpanzees (Table 6). We find higher absolute caloric values, but as with BMR, relative differences between the sexes are practically the same in both our study and in the study of Key and Ross (1999): 12 versus 14% higher in females, respectively.

### CONCLUSIONS

The significant *intraspecific* effects of age and climate on BMR in humans shown by our study are of negligible importance for *interspecific* comparisons of TEE. Further, our expanded chimpanzee sample did not markedly affect the overall results. Our results confirm those of Leonard and Robertson (1997), who proposed a near doubling of energy output in *H. erectus* and early *H. sapiens* over that of the australopithecines. We also support the findings of Key and Ross (1999), indicating that their conclusions regarding the interaction between body size dimorphism and energy investment in reproduction are not affected by

TABLE 6. Comparison with the study of Key and Ross (1999)

Sex	BMR (kcal/d)		TEE (kcal/d)			Reproductive costs (10 <sup>6</sup> kcal)	
	Key and Ross (1999)	This study	Expected <sup>1</sup>	Key and Ross (1999) <sup>2</sup>	This study <sup>2</sup>	Key and Ross (1999)	This study <sup>3</sup>
M	1169	1259 <sup>4</sup>	1559	1515 (-44)	1615 <sup>5</sup> (+56)	3.05	3.25
F	979	1030 <sup>4</sup>	1305	1245 (-60)	1303 <sup>5</sup> (+2)	3.49	3.65

<sup>1</sup> Calculated using the general primate equation for TEE in the study of Key and Ross (1999).

<sup>2</sup> Numbers in parentheses represent the difference between calculated and expected values.

<sup>3</sup> Calculated with data and equations from the study of Key and Ross (1999), using TEE estimates from this study.

<sup>4</sup> Calculated using our new chimpanzee equation.

<sup>5</sup> Calculated from published activity budgets and BMR from this study.

variation in BMR within chimpanzees. This is expected, given the lack of sex differences in chimpanzee BMR. The significant intraspecific variation in BMR that we find does, however, suggest that comparisons between extant human groups (e.g. between different foraging groups) or closely related species should be made with caution. Our results suggest that tropical dwelling humans have BMR values more similar to what is expected from mammals overall, whereas circumpolar and some temperate people diverge from the mammalian pattern to a greater degree. This could have implications for reconstructing the physiological changes that accompanied hominin migration into colder regions, and the origins of climatic variation in BMR in modern humans and possibly Neandertals (e.g. Sorensen and Leonard, 2001; Culotta, 2005).

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