

*Original Research Article***Basal Metabolic Rate in the Yakut (Sakha) of Siberia**J. JOSH SNODGRASS,^{1,2*} WILLIAM R. LEONARD,¹ LARISSA A. TARSKAIA,³ VASILI P. ALEKSEEV,⁴ AND VADIM G. KRIVOSHAPKIN⁴¹Department of Anthropology, Northwestern University, Evanston, Illinois 60208²Institute for Mind and Biology, The University of Chicago, Chicago, Illinois 60637³Institute of Molecular Genetics, Russian Academy of Sciences, Moscow 115478, Russia⁴Institute of Health, Academy of Sciences of the Republic of Sakha (Yakutia), Yakutsk 677010, Russia

ABSTRACT Human indigenous circumpolar populations have elevated basal metabolic rates (BMRs) relative to predicted values; this metabolic elevation has been postulated to be a physiological adaptation to chronic and severe cold stress. The present study examines BMR in the Yakut, an indigenous high-latitude population from the Sakha Republic of Russia to determine (1) whether the Yakut show evidence of an elevated BMR, (2) if the Yakut display evidence of age-related changes in BMR, and (3) whether lifestyle differences influence BMR. BMR was measured during the late summer in 75 women and 50 men (ages 18–56 years) from the Siberian village of Berdygestiakh. Measured BMR (\pm SEM) of the entire sample was significantly elevated (+6.5%) compared to predictions based on body mass ($6,623.7 \pm 94.9$ vs. $6,218.2 \pm 84.7$ kJ/day; $P < 0.001$). Additionally, measured BMR for the entire sample was significantly higher than predictions based on fat-free mass (+20.8%) and surface area (+8.9%). Males and females both showed significant elevations relative to all three standards. The elevated BMR of the Yakut does not appear to be attributable to extreme levels of protein, since the Yakut consume a mixed diet with a substantial proportion of carbohydrates. No significant age-related changes in BMR were found when controlled for body composition. No significant relationship was found between lifestyle variables and BMR, suggesting the possibility of a genetic or developmental mechanism. This study provides additional evidence of metabolic elevation in indigenous circumpolar groups and has important implications for estimating the nutritional requirements of these populations. *Am. J. Hum. Biol.* 17:155–172, 2005. © 2005 Wiley-Liss, Inc.

Beginning in the early part of the 20th century, researchers documented substantial elevations in basal metabolic rates (BMRs) of indigenous high-latitude populations in Alaska and Canada (Heinbecker, 1928; Rabinowitch and Smith, 1936; Crile and Quiring, 1939; Rodahl, 1952; Brown et al., 1954; Brown, 1957; Adams and Covino, 1958; Hart et al., 1962; Rennie et al., 1962; Hildes, 1963; Milan et al., 1963; Milan and Evonuk, 1967). However, some researchers found normal values among traditionally living groups (e.g., Heinbecker, 1931), while others reported elevated values for traditionally living populations but normal values for groups living under more “modernized” conditions (Rodahl, 1952; Hart et al., 1962). Unfortunately, many of these early studies failed to control for the confounding effects of diet, anxiety, and body composition. Additionally, many of the studies relied on small samples.

A number of recent investigations with controlled measurement conditions have docu-

mented significantly elevated BMRs in circumpolar populations. Rode and Shephard (1995) found that BMRs of Inuit participants were greater than those of European individuals living in the same communities as well as higher than predicted values based on European populations. The Buriat and Evenki of Siberia had substantially higher BMRs relative to predicted values derived from European populations and, in the case of the Evenki, relative to non-indigenous individuals (i.e., Russians) living in the same communities (Sorensen et al., 1999; Galloway

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*Correspondence to: J. Josh Snodgrass, Department of Anthropology, Northwestern University, 1810 Hinman Avenue, Evanston, IL 60208. E-mail: j-snodgrass@northwestern.edu

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et al., 2000; Leonard et al., 2002b). Leonard and colleagues (2002b) compiled measurements from indigenous circumpolar North Americans and Asians, including five ethnic groups (Inuit, Chippewa, Athapascan, Evenki, and Buriat), and found elevated BMRs relative to standards based on body mass, fat-free mass, and surface area on the order of +7–19% in men and +3–17% in women.

Numerous researchers (e.g., Roberts, 1978) have hypothesized that elevated BMRs in indigenous northern populations represent an adaptation to chronic and severe cold stress experienced in the circumpolar environment. In addition to cold stress, high-latitude populations are also exposed to a suite of other ecological stressors, including seasonal variation in photoperiod, that may contribute to BMR elevation (Leonard, 2000). In support of the relationship between climate and metabolic rate, an inverse relationship between BMR and mean annual temperature has been documented, which holds true even when controlled for differences in body size (Roberts, 1952, 1978). Although limited in number, preliminary studies of high-latitude populations provide evidence of seasonal variation in BMR, with the highest measurements taken in the winter (Osiba, 1957; Kashiwazaki, 1990). Recent studies of northern European populations, such as work by Plasqui and colleagues (2003), have documented a significant seasonal metabolic elevation with the highest sleeping metabolic rate (SMR) in the winter and the lowest SMR in the summer. However, other studies of northern Europeans have not documented seasonal metabolic fluctuations (e.g., Haggarty et al., 1994).

Elevated BMR in circumpolar populations appears to be at least partially related to upregulation of thyroid hormones (Osiba, 1957; Itoh, 1980; Silva, 1995; Leonard et al., 1999, 2002b). Elevated levels of thyroid hormones (especially tri-iodothyronine [T_3] and thyroxine [T_4]) promote increased thermogenesis in humans and other mammals by increasing rates of oxidative metabolism throughout the body (Hadley, 1996; Bentley, 1998). Research by Leonard and colleagues (1999) demonstrated a link between free thyroxine levels and metabolic variation in indigenous Siberians during a single seasonal period (i.e., the late summer). Other researchers have demonstrated seasonal fluctuations in thyroid hormones in indigenous and non-indigenous high-latitude populations, which appear to be

the related to variation in temperature and photoperiod (Osiba, 1957; Eastman et al., 1974; Smals et al., 1977; Tkachev et al., 1991; Bojko, 1997; Hassi et al., 2001).

Despite recent studies that document systematic and significant elevation of BMR in circumpolar populations, this issue remains controversial within human biology. The most recent review of cold stress in living humans (i.e., Beall and Steegmann, 2000) did not discuss the topic of elevated BMRs in circumpolar populations. The subject has additionally been neglected within the burgeoning literature on interpopulation variation in BMR (e.g., Henry and Rees, 1991; Shetty et al., 1996); virtually all these studies concentrate exclusively on tropical and temperate populations. Many authors continue to attribute these elevated BMR values to heightened anxiety among participants during measurement, interpopulation differences in body size and composition, or the influence of diets with extreme protein content (e.g., Shetty, 1996; Kormondy and Brown, 1998), and consequently dismiss their results. Expert committees responsible for international energy intake recommendations have also failed to recognize the elevated BMR values in circumpolar populations; however, this represents a departure from the stance taken in earlier guidelines. While the FAO (1957) nutritional guidelines incorporated climate into its calculation of energy needs by recommending a 3% addition for every 10°C decrease in annual temperature below the baseline of 10°C, more recent expert panels (e.g., FAO, 1973; FAO/WHO/UNU, 1985) have not included an adjustment and remain identical to those for lower-latitude populations.

While research over the past two decades has demonstrated a systematic elevation of BMR in circumpolar populations, most studies have documented substantial *intrapopulation* variation. Galloway and colleagues (2000), for example, documented considerable variation between Evenki villages within the same region of central Siberia despite similarities in anthropometric measures between these communities. BMRs were found to be substantially elevated in Surinda compared to Poligus and, in the latter village, both sexes had BMRs *below* those predicted by surface area and body mass norms. These researchers attributed this metabolic variation to lifestyle differences between the two villages, with residents of the more northerly Surinda being more “traditional” in lifestyle, with a

higher physical activity level associated with a more nomadic existence, greater exposure to cold stress, and consumption of a more traditional diet higher in protein and fat. In another study, Rode and Shephard (1995) documented elevated BMRs in an Inuit population from Igloodik (Northwest Territories, Canada) but recorded substantial variation between individuals, with the older, more traditionally living men and women having higher BMRs even when controlled for body composition. These studies bring into question the mechanisms involved in BMR elevation and suggest the possibility of reduced metabolic rate as the result of lifestyle changes in northern communities. While recent research documents the existence of a certain degree of metabolic plasticity and suggests a combination of genetic adaptation and functional acclimatization, most past studies of BMR in circumpolar populations relied on relatively small samples. As a consequence, the influence of lifestyle differences on BMR remains a largely unexplored area, despite its important implications for understanding health changes associated with economic modernization in circumpolar populations.

In the current study, we investigate BMR in the Yakut, an indigenous high-latitude population of horse and cattle pastoralists from the Sakha Republic of the Russian Federation. The purpose of this paper is threefold. First, we examine evidence for a metabolic adaptation in a large sample of Yakut adults by comparing BMR measurements with predicted values based on international standards for body mass, fat-free mass, and surface area. Second, we examine BMR variation in the Yakut to test for evidence of age-related changes. Finally, we examine the influence of lifestyle differences on intrapopulation variation in BMR.

METHODS

Study population

The Yakut (Sakha), who number approximately 380,000, are concentrated in north-eastern Siberia and make up nearly 40% of the population of the Sakha Republic of the Russian Federation (Forsyth, 1992; Balzer and Vinokurova, 1996; Jordan and Jordan-Bychkov, 2001). The origin of the Yakut has long been of interest to scholars because their language is most closely related to Turkic languages of the Central Asian

Steppe, while components of their material culture and subsistence behavior show affinities with Buriat and Mongolian populations of the Lake Baikal region (Jochelson, 1933; Krueger, 1962; Tokarev and Gurvich, 1964). Genetic studies indicate that the Yakut have close affinities with other indigenous Siberian groups, including the Evenki, Tuvan, Yukagir, and Buriat, while being more distantly related to other Turkic-speaking populations (Pakendorf et al., 1999, 2003; Zlojutro et al., 2003). The Yakut traditionally practiced a complex and locally variable subsistence strategy that was largely dependent upon regional ecological conditions (Tokarev and Gurvich, 1964). In remote parts of the boreal forest (*taiga*), the Yakut subsisted by hunting and fishing, while in the Lena River Valley the primary subsistence activity was transhumant pastoralism (primarily horse and cattle).

The initial contact between the Yakut and Russians occurred in the early 17th century as Russians expanded eastward through the Siberian plain in search of animal pelts to procure for the burgeoning European fur market (Dmytryshyn et al., 1985; Forsyth, 1992). A key phase of reorganization for Siberia's indigenous people began in the 1930s during collectivization and continued in outlying regions throughout the 1950s (Forsyth, 1992). The Soviet reforms were designed to "enlighten" indigenous people by forcing the abandonment of traditional subsistence practices that were considered primitive; in reality, however, collectivization was an effort to proletarianize the native population and exploit them for the greater good of the Soviet state (Slezkine, 1994). Collectivization for the Yakut began around 1930 as the Soviet government attempted to industrialize and urbanize Siberia, and most rural Yakut were forced to abandon past land-use patterns and settle in farm sites, fishing villages, and fur-trapping collectives (Forsyth, 1992; Mote, 1998). By 1940, almost the entire Yakut population was collectivized, and most resided in large, permanent villages and had shifted to a wage and welfare economy (Forsyth, 1992; Mote, 1998; Jordan and Jordan-Bychkov, 2001). This period brought about major changes for the Yakut, including social transformations of an unprecedented magnitude, dietary shifts, alterations to activity patterns, and changes in land-use patterns (Slezkine, 1994).

Following the collapse of the Soviet Union in 1991, economic and political changes accelerated and unleashed catastrophic changes for the Yakut and other indigenous Siberians who depended on the government for wages and deliveries of food and essential goods (Balzer, 1995; Kempton, 1996; Sorensen, 2003). Many rural Yakut, like other indigenous Siberians, returned to traditional subsistence activities (i.e., herding, fishing, hunting, gathering, and horticulture) to meet the needs no longer met by the government (Fondahl, 1995, 1997; Vinokurova, 1995; Crate, 2001; Jordan and Jordan-Bychkov, 2001; Leonard et al., 2002a; Sorensen, 2003). In recent years, marked lifestyle heterogeneity and economic inequality have emerged in most rural Yakut communities. Many individuals, especially those in large communities or those near urban centers, are involved in wage-earning employment and are tied to regional, national, and global markets (Crate, 2001; Jordan and Jordan-Bychkov, 2001; Sorensen, 2003). These individuals often supplement market foods with local products obtained through subsistence activities, either directly or indirectly through redistribution networks with kin (Crate, 2001). These same communities also have residents that are almost completely reliant on subsistence activities and are minimally connected to larger markets. Today, most rural Yakut populations rely on a mixture of subsistence activities, government wages and pensions, private-sector salaries, and profits from "cottage" industries (Craumer, 1994; Crate, 2001; Jordan and Jordan-Bychkov, 2001).

Participants

Participants included 125 Yakut adult (18–56 years old; 75 females and 50 males) volunteers recruited from the rural Siberian village of Berdygestiakh, 62°N, 127°E (population 4,900), located approximately 180 km west of Yakutsk in the Gorny district of the Sakha Republic (Safronov, 2000) (Fig. 1). Berdygestiakh is located in the subarctic climatic zone and has a mean annual temperature of -11.0°C (12.2°F); mean monthly temperatures range from -40.5°C (-40.9°F) in January to 16.3°C (61.3°F) in July. All data collection took place during the late summer (August) of 2003; the August mean temperature in Berdygestiakh is 12.6°C (54.7°F) (Y.I. Proshin, Sakha Republic Department of Statistics, personal communication).

All participants were ethnically Yakut, based on self-definition, and were healthy at the time of measurement, with no history of metabolic disorders. Pregnant or lactating women were excluded from this study. No information was available on menstrual cycle phase. All measurements were collected at the Gorny Regional Medical Center in Berdygestiakh. This study was conducted in conjunction with the Ministry of Health of the Republic of Sakha. The Institutional Review Board of Northwestern University approved the study protocol and verbal, informed consent (in Yakut or Russian, as preferred) was obtained from all participants.

Anthropometry

Anthropometric dimensions were recorded for all participants according to standard procedures (Lohman et al., 1988). Stature was recorded to the nearest 1.0 mm using a field stadiometer (Seca Corporation, Hanover, MD). Weight was measured to the nearest 0.1 kg using a Tanita BF-558 electronic scale (Tanita Corporation, Tokyo, Japan). Participants were weighed in light clothing, and a correction of 0.5 kg was made to account for the weight of this clothing. Body composition was assessed using two derived measures: body mass index (BMI) and percent body fat (BF). BMI was calculated by dividing mass by height in meters squared (kg/m^2). BF was calculated using two independent methods: bioelectrical impedance analysis (BIA) and sum of skinfolds (SOS). BF_{BIA} was measured using a Tanita BF-558 electronic BIA scale. The Tanita BIA equations are unpublished, and no information is currently available on the reference population. SOS was based on the sum of four skinfolds (triceps, biceps, subscapular, and suprailiac) measured to the nearest 0.5 mm with Lange skinfold calipers (Beta Technology, Santa Cruz, CA); all skinfold measurements were taken without clothing. All skinfold measurements were taken by one experienced observer (J.J.S.) and were repeated three times; the average of the measurements was used in all analyses. BF_{SOS} was calculated according to the sex- and age-specific equations of Durnin and Womersley (1974), which were derived from a sample of Europeans. Although the Durnin and Womersley predictive equations were derived from studies of European populations, studies by Rode and Shephard (1994)



Fig. 1. Map of the Sakha Republic showing the location of the study site (Berdygestiakh). (Inset) Location of the Sakha Republic within the Russian Federation.

documented only a small difference (approximately 1–3%) in young adult males when compared to hydrostatic weighing. Given that previous studies have documented considerable interpopulation differences in body composition and fat distribution, future studies are needed to establish predictive equations for northern populations for assessing body composition from BIA and skinfolds. Fat-free mass (FFM) was calculated as body mass less fat mass calculated by BF_{SOS} . Body surface area (SA) was estimated by measures of mass and height according to the modified

Gehan and George (1970) equation presented in Bailey and Briars (1996).

Basal metabolic rate (BMR)

Participants were familiarized with the procedure and equipment prior to measurement in order to minimize anxiety. BMR (kilojoules [kJ]/day) was measured in a thermoneutral environment (23–27°C), with the participant in a post-absorptive condition (after a 12-h fast). Core body temperature was recorded prior to BMR measurement

using a LifeSource UT-101 infrared ear thermometer (Milpitas, CA).

BMR was measured via indirect calorimetry using a MedGraphics VO2000 open-circuit metabolic analyzer (St. Paul, MN), which measures oxygen consumption (VO_2 , L/min) and CO_2 production (VCO_2 , L/min). All measurements were collected using MedGraphics Breeze Lite software. The AutoCal system was recalibrated for gas volume and composition between every measurement. All measurements were taken with small or medium MedGraphics pre-Vent masks and pneumotachometers and were chosen depending on the size of the individual. Heart rate was simultaneously measured using a Polar S610 heart rate monitor (Woodbury, NY) in order to track participant anxiety level. Barometric pressure was recorded for each participant using a Geneq AP8110 barometer (Montreal, Canada). Laboratory air temperature was measured using an Oregon Scientific EMR-963-HG digital thermometer (Tualatin, OR). The laboratory ambient temperature averaged 25.2°C . A single experienced researcher (W.R.L.) performed all BMR measurements.

Participants had rested quietly in a supine position for a minimum of 20 min prior to measurement of BMR. BMR measurements were recorded for a period of 15–20 min while the participant was lying relaxed in a supine position. All BMR measurements were taken in the morning or early afternoon. Once breathing and heart rate stabilized, VO_2 and VCO_2 were recorded every minute for 10 min; the average of each of these measurements was taken. The respiratory quotient (RQ) was continuously recorded, and an average was calculated for each participant. BMR was then calculated by converting VO_2 to kilojoules per day (kJ/day) based on RQ using the modified Weir formula (Weir, 1949; McArdle et al., 1991). No repeat assessments of BMR were included in this study. However, previous studies have indicated that within-individual variation in BMR is typically less than 8%, although it is generally greater among women (Henry et al., 1989; Spurr et al., 1994; Adriaens et al., 2003).

BMR standards

BMR measurements were compared with predicted values based on standards for body mass, FFM, and SA. BMR standards for body

mass were based on age- and sex-specific norms developed by Schofield (1985) from a large international sample and endorsed by the FAO/WHO/UNU (1985). BMR standards for FFM were developed by Poehlman and Toth (1995) based on sex-specific norms for a U.S. sample. SA standards for predicting BMR were developed by Consolazio and colleagues (1963) based on age- and sex-specific norms for a U.S. sample.

Lifestyle measures

Each participant was given an extensive survey of socioeconomic status (SES) and lifestyle; one experienced researcher (L.A.T.) administered all questionnaires. This survey asked about monthly income, occupation, and education level. Lifestyle questions were focused on participation in subsistence activities and ownership of various consumer goods and livestock. Participants were asked about ownership of 20 items in order to assess their material quality of life. These items included: car, motorcycle, bicycle, television, stereo, VCR, video camera, camera, computer, telephone, washing machine, bath house, ice cellar, barn, tractor, house, cows, horses, pigs, and chickens. For each of the items, participants were asked whether they owned the items and, if so, how many they owned. Participants were also asked to estimate the number of hours per week that they spent viewing television.

Participants were queried about their involvement in subsistence activities, including tending domesticated animals, hay cutting, fishing, hunting, gathering, and horticulture. Participants were also asked to estimate the number of days per year that they engaged in each activity; for tending domesticated animals and horticulture, participants were only asked whether they were involved with each of these activities. Participants were also asked to estimate the amount of food they consumed (as a percent) that was purchased from a store.

A style of life (SOL) scale was created, based on that of Bindon and colleagues (1997), that considered participation in subsistence activities, diet, and ownership of convenience and luxury goods and livestock. Item scores were summed, and a total SOL score was calculated. Items not strongly correlated (i.e., <0.15) with the total summed style of life value were not included in the

final SOL scale. Individuals with lower SOL scores (i.e., more traditional lifestyle) participated in more subsistence activities, consumed less store-bought food, had less formal education, and owned fewer consumer goods. Individuals with higher SOL scores (i.e., more modernized lifestyle) participated in few, if any, subsistence activities, obtained more of their food from a store, had more formal education, and owned more consumer goods. Data were available for 115 individuals (49 males, 66 females). SOL scores ranged from 4 to 20, with a mean of $12.8 (\pm 3.7)$; Cronbach's alpha was 0.62. SOL score was significantly higher in females than males (14.5 ± 2.8 vs. 10.4 ± 3.6 ; $P < 0.001$). The final SOL scale, which includes 16 items, is presented in Table 1.

A subsistence scale was created based on the number of days per year spent in certain

subsistence activities (i.e., hay cutting, fishing, hunting, and gathering) and whether participants were involved in other subsistence activities (i.e., horticulture and tending domesticated animals). This 11-point scale ranged from 0 (participating in all of these subsistence activities) to 10 (participating in no subsistence activities). The orientation of this scale follows the SOL scale, and some variables overlap; the two scales are highly correlated ($r = 0.821$; $P < 0.001$). Data were available for 124 individuals (50 males, 74 females). Subsistence scores ranged from 0 to 9, with a mean of $5.2 (\pm 2.5)$; Cronbach's alpha was 0.63. Subsistence scores were significantly higher in females than males (6.6 ± 1.4 vs. 3.1 ± 2.3 ; $P < 0.001$).

Factor analysis (FA) was used to explore the role and patterns of covariance of various

TABLE 1. Style of life scale for combined sample of males and females; see text for details

Item	Score	Value label	%	Correlation ^a
Bicycle ownership	0	No	58.1	0.331
	1	Yes	41.9	
Stereo ownership	0	No	10.5	0.269
	1	Yes	89.5	
VCR ownership	0	No	21.0	0.152
	1	Yes	79.0	
Video camera ownership	0	No	80.6	0.252
	1	Yes	19.4	
Computer ownership	0	No	75.0	0.278
	1	Yes	25.0	
Ice cellar ownership	0	Yes	28.2	0.232
	1	No	71.8	
Barn ownership	0	Yes	75.8	0.267
	1	No	24.2	
Tractor ownership	0	Yes	10.5	0.320
	1	No	89.5	
Domesticated animal ownership	0	Yes	48.4	0.274
	1	No	51.6	
Domestic animals tending	0	Yes	36.0	0.413
	1	No	64.0	
Subsistence foraging	0	Yes (>16 days per year)	43.2	0.244
	1	Yes (1–16 days per year)	48.8	
	2	No	8.0	
Subsistence hunting	0	Yes (>7 days per year)	28.0	0.552
	1	Yes (1–7 days per year)	7.2	
	2	No	64.8	
Subsistence fishing	0	Yes (>5 days per year)	28.2	0.491
	1	Yes (1–5 days per year)	17.7	
	2	No	54.0	
Subsistence hay cutting	0	Yes (>10 days per year)	28.0	0.671
	1	Yes (1–10 days per year)	19.2	
	2	No	52.8	
Market foods	0	<51%	12.8	0.436
	1	51–75%	27.2	
	2	>75%	60.0	
Education Level	0	Elementary/high school	31.0	0.242
	1	College/university	69.0	

^aCorrelation between item and total score.

socioeconomic and lifestyle variables. FA was used for data reduction by means of principal components analysis (PCA). All FA iterations were performed using Varimax orthogonal rotation with Kaiser normalization and all factor scores were saved by means of the regression method. FA was performed with males and females combined. An initial test using 30 variables (monthly income, education level, number of cars owned, number of motorcycles owned, number of bicycles owned, number of TVs owned, number of stereos owned, number of video players owned, number of video cameras owned, number of cameras owned, number of computers owned, number of telephones owned, number of washing machines owned, ownership of a bath house, ownership of a cellar, ownership of a barn, ownership of a tractor, ownership of a house, number of cows owned, number of horses owned, number of pigs owned, number of chickens owned, whether or not grows own food, number of days forage per year, number of days hunt per year, number of days fishing per year, whether or not tends domestic animals, number of days hay cutting per year, percent of food bought at store, and number of hours watching TV per week) identified six factors with eigenvalues over 1.5. The Kaiser-Meyer-Olkin (KMO) test of sampling ade-

quacy was acceptable at 0.581. Each variable not loading on one of the six factor scores at or above 0.3 was removed, and the analysis was repeated. Six variables were removed (number of chickens owned, whether or not grows own food, number of motorcycles owned, ownership of a barn, number of bicycles owned, and ownership of a house). In the next iteration, FA identified five factors with eigenvalues over 1.5 and a total of eight factors with eigenvalues over 1.0. Only those factors with eigenvalues over 1.5 were used in subsequent analyses. KMO was acceptable at 0.652. Factor loading scores of 0.3 or above were considered acceptable and those at or above 0.5 were given special consideration (Table 2).

Factor analysis was based on socioeconomic and lifestyle data for 111 individuals (46 males, 65 females). Factor 1 has an eigenvalue of 3.65 and explains 15.2% of the observed variance. This factor is related to subsistence activities because it loads heavily on subsistence-related items, such as ownership of cows, number of days of hay cutting per year, and negatively with percent of food bought from a store. Factor 2 has an eigenvalue of 2.76 and explains 11.5% of observed variance. This factor is defined by ownership of horses and pigs and higher education, among other variables. Factor 3

TABLE 2. Rotated component matrix for factor analysis (using principal components analysis) for combined sample of males and females

Variable	Component				
	1	2	3	4	5
Number of cows owned	0.76				
Market foods	-0.72				
Domesticated animal tending	0.63	0.44			
Number of days forage per year	0.50	-0.34	0.32		-0.33
Number of horses owned		0.78			
Number of pigs owned		0.72			
Ownership of tractor	0.30	0.53		-0.34	
Ownership of washing machine		0.46		0.37	
Ownership of cellar		0.41			0.33
Education level			0.67		
Number of video cameras owned			0.64	0.34	
Monthly income			0.62		
Number of computers owned			0.56	0.36	
Number of TVs owned				0.69	
Number of stereos owned				0.65	
Number of telephones owned					0.73
Number of cameras owned					0.58
Number of video players owned					0.58
Number of cars owned	0.38				
Number of days hay cutting per year	0.42				

Note: Only those factors with eigenvalues of at least 1.5 were included. Values represent loading scores for individual factors and are only shown if at or above 0.3. Items with loadings greater than 0.5 are shown in bold. See text for details.

has an eigenvalue of 1.70 and explains 7.1% of the variance. This factor is related to affluence, since it is defined by high monthly income, advanced education, and ownership of electronic goods (i.e., video camera and computer). Interestingly, this factor also associated with number of days foraging. Factor 4 has an eigenvalue of 1.58 and explains 6.6% of the variance. This factor is also related to affluence, with ownership of certain consumer goods (i.e., washing machine, video camera, stereo, computer, and TV), but is not linked with subsistence activities. Factor 5 has an eigenvalue of 1.51 and explains 6.3% of the variance. This factor is associated with certain consumer goods (i.e., camera, telephone, and video player) and is negatively associated with days foraging.

Statistical methods

Measured versus predicted BMR (for body mass, FFM, and SA) were compared using paired-sample *t*-tests (two-tailed). Student's *t*-tests (two-tailed) were used to assess differences between males and females. Multiple regression analysis was used to test the significance of subsistence scale, SOL, FA, age, and body size on BMR. All regression analyses were performed independently by sex. Given the limitations associated with SA in describing metabolic variation (e.g., inherent problems created through the use of a simple ratio, difficulty in obtaining accurate SA measurements, and SA variation between populations resulting from differences in body shape and proportions [Elia, 1992a; Leonard et al., 2002b]), only body mass and FFM were considered in multiple regression models of metabolic variation. All statistical analyses were performed using SPSS 10.0. Comparisons were considered statistically significant at $P < 0.05$. All results are expressed as means \pm standard deviations unless otherwise noted.

RESULTS

Descriptive statistics for age and anthropometric data are presented in Table 3. Participants ranged in age from 18 to 56 years old; there were no significant differences in age between females and males (31.6 ± 10.7 vs. 30.1 ± 10.5 years; NS). Males were significantly larger than females in body mass (66.6 ± 12.9 vs. 60.4 ± 13.8 kg;

TABLE 3. Descriptive statistics for age and anthropometric data^{a,b}

Measure	Females (<i>n</i> = 75)	Males (<i>n</i> = 50)
Age (years)	31.6 (10.7)	30.1 (10.5)
Height (cm)	156.7 (5.5)***	170.1 (6.1)
Weight (kg)	60.4 (13.8)*	66.6 (12.9)
BMI (kg/m ²)	24.6 (5.2)	23.0 (4.0)
Surface area (m ²)	1.65 (0.25)**	1.77 (0.23)
Sum of skinfolds (mm)	95.9 (33.8)***	52.7 (27.8)
Percent body fat (BIA)	29.9 (8.7)***	17.6 (7.2)
Percent body fat (SOS)	36.2 (6.1)***	19.9 (7.2)
Fat-free mass (kg)	37.9 (5.9)***	52.5 (6.3)
Respiratory quotient (RQ)	0.90 (0.10)	0.89 (0.10)
Heart rate (beats/min)	68.8 (8.5)	68.1 (9.5)

^aAll values are presented as means and standard deviations.

^bDifferences between females and males are statistically significant at * $P < 0.05$; ** $P < 0.01$; and *** $P < 0.001$.

$P < 0.05$) and stature (170.1 ± 6.1 vs. 156.7 ± 5.5 cm; $P < 0.001$). However, there were no significant sex differences in BMI (23.0 ± 4.0 in males vs. 24.6 ± 5.2 in females; NS). Among females, 16.0% of individuals were classified as obese (i.e., BMI ≥ 30.0), 14.7% were classified as overweight (BMI = 25.0–29.9), and 69.3% of individuals were classified as of normal body weight or underweight (BMI < 25.0) according to WHO (2000) categories. Among males, 8.0% of individuals were classified as obese, 14.0% were classified as overweight, and 78.0% of individuals were classified as of normal body weight or underweight. BF_{BIA} was significantly higher in females than males (29.9 ± 8.7 vs. 17.6 ± 7.2 %; $P < 0.001$). SOS was significantly higher in females than males (95.9 ± 33.8 vs. 52.7 ± 27.8 mm; $P < 0.001$). BF_{SOS} was significantly higher in females than males (36.2 ± 6.1 vs. 19.9 ± 7.2 %; $P < 0.001$). FFM, calculated using BF_{SOS}, was significantly higher in males than females (52.5 ± 6.3 vs. 37.9 ± 5.9 kg; $P < 0.001$). SA was significantly higher in males than females (1.77 ± 0.23 vs. 1.65 ± 0.25 m²; $P < 0.01$). There were no significant sex differences in RQ (0.90 ± 0.1 in females vs. 0.89 ± 0.1 in males; NS).

Evidence of BMR elevation

Measured and predicted BMRs (\pm standard error of the mean [SEM]) for males ($n = 50$) and females ($n = 75$) relative to standards for body mass, FFM, and SA are presented in Table 4. Males had significantly

TABLE 4. Measured BMR (means and standard error of the mean) versus predicted BMR^a

	Females (n = 75)	Males (n = 50)
BMR vs. body mass		
Measured (kJ/day)	6,072.0 (89.0)***	7,451.3 (125.4)***
Predicted (kJ/day)	5,703.5 (81.5)	6,990.3 (100.1)
Percent deviation (%)	+6.5	+6.6
BMR vs. fat-free mass		
Measured (kJ/day)	6,072.0 (89.0)***	7,451.3 (125.4)***
Predicted (kJ/day)	4,930.3 (53.4)	6,314.8 (70.0)
Percent deviation (%)	+23.2	+18.0
BMR vs. surface area		
Measured (kJ/m ² /h)	154.5 (2.2)***	176.3 (2.2)***
Predicted (kJ/m ² /h)	144.3 (0.6)	158.1 (0.7)
Percent deviation (%)	+7.1	+11.5

^aDifferences between measured and predicted are statistically significant at ****P* < 0.001.

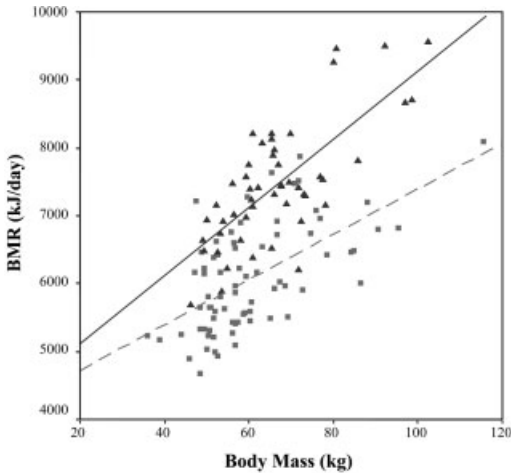


Fig. 2. Scaling relationship of BMR (kJ/day) and body mass (kg) in Yakut males and females. The scaling relationship in Yakut males is 50.3 [body mass] + 4,099 (*r* = 0.73; *P* < 0.001). The scaling relationship in Yakut females is 33.4 [body mass] + 4,055 (*r* = 0.60; *P* < 0.001). Symbols: (- - -, ■) females; (—, ▲) males.

higher measured BMRs than females (7,451.3 ± 125.4 vs. 6,072.0 ± 89.0 kJ/day; *P* < 0.001). Figure 2 shows the scaling relationship of BMR and body mass for Yakut males and females. Measured BMR of the entire sample was significantly elevated (+6.5%) compared to predictions based on body mass (6,623.7 ± 94.9 vs. 6,218.2 ± 84.7 kJ/day; *P* < 0.001). Both males and females showed similar and statistically significant elevations in BMR over that pre-

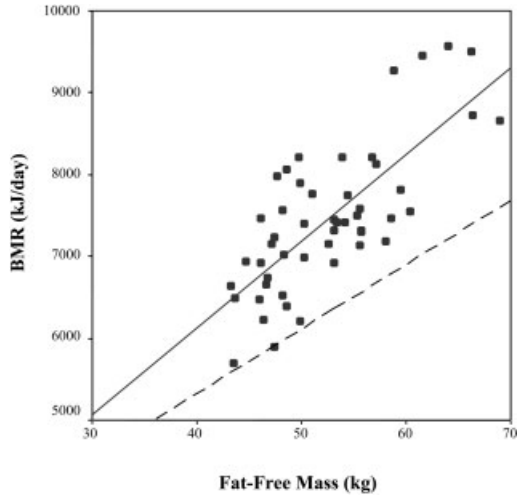


Fig. 3. Scaling relationship of BMR (kJ/day) and fat-free mass (FFM; kg) in Yakut males compared to BMR norms for FFM in U.S. males from Poehlman and Toth (1995). The scaling relationship in Yakut males is 105.9 [FFM] + 1,884 (*r* = 0.75; *P* < 0.001). The scaling relationship in U.S. males is 78.8 [FFM] + 2,174 (*r* = 0.69; *P* < 0.01). Symbols: (- - -) predicted values; (—, ■) Yakut.

dicted by body mass (7,451.3 ± 125.4 vs. 6,990.3 ± 100.1 kJ/day in males [*P* < 0.001] and 6,072.0 ± 89.0 vs. 5,703.5 ± 81.5 kJ/day in females [*P* < 0.001]).

Measured BMR for the entire sample was significantly higher (+20.8%) than predictions based on FFM (6,623.7 ± 94.9 vs. 5,484.1 ± 74.2 kJ/day; *P* < 0.001). Figure 3 shows the scaling relationship of BMR and FFM in Yakut males compared to BMR standards for FFM. The scaling relationship in Yakut males is 105.9 (FFM) + 1,884, whereas the relationship for the US males is 78.8 (FFM) + 2,174. Figure 4 shows the scaling relationship of BMR and FFM in Yakut females compared to BMR standards for FFM. The scaling relationship in Yakut females is 74.4 (FFM) + 3,252, whereas the relationship for the U.S. females is 78.8 (FFM) + 1,944. Both males and females showed statistically significant elevations in BMR over predicted for FFM (7,451.3 ± 125.4 vs. 6,314.8 ± 70.0 kJ/day in males [*P* < 0.001] and 6,072.0 ± 89.0 vs. 4,930.0 ± 53.4 kJ/day in females [*P* < 0.001]).

Measured BMR for the entire sample was significantly higher (+8.9%) than predictions based on SA (163.2 ± 1.8 vs. 149.8 ± 0.8 kJ/m²/h; *P* < 0.001). Both males and

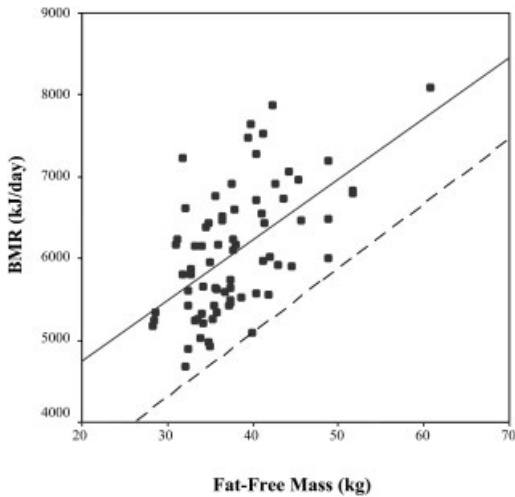


Fig. 4. Scaling relationship of BMR (kJ/day) and fat-free mass (FFM; kg) in Yakut females compared to BMR norms for FFM in U.S. females from Poehlman and Toth (1995). The scaling relationship in Yakut females is $74.4 [\text{FFM}] + 3,252$ ($r = 0.57$; $P < 0.001$). The scaling relationship in U.S. females is: $78.8 [\text{FFM}] + 1,944$ ($r = 0.73$; $P < 0.001$). Symbols: (---) predicted values; (—, ■) Yakut.

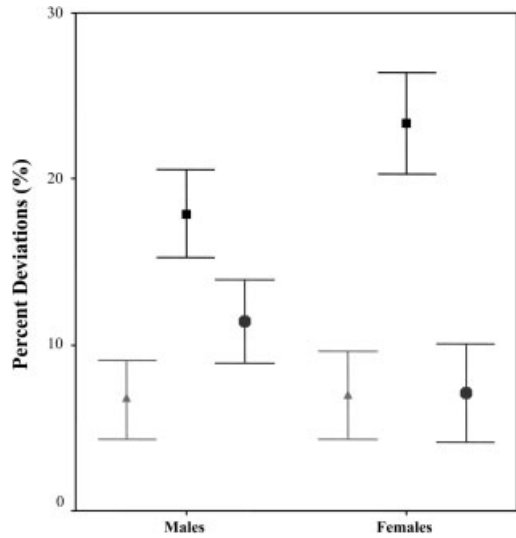


Fig. 5. Summary of percent deviations showing means and 95% confidence intervals for measured and predicted BMRs in Yakut males and females. Body mass (▲) predictions are derived from Schofield (1985) standards, fat-free mass (■) predictions are derived from Poehlman and Toth (1995), and surface area (●) predictions are derived from Consolazio and colleagues (1963).

females showed statistically significant elevations in BMR over predicted for SA (176.3 ± 2.2 vs. 158.1 ± 0.7 $\text{kJ}/\text{m}^2/\text{h}$ in males [$P < 0.001$] and 154.5 ± 2.2 vs. 144.3 ± 0.6 $\text{kJ}/\text{m}^2/\text{h}$ in females [$P < 0.001$]).

Overall, results indicated that, regardless of which reference standard was used, Yakut men and women had significant elevations in BMR (Fig. 5). Yakut male deviations from predicted BMR ranged from +7% to +18%, while females ranged from +7% to +23%.

Age and BMR

In a multiple regression model, males showed a significant decrease in BMR (dependent variable) for body mass ($P < 0.001$; $\beta = 0.828$) with age ($P < 0.01$; $\beta = -0.273$) ($r^2 = 0.605$). However, in a multiple regression model of BMR (dependent variable) on FFM, there was no significant decrease in BMR with age ($P = 0.279$). For females, in a multiple regression model of BMR (dependent variable) on body mass, there was no significant decrease in BMR with age ($P = 0.299$). Similar results were obtained from a multiple regression model of BMR (dependent variable) on FFM; in this model,

there was no significant decrease in BMR with age ($P = 0.695$).

Lifestyle variation and BMR

Participants were classified on a SOL scale that measured more traditional versus more modernized lifestyles. For males, multiple regression analysis of BMR (dependent variable) on body mass and SOL score showed that SOL score ($P = 0.858$) was not significant in explaining BMR variation. Similar results were obtained when FFM was substituted for body mass; SOL score ($P = 0.841$) was not significant in explaining BMR variation. For females, multiple regression analysis of BMR (dependent variable) on body mass and SOL score showed that SOL score ($P = 0.678$) was not significant in explaining BMR variation. Similar results were obtained when FFM was substituted for body mass; SOL score ($P = 0.821$) was not significant in explaining BMR variation.

Participants were classified on a scale that measured their involvement in subsistence activities, and included domesticated animal tending, hay cutting, foraging, hunting, fishing, and horticulture (i.e., growing fruits and

vegetables in "kitchen" gardens). Individuals with lower subsistence scores, following the orientation of the SOL scale, participated in more subsistence activities and engaged in these activities for more days per year. Conversely, individuals with higher scores participated in fewer subsistence activities and engaged in these activities for fewer days per year. For males, multiple regression analysis of BMR (dependent variable) on body mass and subsistence score showed that subsistence score ($P = 0.681$) was not significant in explaining BMR variation. Similar results were obtained when FFM was substituted for body mass; subsistence score ($P = 0.759$) was not significant in explaining BMR variation. For females, multiple regression analysis of BMR (dependent variable) on body mass and subsistence score showed that subsistence score ($P = 0.918$) was not significant in explaining BMR variation. Similar results were obtained when FFM was substituted for body mass; subsistence score ($P = 0.548$) was not significant in explaining BMR variation.

Factor analysis was used to explore the patterns of covariance between various socioeconomic and lifestyle variables; these factor scores were then used as predictors of BMR using multiple regression analysis. In a multiple (stepwise) regression model for males, body mass was the only significant predictor of BMR (dependent variable) variation ($P < 0.001$; $\beta = 0.722$; $r^2 = 0.522$); none of the five factors was a significant predictor in this model (Factor 1 [$P = 0.097$]; Factor 2 [$P = 0.229$]; Factor 3 [$P = 0.278$]; Factor 4 [$P = 0.885$]; Factor 5 [$P = 0.772$]). In a multiple (stepwise) regression model for males, FFM was the only significant predictor of BMR (dependent variable) variation ($P < 0.001$; $\beta = 0.742$; $r^2 = 0.551$); none of the five factors was a significant predictor (Factor 1 [$P = 0.124$]; Factor 2 [$P = 0.212$]; Factor 3 [$P = 0.189$]; Factor 4 [$P = 0.804$]; Factor 5 [$P = 0.689$]). In a multiple (stepwise) regression model for females, body mass was the only significant predictor of BMR (dependent variable) variation ($P < 0.001$; $\beta = 0.622$; $r^2 = 0.387$); none of the five factors was significant in the model (Factor 1 [$P = 0.846$]; Factor 2 [$P = 0.363$]; Factor 3 [$P = 0.817$]; Factor 4 [$P = 0.541$]; Factor 5 [$P = 0.166$]). In a multiple (stepwise) regression model for females, FFM was the only significant predictor of BMR (dependent variable) variation ($P < 0.001$; $\beta = 0.599$; $r^2 = 0.358$); none of the five factors was a significant predictor (Factor 1 [$P = 0.955$]; Factor 2

[$P = 0.299$]; Factor 3 [$P = 0.765$]; Factor 4 [$P = 0.558$]; Factor 5 [$P = 0.221$]).

DISCUSSION

Evidence of BMR elevation

The results of this study indicate that, regardless of which reference standard is used, Yakut men and women have significant elevations in BMR. Yakut male deviations from the predicted BMR range from +7% to +18%, while those from females range from +7% to +23%.

Early metabolic studies of circumpolar populations primarily used SA as the reference standard, but as previously noted, there are a number of problems with this approach. Over the past century there has been a general trend away from the use of SA in metabolic studies, both within human biology and comparative physiology; this represents a dramatic shift in perspective from one concerned primarily with heat loss to one that emphasizes heat production (Elia, 1992a). In order to compare data from the current study to that of earlier studies, we compared BMR measurements in the Yakut to standards for SA. This study documented significant elevations (+8.9%) based on SA norms; these elevations were somewhat higher in males (+11.5%) than females (+7.1%) but both were significantly elevated.

When compared to Schofield's (1985) norms for body mass, measured BMR was significantly elevated (+6.5%) and both males and females showed similar and statistically significant elevations in BMR over predicted for body mass. The Schofield (1985) norms, which were endorsed by the FAO/WHO/UNU (1985) and represent the current standard for assessing population-level energy needs, are widely regarded to overestimate BMR in many populations because of sampling issues (Hayter and Henry, 1993; Shetty et al., 1996). In all likelihood, when compared to other weight-specific BMR standards, the metabolic rate of the Yakut would be further elevated; however, this has not been evaluated.

Yakut BMR elevation is unlikely to reflect body composition differences between circumpolar populations and lower latitude groups, since we controlled for body composition through use of FFM. FFM standards for BMR, which ease comparisons between different populations with diverse body

shapes and sizes, have increased in use in recent years as empirical data support FFM as the best single predictor of BMR; FFM explains approximately 70–80% of BMR variation (Ravussin and Bogardus, 1989; Elia, 1992a; Nelson et al., 1992; Weinsier et al., 1992; Sparti et al., 1997). Measured BMR showed the greatest elevation (+20.8%) when FFM standards were used, and the elevations were substantial and significantly elevated in both males (+18.0%) and females (+23.2%). Although the data are not presented here, similar results were obtained when FFM was calculated using BIA; measured BMR for the entire sample was significantly higher (+16.4%) than predictions. Further, a subsample of individuals ($n = 28$), measured as part of a doubly labeled water study, had body fat assessed using the isotope dilution technique; isotope dilution gave the lowest estimates of FFM of all three techniques (Snodgrass, 2004). These results argue against the view that Yakut BMR elevation is erroneously high because FFM was underestimated. The discrepancy between BMR deviations calculated for FFM and body mass may result from increased amounts of body fat in some individuals; although this issue needs further study, increased levels of adipose tissue, with its low mass-specific tissue metabolic rate (Elia, 1992b), could have the effect of depressing mass-specific BMR.

The Yakut have similar metabolic rates as other indigenous circumpolar populations and the deviations from predicted BMR for different standards are strikingly similar to those found by Leonard and colleagues (2002b) in their meta-analysis. In that study, Leonard and colleagues (2002b) documented substantial elevations in BMR in males (+18.5%) and females (+17.1%) over predicted for FFM. Results were similar when assessed using body mass and SA.

In this study, BMR elevation in the Yakut is unlikely to be the consequence of heightened anxiety, as steps were taken to minimize acute anxiety. In addition, this study incorporated simultaneous heart rate monitoring, which allowed the tracking of heart rate changes; the current study follows other investigations that have incorporated this methodology (e.g., Rode and Shephard, 1995; Galloway et al., 2000). BMR was recorded only after heart rate stabilized, and heart rate changes were also monitored during the measurement period.

The mixed diet of the Yakut, which includes a substantial proportion of carbohydrates (Sorensen, 2003; Snodgrass, 2004), makes it unlikely that BMR elevation is the result of extreme levels of dietary protein. In a study of six rural Yakut villages, including Berdygestiakh, Sorensen (2003) found that Yakut adults obtained roughly 52% of their calories from carbohydrates, 34% from fats, and 14% from protein. Metabolic and nutritional studies of other indigenous Siberians (Buriat and Evenki [Leonard et al., 2002b]) and North Americans (Inuit [Hart et al., 1962; Rode and Shephard, 1995]) suggest that dietary factors are unlikely to play a significant role in the systematic elevation in BMR found in circumpolar populations. However, it should be noted that the traditional diet of Inuit groups, with extremely high levels of protein, might have further increased BMR in some of the earlier metabolic studies (e.g., Rodahl, 1952) and in certain segments of the population (i.e., older, more traditionally living individuals) in a recent study (Rode and Shephard, 1995). Finally, although not conclusive, a number of laboratory-based studies indicate that while protein influences metabolic rate following a meal and can lead to elevations of up to 30%, metabolic rate generally returns to normal levels within 12 h; therefore, dietary protein does not appear to elevate metabolic rate when measured in basal conditions (Soares et al., 1989; Guyton and Hall, 1996; Reed and Hill, 1996). The thermic effect of other macronutrients appears to be far smaller than protein, both in terms of the magnitude and duration of the effect. Metabolic rate generally increases by less than 5% for the first few hours after a meal containing large amounts of carbohydrates and fats and current evidence suggests that fats have a considerably smaller thermic effect than carbohydrates (Blaxter, 1989; Guyton and Hall, 1996; Rolfe and Brown, 1997; Schutz and Jequier, 1998). Overall, the thermic effect of food accounts for approximately 10% of total daily energy costs (Reed and Hill, 1996). Considering the low protein diet of the Yakut and the study design employed here (i.e., measurement of metabolic rate with participants having fasted for at least 12 h), dietary factors are unlikely to play a substantial role in explaining BMR elevation in the Yakut.

Age and BMR

A number of studies have documented an age-related decrease in BMR (see review in

Henry, 2000), although the extent of this decline may have been exaggerated previously through cross-sectional sampling issues, changes in body composition with age, and measurement of relatively inactive and unhealthy older individuals in industrialized countries (Keys et al., 1973; Murray et al., 1996; Henry, 2000). In fact, recent studies indicate that the BMR decline during adulthood—measured using FFM or lean body mass (LBM)—is more modest than previously described, and likely results from reductions in metabolically active tissues and slight changes in cellular metabolism (Fukagawa et al., 1990; Murray et al., 1996; Chumlea et al., 1998; Henry, 2000; Wilson and Morley, 2003). Although BMR generally shows a modest decline with age at the population level, not all individuals experience a reduction in BMR, and some show an increased BMR with age (Tzankoff and Norris, 1978; Henry, 2000). Data from Rode and Shephard (1995) on Iglolik Inuit document moderately *higher* BMRs in older adults of both sexes, and this remained when controlled for differences in body composition; the researchers attributed these metabolic differences to secular differences in lifestyle, with older individuals being exposed to greater cold stress through greater dependence on subsistence activities, as well as consuming a diet higher in protein and fats.

The current study, which did not include adults over 56 years old, found a significant decline in BMR with age among males. This decline was not evident in females. However, when FFM was used to control for the effects of body composition, no significant age-related declines in BMR were found in males or females, although a slight decline in BMR with age was evident. Therefore, it appears that changes in body composition (i.e., increased levels of fat) are the primary factor in explaining the apparent age decline in BMR. The data presented here do not show evidence of a recent secular change in BMR after controlling for body size, despite evidence for a recent secular increase in adult stature and FFM among the Yakut (Snodgrass, 2004).

Lifestyle variation and BMR

Previous metabolic research in northern populations has documented substantial intrapopulation variation in BMR, which has generally been attributed to differences in lifestyle (e.g., Rode and Shephard, 1995; Galloway et al., 2000). In addition to these

metabolic studies, a large literature in anthropology has examined the health consequences of cultural and economic changes (i.e., economic modernization) (e.g., Baker et al., 1986; Friedlaender, 1987; McGarvey et al., 1989; Huss-Ashmore et al., 1992; Shephard and Rode, 1996). These studies have generally found that lifestyle transition in subsistence populations is associated with an increased prevalence of obesity and hypertension and an elevated risk for various chronic conditions, such as cardiovascular disease and type 2 diabetes, as well as declines in measures of fitness and physiological work capacity.

The current study used extensive data on lifestyle variation, which included information on socioeconomic status, material style of life, and participation in subsistence activities and demonstrated no significant relationship between these variables and BMR. These findings suggest that lifestyle factors have a minimal role in explaining metabolic elevation in the Yakut. However, it is possible that other lifestyle factors not measured in this study may influence BMR variation in the Yakut. No direct measure of exposure to cold was included in this study, but future studies should quantify outdoor exposure during the cold season and should measure internal house temperature during winter. The latter is important since most rural Yakut houses are Russian notched-log style and rely on a single wood-burning stove for heat. Even though some wealthier households use a boiler to distribute heat throughout the house via steam and hot water, virtually all houses are exclusively heated with wood, which is cut from local forests and is heavily regulated and taxed. A small number of Berdygestiakh residents (<5%) inhabit small, centrally (wood) heated apartment buildings. Given the long duration (~8 months) of the Siberian winter, vast quantities of wood are required to heat a home and livestock pens. The current study (and virtually all metabolic studies of circumpolar populations) used metabolic data collected during one season (i.e., during the late summer), and future studies are needed to examine whether BMR measurements collected during the winter are more closely related to lifestyle variation. Despite these caveats, this study provides preliminary evidence that lifestyle factors have a minimal role in explaining metabolic elevation in circumpolar groups. However, BMR elevation

may result from similarities in cold exposure irrespective of lifestyle or may reflect developmental or genetic factors. The latter has been suggested by recent studies of mitochondrial DNA (mtDNA) (Mishmar et al., 2003; Ruiz-Pesini et al., 2004) yet awaits investigations of direct links between BMR and mtDNA variation. We hypothesize that genetic factors play an important role in metabolic elevation in the Yakut and other indigenous circumpolar groups but that short-term functional responses to acute cold stress will further elevate cold stress under certain conditions and will be structured by lifestyle variation.

Population-level energy requirements

International recommendations on energy intake for circumpolar populations remain identical to those for lower latitude populations and, despite the recent evidence for elevated BMRs, do not adjust for the additional energy costs of elevated BMR. This, however, reflects a change in stance over the past half-century. The FAO (1957) guidelines incorporated climate into calculation of energy needs by recommending a 3% addition for every 10°C decrease in annual temperature below the baseline of 10°C. More recent panels (e.g., FAO, 1973; FAO/WHO/UNU, 1985) reversed this position and no longer include a correction for temperature. The FAO/WHO/UNU (1985) guidelines predict energy needs of adults based on multiples of BMR; in these equations, BMR is estimated from body mass according to the sex- and age-specific Schofield equations, while activity level is estimated from occupational categories of physical activity level. The underestimation of basal energy needs in absence of a temperature correction, combined with underestimates of physical activity costs in subsistence-level populations stemming from problems with the use of time allocation methods (Haggarty et al., 1994; Leonard et al., 1997), imply that current nutritional guidelines for indigenous northern populations are inadequate. For these reasons, future international panels should consider evidence for including a temperature adjustment in future nutritional guidelines. This will require a systematic examination of data on BMR and temperature—preferably mean annual temperature or effective temperature—and should also include measurements using

FFM. Finally, these studies should examine data on seasonal variation in BMR.

Any future changes in nutritional guidelines must be carefully considered within the context of an increasing prevalence of obesity and its attendant comorbidities among indigenous Siberians and other circumpolar groups. In the current study, 16% of females and 8% of males were obese, while an additional 15% of females and 14% of males were overweight. A larger study, which included data on 900 adults (537 females and 363 males) from four Siberian ethnic groups (Buriat, Evenki, Ket, and Yakut), found generally comparable results; approximately 12% of females and 7% of males were obese, while approximately 24% of females and 18% of males were overweight (Snodgrass, 2004). Recent increases in the rates of overweight and obesity have been documented among indigenous circumpolar populations from North America (Shephard and Rode, 1996) and in many other populations around the world (WHO, 2000). In addition, data from the nationally representative Russian Longitudinal Monitoring Survey documented a recent rise in the prevalence of adult obesity (Zohoori et al., 2003). Despite this evidence for increasing overnutrition, Russia suffers from a double burden of disease, as undernutrition remains an acute problem, especially among children and young adults (Doak et al., 2000; Zohoori et al., 2003). Although very few data exist on undernutrition in indigenous Siberians, studies conducted in the early 1990s on Evenki children documented sharp reductions in growth and nutritional status associated with increased economic marginalization in the early post-Soviet period (Leonard et al., 2002c). Without accurate nutritional guidelines for indigenous circumpolar populations, attempts to assess energy balance will be problematic and, in all likelihood, will minimize evidence of nutritional stress.

CONCLUSIONS

In summary, BMR among the Yakut was found to be similar to other indigenous high-latitude populations, and for males and females was significantly higher than predicted for body mass, FFM, and SA (with deviations from +7% to +23%). This elevation in BMR is unlikely to be the consequence of body composition differences

between circumpolar and lower-latitude populations. In fact, when body composition was controlled through measurement of FFM, measured BMR was significantly elevated (+20.8%) and was the highest of all the BMR standards. Likewise, the Yakut diet, which includes a sizeable portion of carbohydrates, is an unlikely culprit for explaining elevated BMR. This study did not find significant age-related changes in BMR once measurements were controlled for body composition. This study did not find any significant relationships between lifestyle measures and BMR, suggesting that genetic factors play an important role in BMR elevation. This study provides additional evidence of a metabolic elevation in indigenous circumpolar populations and adds to data from recent studies of other Siberian populations, as well as North American groups. This study has important implications for understanding the biological adaptations that allowed modern human populations to successfully colonize the high-latitude environment. Finally, this study has implications for public health recommendations, as current population-level energy requirements are likely to systematically underestimate the energy demands of indigenous Siberians.

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