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Original Research Article

Adaptive Dimensions of Health Research Among Indigenous Siberians

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ABSTRACT Present evidence suggests that modern humans were the first hominid species to successfully colonize high-latitude environments ($\geq$55°N). Given evidence for a recent (<200,000 years) lower latitude naissance of modern humans, the global dispersal and successful settlement of arctic and subarctic regions represent an unprecedented adaptive shift. This adaptive shift, which included cultural, behavioral, and biological dimensions, allowed human populations to cope with the myriad environmental stressors encountered in circumpolar regions. Although unique morphological and physiological adaptations among contemporary northern residents have been recognized for decades, human biologists are only now beginning to consider whether biological adaptations to regional environmental conditions influence health changes associated with economic modernization and lifestyle change. Recent studies have documented basal metabolic rates (BMRs) among indigenous Siberian populations that are systematically elevated compared to lower latitude groups; this metabolic elevation apparently is a physiological adaptation to cold stress experienced in the circumpolar environment. Important health implications of metabolic adaptation are suggested by research with the Yakut (Sakha), Evenki, and Buriat of Siberia. BMR is significantly positively correlated with blood pressure, independently of body size, body composition, and various potentially confounding variables (e.g., age and smoking). Further, this research has documented a significant negative association between BMR and LDL cholesterol, which remains after controlling for potential confounders; this suggests that high metabolic turnover among indigenous Siberians has a protective effect with regard to plasma lipid levels. These results underscore the importance of incorporating an evolutionary approach into health research among northern populations. Am. J. Hum. Biol. 19:165–180, 2007.

Based on present evidence, modern humans (*Homo sapiens sapiens*) were the first hominid species to permanently settle high-latitude environments (i.e., $\geq$55°N); all earlier species, including *Homo erectus*, archaic *Homo sapiens*, and Neandertals, were restricted to lower latitudes (Goebel, 1999; Klein, 1999; Pavlov et al., 2001). Given genetic, archaeological, and paleontological evidence for a lower latitude origin of modern humans within the last 200,000 years (Ingman et al., 2000; Klein, 1999; White et al., 2003), the global dispersal and successful settlement of arctic and subarctic regions represents an unprecedented adaptive shift. This adaptive shift, which included cultural, behavioral, and biological dimensions, allowed human populations to cope with the myriad climatic and ecological stressors encountered in circumpolar environments. While unique morphological and physiological adaptations among contemporary northern residents have been recognized for decades (Itoh, 1980; Roberts, 1953, 1978; Steegmann, 1975) researchers

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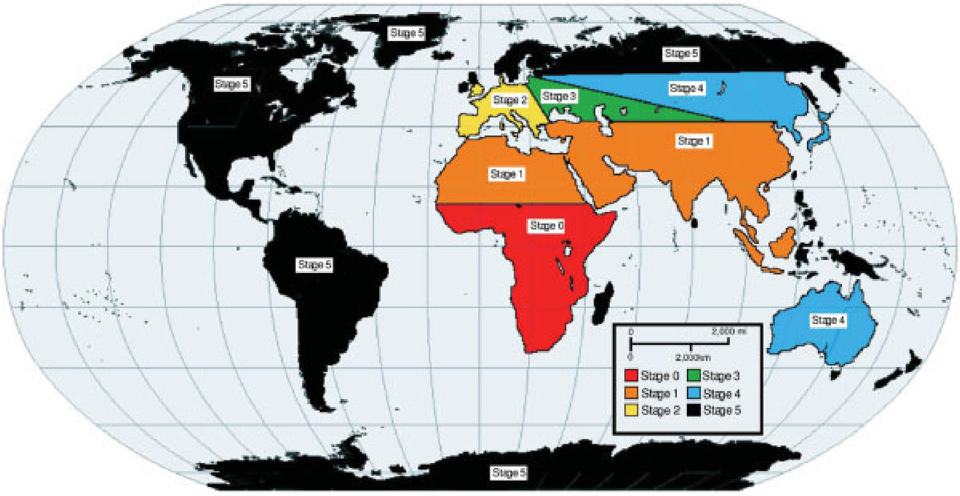

Fig. 1. World map with settlement pattern of middle and northern latitudes. See text for details. Reproduced with permission from Hoffecker (2005).[Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

have given much less attention to the question of whether biological adaptations to specific environmental conditions influence health changes associated with economic modernization and lifestyle change (but see Ruiz-Pesini et al., 2004; Shephard and Rode, 1996; Snodgrass, 2004; Wallace, 2005).

Research over the past three decades has revealed that health effects relating to lifestyle change are not uniform across populations (Harrison et al., 1988). Such differences are likely the consequence of the interaction between underlying physiological and genetic differences and unique economic, political, and social histories. However, very few studies have attempted to explore the interaction of these domains for understanding the origins of regional differences in health changes that occur with economic development. In this paper, we describe the role of biological adaptations to the cold and marginal high-latitude environment in shaping the health transition that northern populations experience with economic development. Specifically, we concentrate on how metabolic adaptation (i.e., elevated basal metabolic rate [BMR]) influences cardiovascular risk factors (e.g., blood pressure and serum lipid levels) observed among indigenous Siberians in the post-Soviet period. These results underscore the importance of incorporating an evolutionary approach into health research among northern populations.

THE SETTLEMENT OF NORTHERN ENVIRONMENTS

Early hominid evolution was confined to tropical and subtropical Africa, but beginning in the early Pleistocene, hominids began to disperse into temperate latitudes (Antón and Swisher, 2004; Gabunia et al., 2000, 2001). The hominid settlement of northern environments occurred in a series of relatively rapid dispersals; this progressive northward advance has been arranged into a five-stage model of high-latitude settlement by Hoffecker (2005) (Fig. 1). The initial early Pleistocene (1.7–1.8 Ma) dispersal out of Africa by *Homo erectus* led to the settlement of middle latitude Asia (Stage 1); the northern boundary of this advance is represented by sites, such as Dmanisi, Georgia and Majuangou, China (Antón and Swisher, 2004; Gabunia and Vekua, 1995; Gabunia et al., 2000, 2001; Zhu et al., 2004). Despite the dramatic geographic range expansion of this species, present evidence suggests that *H. erectus* was unable to permanently settle latitudes above 40°N even during warmer, interglacial periods (Antón, 2002, 2003; Klein, 1999).

The subsequent northward expansion, documented by fossils from Mauer, Germany (49°N) and Boxgrove, England (51°N), represents the first hominid settlement of Europe (Stage 2) (Hoffecker, 2005; Klein, 1999). This range expansion, associated with *Homo heidelbergensis*, occurred principally during the warm interglacial periods beginning ~500,000 years ago.

These hominids were able to settle in a range of environmental settings (e.g., temperate woodlands and cold steppe biomes), including outlying areas of central Europe, as represented by the 500,000-year-old site of Korolevo from the Carpathian Mountains of Ukraine (at about 48°N) (Hoffecker, 1999; Roebroeks, 2006). The climatically favorable Mediterranean region of southern Europe was apparently inhabited considerably earlier in time, as represented by ~800,000-year-old fossils from the TD6 component of Atapuerca, Spain and the Ceprano (Italy) calvaria (Bermúdez de Castro et al., 1997; Falguères et al., 1999; Manzi et al., 2001). Recent flint artifacts recovered from the English site of Pakefield (52°N) reveal a hominid presence in northern Europe at ~700,000 years ago; however, paleoclimatic and ecological data indicate that the occupation occurred during a warm interglacial period when the region was characterized by a Mediterranean climate (Parfitt et al., 2005). Thus, the initial settlement of northern parts of Europe apparently reflects an opportunistic expansion of hominid populations into higher latitudes during climatically favorable circumstances (Hoffecker, 2005; Roebroeks, 2006).

Neandertals (*Homo neanderthalensis*) further extended the geographic range of hominids, successfully settling previously uninhabited regions of eastern Europe and southwestern Siberia during the last 130,000 years (Stage 3). While Neandertals minimally extended the northernmost boundary of colonization, this stage is noteworthy for two reasons. First, Neandertals inhabited Europe principally during glacial times when temperatures were considerably colder than during earlier occupation. Second, Neandertals were able to settle unoccupied locales to the east (i.e., eastern Europe and southwestern Siberia), where the moderating effects of the Atlantic gave way to colder and drier climates (Goebel, 1999; Hoffecker, 2002, 2005). Neandertals do not appear to have been able to successfully settle subarctic or Arctic Siberia, as all Neandertal sites from southwestern Siberia are located at or below 55°N (Goebel, 1999). However, during much of their occupation of Europe and southwestern Siberia, temperatures were generally colder than today (Hoffecker, 2005). Based on current evidence, Neandertals were unable to inhabit the colder, drier high-latitude arctic or subarctic zones where winter temperatures fell substantially below freezing (Hoffecker, 2005; Hoffecker and Elias, 2003).

The final two stages of hominid settlement of the North occurred with modern humans. The initial dispersal of modern humans from Africa and southwestern Asia between ~46,000 and 24,000 years ago saw the settlement of subarctic Eurasia, including previously uninhabited areas of southern Siberia and eastern Asia (Stage 4) (Goebel, 1999; Hoffecker, 2005; Mellars, 2006; Vasil'ev et al., 2002). Sites from this expansion include the northern Russian sites of Sungir (56°N) and Kostenki (52°N), as well as Kara-Bom, from the Altai region of southern Siberia (50°N) (Hoffecker, 2005). Present evidence, however, does suggest a limitation on the northern range expansion of early Upper Palaeolithic populations with the northern boundary represented by Russian sites near the Arctic Circle, such as Mamontovaya Kurya (66°N) (Pavlov et al., 2001). Some recent discoveries from northern Siberia (e.g., Yana RHS site at 71°N), however, suggest that Upper Palaeolithic humans might have occupied northern regions during warmer times during the Middle Pleniglacial (Hoffecker, 2005; Pitulko et al., 2004). Subsequently, modern human geographic range in northern regions contracted during the harsh climate at the peak of the Last Glacial Maximum (24,000–20,000 years ago), leading to the abandonment of vast areas of northern Europe, the eastern European plain, and Siberia (Hoffecker, 2005).

The second wave of modern human high-latitude settlement occurred during only the last 20,000 years as populations reoccupied previously abandoned regions and expanded into circumpolar Europe and Asia and later into North America and Greenland (Stage 5) (Hoffecker, 2005). This expansion took place within the context of a period of climatic amelioration that began ~20,000 years ago. Most Eurasian Arctic sites, such as those in Scandinavia, were not permanently occupied until the Holocene, and much of the North American Arctic was not inhabited until only the last 7000 years. The Holocene has seen both the emergence of environmental heterogeneity (e.g., tundra and boreal forest) and extensive population movement in northern regions; some contemporary populations, in fact, are only recent settlers in the Arctic (Hoffecker, 2005). For instance, the full development of arctic maritime economies occurred only within the past few thousand years, and the major phase of Inuit expansion occurred within only the last 1000 years, in part as a result of the Medieval Warm Period climatic amelioration.

HUMAN ADAPTATION TO NORTHERN ENVIRONMENTS

Circumpolar (i.e., subarctic [55–66.5°N] and Arctic [≥66.5°N]) populations, as a result of their residence at high latitudes, are exposed to a unique suite of ecological stressors including chronic and severe cold stress, marked seasonality, variation in photoperiod, sparse vegetation, and low overall energy availability (Cox and Moore, 1993; Krebs, 1972). Northern populations are subjected to prolonged intense cold stress in arctic and subarctic areas, where mean monthly temperatures can drop to below −40°C in places and isolated temperatures to below −60°C (Folk et al., 1998; Romanovsky, 2003). Colonization and long-term residence in this environment imply successful adaptation through biological, behavioral, and cultural means.

In addition to the plethora of cultural and behavioral adaptations (e.g., clothing, shelter, timing of outdoor activity, seasonal migration, etc.), humans are able to survive in cold regions as a result of two types of biological adaptation: those that promote heat conservation and those that increase heat production (Frisancho, 1993). Human populations native to cold regions, for example, have large absolute body mass and relatively short legs, which both serve to minimize surface area and reduce heat loss in cold environments (Hanna et al., 1989; Katzmarzyk and Leonard, 1998; Newman, 1953; Roberts, 1953, 1978; Ruff, 1994). It is presently unclear the extent to which measures of body size and proportions are controlled by genetic mechanisms as a result of adaptation by natural selection or proximate factors experienced during ontogeny, such as nutrition or disease environment (Bogin et al., 2001; Norgan, 1998; Stinson and Frisancho, 1978; Stinson, 2000). These ecogeographical patterns among humans are, in part, a reflection of differences in lifestyle and, in particular, of economic development between tropical and temperate populations; this explanation, however, cannot account for the entirety of these patterns. Body proportions appear to be fairly conserved and, although some secular changes have occurred (i.e., relative increases in the length of the limbs), body proportions appear to be strongly shaped by genetic factors (Eveleth, 1966; Katzmarzyk and Leonard, 1998; Shapiro, 1939; Trotter and Gleser, 1958). Additional evidence for this comes from growth studies demonstrating that interpopulation variation in body proportions first appears prenatally (Eveleth and Tanner, 1991; Schultz, 1923, 1926; Y'Edynak, 1978). In contrast, body mass is strongly shaped by proximate environmental influences, such as dietary factors and physical activity, that can occur during ontogeny or adulthood and lead to shifts in body composition; however, the role of genetic factors in structuring body mass is not negligible. Human populations in northern regions are also relatively muscular and exhibit a regional tissue (muscle and fat) distribution that maximizes insulation and is consistent with cold adaptation (Beall and Steegmann, 2000; Hanna et al., 1989).

Various short-term physiological responses enhance the ability of northern populations to conserve heat and maintain functionality at cold temperatures (Beall and Steegmann, 2000; Frisancho, 1993; Hanna et al., 1989; Young, 1988). The main heat conserving response in humans is peripheral vasoconstriction, in which lowered skin temperature causes subcutaneous vessels to constrict, which shunts blood away from superficial tissues (e.g., skin, fat, and muscle) and towards deep vessels and internal organs where it is more easily retained (Burton and Edholm, 1955; Frisancho, 1993; Stroud, 1993). Additionally, this further reduces skin temperature, which lowers the temperature gradient between the skin and the environment (maximizing insulative value of the skin and subcutaneous fat), and slows the rate of heat loss from the body. However, peripheral vasoconstriction affects cardiovascular function by increasing hematocrit, elevating metabolic rate, and increasing blood pressure; thus, susceptibility to acute coronary events is increased by peripheral vasoconstriction (Beall and Steegmann, 2000; Burton and Edholm, 1955; Guyton and Hall, 1996; Houdas et al., 1992; Pääkkönen and Leppäluoto, 2002; Vogelaere et al., 1992). Peripheral vasoconstriction also impairs the functioning of the hands and feet, which, during severe stress, can lead to frostbite. Northern populations are apparently less prone to cold-induced blood pressure increase and cardiovascular mortality than lower latitude populations (Donaldson et al., 1998a,b; LeBlanc, 1975).

If cold stress continues, the vasoconstrictive response is followed by vasodilation (i.e., cold-induced vasodilation [CIVD]), which returns blood to peripheral tissues (Folk et al., 1998; Stroud, 1993). Alternating peripheral vasoconstriction and vasodilation in the extremities maximizes heat conservation yet protects from cold injury and maintains function in cold temperatures. Present evidence suggests that the timing and intensity of CIVD differs between populations; this has been attributed to a combination of acclimatization and genetic factors (Beall and Steegmann, 2000; Stroud, 1993). For example, northern populations (e.g., Inuit) appear to sustain the highest extremity temperatures upon acute localized cold stress (Frisancho, 1993; Steegmann, 1975).

Increased heat production can be accomplished through short-term metabolic elevation (e.g., voluntary physical activity, shivering thermogenesis, and short-term increases in nonshivering thermogenesis [NST]) or long-term metabolic upregulation (Frisancho, 1993; Hanna et al., 1989; Roberts, 1978; Stroud, 1993; Young, 1988). Although increased voluntary physical activity and shivering can substantially increase metabolic rate, both also increase heat loss due to increased air flow over the body and require increased energy intake to sustain; additionally, the involuntary nature of shivering limits the ability to perform many normal tasks (Hanna et al., 1989; Shephard, 1991). Adult humans also have the ability to increase metabolic rate to a limited extent ($\sim$10–15%) through NST. This can be accomplished through sympathetic nervous system or catecholamine-mediated increases in cellular metabolism and increased uncoupling of oxidative phosyphorylation (OXPHOS), which uses futile metabolic cycles to increase heat liberation at the expense of energy for work (Guyton and Hall, 1996). NST does contribute to a more sizable increase (up to 100%) in metabolic rate in human infants (as well as a number of small mammals) because of the presence of deposits of brown adipose tissue (BAT), a highly thermogenically active tissue rich in mitochondria (Guyton and Hall, 1996; Himms-Hagen and Ricquier, 1998). Although the limited evidence presently available from humans points to the loss of functional BAT by adulthood among individuals in industrialized settings (Astrup et al., 1985), a few studies of humans (e.g., outdoor workers in Finland) and nonhuman primates (e.g., *Macaca mulatta*) exposed to chronic cold stress suggest that functional BAT may be present in some adults (Chaffee et al., 1975; Huttunen et al., 1981). The large body size of human adults, however, precludes effective cold climate thermogenesis via BAT (Wallace, 2005).

One aspect of northern physiology that has attracted considerable attention is the long-term upregulation of basal metabolic rates (BMRs) of high-latitude populations. Indigenous northern residents of North America, including the Inuit of Alaska and Canada, have BMRs that are significantly higher than those found among lower latitude reference populations (Adams and Covino, 1958; Crile and Quiring, 1939; Heinbecker, 1928). Metabolic elevation, which is likely mediated at least in part by thyroid hormones (particularly triiodothyronine [T_3] and thyroxine [T_4]), appears to represent a physiological adaptation to chronic and severe cold stress experienced in the circumpolar environment (Leonard et al., 1999, 2005a; Roberts, 1978). This relationship with climate is supported by distributional studies that demonstrate a strong negative correlation between BMR and mean annual temperature, which remains when controlled for differences in body size (Roberts, 1952, 1978). However, a causal relationship remains to be established, and the mechanism or mechanisms responsible for metabolic elevation has yet to be fully elucidated. Although the results of early metabolic studies were criticized for their small sample sizes and for failing to control for the potentially confounding effects of anxiety, diet, and body composition, more recent studies with controlled measurement conditions (Rode and Shephard, 1995a) have confirmed earlier findings.

Findings from studies of native Siberians are consistent with the hypothesis that indigenous northern populations show distinctive metabolic adaptations to their cold and marginal environment. Our research among three indigenous Siberian populations (the Evenki of central Siberia, the Buriat of southern Siberia, and the Yakut of eastern Siberia) parallels findings from North American groups and demonstrates systematically elevated BMRs relative to body mass, fat-free mass, and surface area norms (Galloway et al., 2000; Leonard et al., 2002a, 2005a; Snodgrass et al., 2005a; Sorensen et al., 1999). Among the pooled Siberian sample, BMR measurements among males were 16% above and females 19% above predicted values using fat-free mass standards (Leonard et al., 2005a) (Fig. 2). BMR was also significantly elevated among males (+6%) and females (+4%) according to Schofield (1985) norms. Despite endorsement of the Schofield norms by the FAO/WHO/UNU (1985), these standards are widely regarded as overestimating BMR; thus, when compared to other mass-specific BMR standards, the metabolism of indigenous Siberians would likely be further elevated (Hayter and Henry, 1993; Shetty, 1996). Further, Evenki BMRs are substantially higher than non-indigenous individuals (i.e., Russians) living in the same communities (Galloway et al., 2000; Leonard et al., 2002a). The results of these

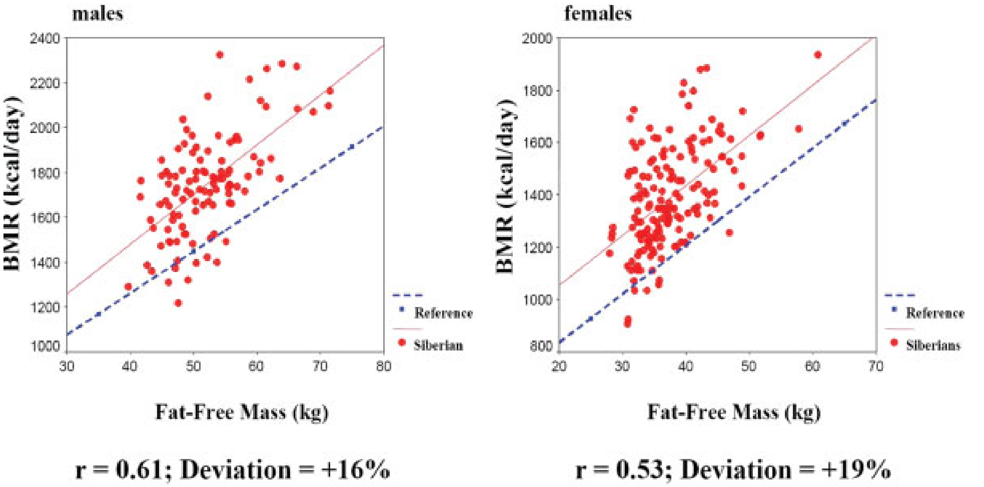

Fig. 2. Relationship between basal metabolic rate (BMR; kcal/day) and fat-free mass (kg) in indigenous Siberian (a) men and (b) women compared to estimated values from reference norms (Poehlman and Toth, 1995). BMRs of Siberian men average 1746 kcal/day (7,400 kJ/day), 16% higher than predicted values. Siberian women average 1,388 kcal/day (5,800 kJ/day), 19% higher than predicted values. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

studies indicate that, regardless of which reference standard is used, indigenous Siberians have systematically elevated BMRs compared to lower latitude populations.

BMR elevation in native Siberians is unlikely to be a consequence of body composition differences between northern and lower-latitude populations, as the use of fat-free mass standards adjusts for variation in body composition. Further, elevated BMR among indigenous Siberians does not reflect a diet high in protein, as each of the study populations consume a mixed diet with a similar daily protein concentration as United States adults (Leonard et al., 2005a; Snodgrass et al., 2005a). Instead, BMR elevation likely reflects an adaptation to severe climatic stress experienced in the circumpolar environment. Present evidence suggests that thyroid hormones play an important role in structuring metabolic adaptation among indigenous Siberians, and likely control short-term upregulation of metabolic rate during winter months (Leonard et al., 1999, 2005a). Genetic factors are likely involved in metabolic elevation, given that BMR is elevated during warm months in the summer and early fall. Though no multiseason studies have been conducted among indigenous Siberians, certain European and Japanese populations have metabolic rates that are higher during the winter months (Kashiwazaki, 1990; Osiba, 1957; Plasqui et al., 2003; but see Haggarty et al., 1994). We hypothesize that genetic factors play an important role in shaping metabolic adaptation among indigenous Siberians, but that short-term functional responses to acute cold stress during winter months further elevate metabolic rates.

Elevated metabolic rates likely help maintain homeostasis in cold temperatures and contribute to survival in northern environments. However, this metabolic adaptation is not without its consequences. Within the context of the relatively low energy circumpolar environment, the elevated caloric demands necessitated by heightened maintenance costs place increased dietary stress on northern populations. Because environmental energy is not unlimited, relatively high BMRs mean that less energy is available for other somatic functions, such as growth and reproduction. As a consequence, energy trade-offs shape life history variables (e.g., fecundity, age at maturity, lifespan, growth rate, and body size) (Charnov, 1993; Hill and Hurtado, 1996; Hill, 1993; Stearns, 1992). At present, the influence of environmental factors on life history patterns in northern populations remains largely unexplored, although the delayed menarche and slow somatic growth schedule documented among northern populations are thought to be shaped by relatively high maintenance costs (Leonard et al., 1994; Roberts, 1978). Finally, various lines of evidence suggest that there are important health implications of

BMR elevation. For example, upregulated cellular metabolism among mammals increases production of reactive oxygen species (i.e., free radicals), which cause DNA and cellular damage and can shorten lifespan (Adelman et al., 1988; Speakman et al., 2002). However, if OXPHOS is uncoupled to a greater extent among northern human groups (generating greater amounts of heat at the expense of chemical energy for work), as proposed by Wallace and colleagues (Mishmar et al., 2003; Ruiz-Pesini et al., 2004; Wallace, 2005), elevated metabolic rates could actually lead to decreased production of reactive oxygen species and increased longevity. Future research is needed to resolve this important question.

Most reconstructions of the human high-latitude settlement have generally emphasized the role of technological developments (e.g., sophisticated fur clothing and thermally efficient shelters) and dietary strategies (e.g., consumption of large quantities of protein and fat) for coping with climatic and ecological stressors, while minimizing the importance of biological adaptations (although the opposite is true for most studies of Neandertals). In part, this relates to the dramatic expansion of material culture first seen among modern humans, and clear evidence of technology associated with protection from environmental stressors (Klein, 1999). In addition, evidence that the earliest modern humans in Europe had postcranial morphology similar to tropical-living groups (i.e., a more linear build with relatively long limbs and a relatively low body mass) (Holliday, 1999), combined with the lower latitude naissance of these populations, has led some to dismiss the importance of biological adaptation.

This perspective neglects the wealth of evidence of biological adaptations among past and present northern populations, many of which appear to have substantial genetic components. Further, it oversimplifies a complicated history of northern expansion, in which early modern humans moved into subarctic Eurasia during a period of climatic amelioration, yet were unable to permanently settle much of arctic and subarctic Eurasia until considerably later in time (Hoffecker, 2005; Hoffecker and Elias, 2003; Mellars, 1998). In fact, the deteriorating climate of the Upper Pleniglacial ($\sim$30,000–20,000 years ago) appears to have forced a range contraction among modern human populations that left them confined to more southern regions. Following this period, human populations expanded northward and fossil evidence documents a shift in body size and proportions in later European populations to a morphological plan consistent with contemporary cold-living human populations in Europe, Asia, and North America (i.e., a more compact build with relatively long trunks and short limbs, and a relatively high body mass) (Hoffecker and Elias, 2003; Hoffecker, 2005; Holliday, 1997, 1999; Pearson, 2000). While humans in high-latitude regions, both past and present, are highly dependent on cultural and behavioral mechanisms to cope with environmental stressors, these act in concert with biological adaptations in an additive fashion. In fact, it may have been the evolution of morphological and physiological adaptations to cold stress, operating in tandem with cultural and behavioral adaptations, that enabled later modern human populations to successfully expand their range into the previously uninhabited high-latitude regions of Europe, Asia, and North America (Hoffecker and Elias, 2003; Hoffecker, 2005). The systematically elevated BMRs documented among the northern populations, within the context of low energy northern ecosystems, strongly suggest that this aspect of northern physiology was an important component of the adaptive shift that allowed modern humans to successfully colonize the circumpolar environment.

RECENT LIFESTYLE CHANGE AMONG INDIGENOUS SIBERIANS

Lifestyle changes that occur with economic development have been linked to a variety of negative health outcomes, including an increased prevalence of obesity, type 2 diabetes, hypertension, an elevated risk for various chronic degenerative conditions (e.g., cardiovascular disease), and declines in fitness and physiological work capacity (Baker et al., 1986; Friedlaender et al., 1987; Huss-Ashmore et al., 1992; Shephard and Rode, 1996; Trowell and Burkitt, 1981). The mechanisms responsible for this health transition remain incompletely understood, although dietary changes, alcohol consumption, tobacco use, chronic psychosocial stress, and physical inactivity have all been implicated (Durnin, 1990; Popkin et al., 1995; Shephard and Rode, 1996; WHO/FAO, 2003; Yach et al., 2004).

The transition from traditional subsistence-oriented economies among circumpolar groups in North America has been accompanied by extensive changes in health, including dramatic increases in cardiovascular risk and the prevalence of obesity, as well as declines in aerobic fitness and muscular strength (Kuhnlein et al., 2004; Rode and Shephard, 1995b; Shephard and Rode, 1996; Young et al., 1993). This health transition, which has been extensively studied in the Igloolik (Northwest Territories, Canada) Inuit, appears to be largely the result of the transition away from a traditional hunting-based subsistence economy during the process of economic development (Godin and Shephard, 1973; Shephard and Rode, 1996). Total energy expenditure declined in most individuals as a result of this decreased participation in subsistence activities. In addition, the Igloolik Inuit and other North American circumpolar groups experienced massive dietary changes during this period, including an overall increase in energy intake, heightened stability of the food supply, increased consumption of refined carbohydrates and saturated fats, and a decline in the intake of polyunsaturated ω-3 fatty acids (Kuhnlein and Receveur, 1996; Kuhnlein et al., 2004).

Our understanding of the effects of economic modernization on indigenous Siberians is complicated by recent political, economic, and social changes that followed the collapse of the Soviet Union, as well as by the political conditions of the Soviet period that isolated these populations. The application of a centrally planned socialist system during the Soviet period—part of the plan to modernize and industrialize Siberia—profoundly affected native Siberian lifeways. These social and economic transformations included forced relocation and settlement into large, permanent villages, the forced abandonment of traditional cultural practices (e.g., shamanism), and a shift to a wage and welfare economy (Forsyth, 1992; Jordan and Jordan-Bychkov, 2001; Mote, 1998; Slezkine, 1994). At the end of the Soviet period, however, many of the promises of modernization were left unfulfilled (Pika, 1999; Slezkine, 1994).

The collapse of the Soviet Union in 1991 triggered massive economic and political changes that dramatically altered the lives of rural Siberians who were dependent on the government for wages and deliveries of food and essential goods. Many native Siberians returned to traditional subsistence practices (e.g., herding, fishing, hunting, and foraging) to meet needs no longer met by the government, although many of these activities had been transformed during the Russian and Soviet periods (Crate, 2001; Fondahl, 1997; Jordan and Jordan-Bychkov, 2001; Leonard et al., 2002b; Snodgrass, 2004; Vinokurova, 1995). Within the last few years, economic development has again accelerated in many parts of Siberia, although in dramatically different form than during Soviet times. Many native Siberians, especially those in large communities or near urban centers, are now involved in wage earning employment and are tied to regional, national, and global markets, (e.g., diamond and petroleum industries) (Crate, 2001; Jordan and Jordan-Bychkov, 2001; Snodgrass, 2004; Sorensen, 2003). As a result, marked lifestyle heterogeneity and economic inequality have emerged in many rural Siberian communities, with some individuals involved in wage-earning employment and others almost completely dependent on subsistence activities.

Since the breakup of the Soviet Union, there has been a marked decline in Russian health (Notzon et al., 2003); however, the effects of the Russian market reforms on the health of native Siberians remain largely unknown. Further, relatively few studies have examined health among indigenous Siberians during the post-Soviet period, and nationally representative health studies typically have not disaggregated data by ethnicity and location. Over the past decade and a half, we have conducted a series of studies among several native Siberian groups (Evenki, Ket, Buriat, and Yakut) in collaboration with Russian, Canadian, and American researchers (Leonard et al., 1994, 2002a,b,c; Snodgrass, 2004; Snodgrass et al., 2006a; Sorensen, 2003; Sorensen et al., 2005) that have investigated the health effects of economic development. This research has been largely focused on cardiovascular risk and, in particular, body composition, blood pressure, and serum lipids.

Obesity has recently emerged as an important health issue among native Siberian adults and particularly for women, whose obesity rates are nearly double those of men (12% vs. 7%) (Snodgrass et al., 2006a). This sex difference in obesity prevalence is also evident in studies of the Siberian Nganasan (Rode and Shephard, 1995b) and may reflect the differential participation by men and women in subsistence activities. This reflects the continuation of Soviet-era labor restructuring policies, which made men primarily responsible for herding, haycutting, and other intense manual labor tasks, into the post-Soviet period (Jordan and Jordan-Bychkov, 2001; Seroshevski, 1993; Tokarev and Gurvich, 1964). Our studies of the Evenki, Ket, and Yakut have documented lower levels of energy expenditure and physical activity among women, which appears to be related to their participation in fewer subsistence tasks (e.g., herding and hay cutting) (Katzmarzyk et al., 1994; Leonard et al., 2002b; Snodgrass et al., 2006b). Despite the emergence of obesity as an important health concern among native Siberian groups, prevalence rates are still lower than those documented in most North American circumpolar groups (e.g., Canadian Inuit and Alaska Natives) and much of the developed world (Snodgrass et al., 2006a).

Indigenous Siberians have relatively low levels of serum cholesterol and other blood lipids (e.g., triglycerides), even though levels of overweight and obesity are increasing (Leonard et al., 1994, 2005a; Rode and Shephard, 1995b; Sorensen et al., 2000, 2005). Total cholesterol and LDL cholesterol levels among all Siberian populations are low compared to median values from the United States, with extremely low serum lipid levels in groups that follow more traditional life ways (e.g., Evenki reindeer herders) (Leonard et al., in press). Our research suggests that lifestyle changes, such as reduced physical activity levels and a dietary shift to foods higher in saturated fat and refined sugars, have contributed to recent increases in serum lipid levels among many Siberian groups. These findings are similar to studies of North American circumpolar populations that document low serum lipid concentrations in relatively unacculturated groups, but higher concentrations among more economically developed groups. However, our studies have also revealed important differences both within and between Siberian populations. For example, we documented higher lipid levels and greater cardiovascular risk among Yakut residents of small, rural communities, even though individuals consumed few market foods and were heavily involved in the subsistence economy (Sorensen et al., 2005).

Blood pressure among native Siberian men and women is consistently higher than that documented in most traditionally living indigenous groups and isolated populations in developing nations, as well as higher than reference values from the United States (Kozlov et al., 2003; Leonard et al., 2005b, in press; Snodgrass, 2004; Sorensen, 2003). There is some variation among native Siberian populations, however, as studies have documented lower blood pressure among a few Siberian coastal groups (Nikitin et al., 1981; Shephard and Rode, 1996). Our research among the Yakut, Evenki, and Buriat documents that hypertension (systolic blood pressure $\geq$140 mm Hg and diastolic blood pressure $\geq$90 mm Hg) occurs at a similar frequency as that seen in many developed nations, including Canada and the United States, but below the levels found in much of Europe (Leonard et al., 2005b; Snodgrass, 2004; Sorensen, 2003). Overall, 57% of Siberian men and 47% of women have suboptimal blood pressure according to NIH (2003) guidelines (i.e., systolic blood pressure $\geq$120 mm Hg and/or diastolic blood pressure $\geq$80 mm Hg) (Leonard et al., in press). In general, these levels are considerably higher than many other northern groups, including the North American and Greenland Inuit.

These studies of indigenous Siberians documented certain similarities with other populations in regards to the effects of economic development on chronic disease patterns. For example, like other populations, prevalence rates of overweight and obesity have risen among indigenous Siberians with economic development and urbanization. This is largely the result of the incorporation of Western foods high in saturated fats and refined sugars, and decreases in physical activity levels (McGarvey et al., 1989; Snodgrass et al., 2006b; WHO, 2000; WHO/FAO, 2003).

Native Siberians, however, also appear to differ from other modernizing populations in a number of important ways. Several factors likely contribute to variation in health between populations undergoing economic modernization. First, the timing, pace, intensity, and pervasiveness of economic modernization clearly have the potential to influence health changes at the population level. For example, a rise in gross national product (GNP) generally heralds an increase in alcohol and tobacco use, as well as an elevated intake of nutrient dense foods (Yach et al., 2004); thus, the pace of economic development can have important effects on health through its influence on risk factors for disease. Second, government policy actions and intervention by nongovernmental organizations can alter the course of lifestyle changes associated with economic modernization and, consequently, affect health. One example comes from Poland, where the national government removed subsidies and levied taxes on animal fats during the period of economic modernization of the last decade; this increased prices of these products, reduced their overall consumption, and led to a greater reliance on vegetable oils (Mitka, 2004). As a result of this policy decision, mortality from heart disease decreased at a national level. Third, cultural factors can contribute to variation in health outcomes. For example, cultures that prohibit smoking or alcohol consumption can alter risk factor profiles for chronic conditions, such as CVD. Likewise, cultural factors that increase these behaviors, such as those in Russia that promote high rates of smoking and alcohol consumption, can accelerate health declines during economic modernization (Yach et al., 2004). The anti-alcohol campaign of the late Soviet-era drastically reduced alcohol consumption and led to a brief, but marked, improvement in life expectancy among Russians (Shkolnikov and Cornia, 2000); these anti-alcohol policies also were associated with substantial reductions in mortality rates among native Siberians (Boiko, 1992; Leonard et al., 1997; Pika, 1993). Fourth, the disease burden from unrelated conditions can influence the intensity and character of health declines associated with development. For example, many sub-Saharan African populations have a high burden of infectious disease that is primarily the result of recent increases in HIV/AIDS, malaria, and tuberculosis, yet many of these populations are simultaneously undergoing economic transitions (WHO/FAO, 2003; Yach et al., 2004). South Africa, for example, has a double burden of disease with a high infectious disease mortality rate (accounting for $\sim$28% of mortality) that is compounded by an increasing burden of chronic diseases (comprising $\sim$25% of mortality); a high infectious disease mortality rate in prime-aged adults can severely alter the course of development of chronic diseases. Finally, biological adaptations to local or regional environmental conditions can influence the experience of health changes resulting from economic modernization. The high prevalence of type 2 diabetes in economically modernizing Native American populations has been hypothesized to represent an interaction between lifestyle changes resulting from economic modernization (e.g., diet, physical activity, etc.) and a genetic mechanism that has been selected to allow metabolic efficiency (i.e., a "thrifty" genotype) in populations that, in the past, experienced periodic fluctuations in food availability (Neel, 1982; Weiss et al., 1984). Although a number of researchers have questioned the validity of this hypothesis, it remains a prominent explanatory model for the high prevalence of type 2 diabetes among Native Americans.

HEALTH AND ADAPTATION IN THE CIRCUMPOLAR ENVIRONMENT

The limited attention to interpopulation health differences with lifestyle change in part reflects the theoretical approach used in most studies of economic modernization. These studies (Baker, 1986; Rode and Shephard, 1994) have generally approached the issue of health change as stemming from lifestyle changes (e.g., diet, physical activity, etc.) that disrupt the homeostatic (or adaptive) equilibrium between human populations and their traditional environments. Such an approach, however, minimizes the differential impact that lifestyle change may have on distinct groups as a result of underlying biological differences.

A few recent studies (Fridlyand and Philipson, 2006; Ruiz-Pesini et al., 2004; Shephard and Rode, 1996; Wallace, 2005) have suggested that biological adaptations to the high-latitude environment may influence the health changes that northern populations experience with economic modernization and lifestyle change. For example, Ruiz-Pesini et al. (2004) propose that although certain mtDNA variants (i.e., those that increase heat generation through greater uncoupling of OXPHOS) helped some human populations successfully colonize northern environments, within the context of economic development these adaptations have consequences for health and longevity. While provocative, this hypothesis remains untested; mtDNA variants have not been directly linked with variation in energy metabolism in northern populations.

Our research among indigenous Siberians underscores both the importance of recognizing the unique aspects of health transition that occur in different populations, and of incorporating an evolutionary approach for understanding these differences. Like other modernizing populations, rates of overweight and obesity are increasing among indigenous Siberians. However, cholesterol levels remain relatively low among Siberians, and the limited information on blood glucose levels suggests that diabetes remains relatively uncommon. Hypertension appears to be a particularly acute problem among Siberians, especially among men. Taken together, this suite of cardiovascular risk factors differs from those observed in other modernizing populations, such as the

Pima of North America (Weyer et al., 2000). In part, these differences reflect the distinct social and political history of native Siberians and, specifically, the effects on indigenous health of idiosyncratic lifestyle changes in post-Soviet Russia. Additionally, there is evidence that physiological adaptation among northern residents structures the pattern of chronic disease within the context of this health transition.

The ongoing social and economic changes occurring in post-Soviet Russia have had profound and distinctive influences on the health of native Siberians. Although development is occurring in Siberia, the region remains relatively isolated because of its vast geographic area and limited infrastructure (e.g., few paved roads and little mobility). This geographic marginalization of rural Siberians has contributed to divergent health outcomes among different sectors of the population. For example, while conditions of undernutrition and growth stunting continue to be important problems for young children (Leonard et al., 2002c), diseases of 'overnutrition'—obesity and associated cardiovascular diseases—are on the rise among adults (Snodgrass et al., 2006a; Sorensen et al., 2005). In addition, even among adults, the relative risks of obesity and cardiovascular diseases appear to vary by sex. Higher levels of physical activity, often related to subsistence, contribute to the lower rates of overweight and obesity seen in Siberian men relative to women (Snodgrass et al., 2006b).

We have documented a variety of lifestyle factors associated with elevated blood pressure, including increased age, excess body fat, low physical activity, low income, and prolonged television viewing, among indigenous Siberians (Leonard et al., 2005b; Snodgrass et al., 2005b; Snodgrass, 2004). Variation in blood pressure among indigenous Siberians is explained in part by increased adiposity and recent declines in physical activity level. However, our research among the Yakut strongly suggests that chronic psychosocial stress related to economic marginalization and emerging economic inequality in the post-Soviet period contributes to elevated blood pressure, especially among men. Economic modernization exposes individuals to increased levels of chronic psychosocial stress as a result of the transformation of social and economic systems, which appear to lead to increases in blood pressure (Bindon et al., 1997; Dressler et al., 1987; Dressler, 1982, 1999; Schall, 1992). Psychosocial stress associated with catastrophic economic and social changes in Russia over the past two decades has likely contributed to increased blood pressure among Russians, including among indigenous Siberians (Bobak and Marmot, 1996; Kozlov et al., 2003; Marmot and Bobak, 2000). This problem is particularly severe among Russian men, possibly as a result of gender differences in coping strategies related to unemployment and underemployment, as well as low levels of autonomy (Jahns et al., 2003; Marmot and Bobak, 2000). This gender difference is also apparent from our research among the Yakut. Higher levels of chronic psychosocial stress have been documented in Yakut men compared to women using Epstein-Barr virus antibodies, a marker of cell-mediated immune function that serves as a proxy measure of stress (Sorensen et al., 2002). Those men with low individual incomes had higher blood pressure, and this was independent of body composition and age (Snodgrass, 2004; Snodgrass et al., 2005b). It is possible that these individuals suffered from elevated levels of psychosocial stress that resulted from their low incomes and inability to purchase consumer goods and luxury items. Finally, television viewing patterns were found to be associated with blood pressure among Yakut men, even when controlled for body composition and other potential confounders. Prolonged television viewing may contribute to increased psychosocial stress within the context of economic development, given that television serves as a powerful source of social and economic ideas of modernization that may be unattainable (Dressler, 1991).

To explore the adaptive dimensions of this health transition, we investigated whether heightened maintenance costs (i.e., elevated BMR) affect blood pressure and serum lipid concentrations among three indigenous Siberian groups (Evenki, Buriat, and Yakut). When controlled for body size and composition, as well as a variety of potentially confounding variables, such as age and smoking, BMR is positively correlated with both systolic blood pressure ($P < 0.01$) and approaches significance for diastolic blood pressure ($P = 0.10$) among the study participants ($n = 289$). Thus, higher BMR is associated with higher blood pressure. BMR is the strongest predictor of blood pressure of all variables in multiple regression models.

Our findings mirror those from a large study of Nigerians ($n = 997$) and African Americans ($n = 452$) (Luke et al., 2004). This relationship is opposite that between physical activity and blood pressure, as a number of studies have documented lower blood pressure with increased physical activity (Luke et al., 2004; Paffenbarger et al., 1991; Simons-Morton, 2003; Wareham et al., 2000). At present, the mechanism responsible for the association between BMR and blood pressure is unknown, and it remains to be confirmed whether the relationship is causal. Luke et al. (2004) postulated that heightened sympathetic tone or increased transmembrane ion exchange associated with increased BMR could potentially elevate blood pressure. Alternatively, increased formation of reactive oxygen species through upregulated cellular metabolism may heighten oxidative damage and lead to an increase in blood pressure (Harrison and Griendling, 2003).

Further, our research suggests a link between BMR and serum cholesterol concentrations. In an analysis of data from research with the Evenki and Buriat ($n = 175$), we found a negative correlation between BMR and LDL cholesterol, which remained even when adjusted for a variety of potentially confounding variables, including body size and composition, age, smoking status, and residence pattern ($P < 0.05$). This is suggestive of a protective effect of heightened metabolic turnover on plasma lipid levels. Taken together, this research suggests a potential pathway for environmental influence on health, given the systematically elevated BMRs among indigenous Siberians. Thus, evidence suggests that biological adaptations to northern environments, combined with a unique suite of lifestyle changes, may structure the distinctive health changes documented among native Siberians.

INTEGRATING ADAPTIVE AND BIOCULTURAL PERSPECTIVES

Over the past few decades, the study of variation in human health has become increasingly sophisticated as we have witnessed important growth in both evolutionary (adaptive) and biocultural approaches. Yet, despite these advances, research on human biology and health is typically framed as either evolutionary or biocultural. The evolutionary approach (Beall et al., 2002; Beall, 2001; Frisancho, 1993) primarily relies on an adaptive framework for understanding human biological variation and minimizes the importance of proximate causes, such as political, economic, and historical factors. In contrast, biocultural approaches (Goodman and Leatherman, 1998; Leatherman and Goodman, 1997) focus primarily on macro-level processes, while minimizing the attention to specific mechanisms affecting health, as well as underlying genetic and physiological variation within and between populations. This is a false dichotomy that moves us away from the historic strengths of the discipline and limits the explanatory power of our models. More effective integration of social, cultural, and economic information into our research can provide a better understanding of the adaptive options available to human populations. Conversely, information on the underlying genetic and physiological variation within human populations is critical for gaining insights into how forces of social change and economic development affect variation in health outcomes.

CONCLUSIONS

In summary, contemporary northern inhabitants possess a variety of biological adaptations for heat conservation and heat production, some of which appear to have a genetic basis. Studies of economic modernization are increasingly revealing that health effects relating to lifestyle change are not uniform across populations. No consensus currently exists on the cause or causes of variation in health between populations undergoing economic development, although a variety of sources could potentially influence health outcomes. Although preliminary, our research among indigenous Siberians suggests an important role for adaptation to regional environmental conditions (i.e., the circumpolar environment) in structuring health changes associated with economic development. Finally, we believe that framing human biology as both evolutionary and biocultural increases our ability to recognize distinctive health outcomes between populations and identify causal mechanisms associated with the production of variation. More effective integration of these research approaches is critical to understanding health change among northern populations.

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