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Human Bodies in Extreme Environments

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Abstract

Human habitation and adaptation to extreme environments have a deep history in anthropological research. Anthropologists' understanding of these ecological pressures and how humans respond to them has grown substantially over the last 100+ years. This review covers long-standing knowledge on adaptation to classic extreme conditions of heat, cold, and high altitude, while also updating the areas in which recent research has broadened our understanding of human adaptation, acclimatization, and resilience. Unfortunately, the intersecting stresses of structural inequality and climate change have made these extremes more extreme, with drastic negative impacts on health and well-being. Future research will need to explore how extreme environments, structural inequality, and climate change are embodied as well as mitigated so that humans are better prepared to face a rapidly changing world.

INTRODUCTION

Human habitation of extreme environments is a long-standing area of interest within biological anthropology and human biology, and with good reason because humans have successfully inhabited every continent on this planet. Humans in extreme environments offer the opportunity to document evidence of multiple levels of adaptation from genetic to functional. We have come a long way over more than a century and gained a better understanding of human biological flexibility, phenotypically and genetically, in the face of extreme environments in terms of both adaptation and acclimatization, though there is still a great deal more to learn.

Adaptation: change over time in response to the environment (genetic, cultural, developmental, physiological, anatomical) that improves function/fitness that can be inherited

Acclimatization: rapid change (over ~10 days) in response to the environment (cultural, anatomical, physiological) that improves function; cannot be inherited and can quickly reverse

Acclimation: rapid accommodation to immediate environment to maintain homeostasis; for example, shivering when cold, an accommodation that disappears when stress disappears

Adaptability: one's ability to adapt to an environment

Thermoregulation: various processes (biological and behavioral) involved in maintaining the body's core temperature within a normal range of 36.1–37.2°C

Unfortunately, there is a pressing need now more than ever to improve our understanding of how human bodies survive and thrive in extreme environments. The Intergovernmental Panel on Climate Change released its sobering sixth assessment report, which unequivocally states that human activity is driving global climate change (IPCC 2021). Human-induced climate change has resulted in increasingly variable and extreme weather events across the globe. Just within the United States in 2021, the state of Texas experienced an uncharacteristic ice storm, the Pacific Northwest grappled with extreme heat and extensive wildfires, and hurricanes flooded parts of the South and Northeast coasts. Globally, the 2022 men's World Cup in Qatar experienced unseasonably high temperatures and humidity, and in December 2022, the Horn of Africa was experiencing its worst drought in decades, devastating people through severe hunger, malnutrition, and dehydration.

Climate change–driven extreme weather events have killed hundreds of people, uprooted families and businesses, and cost hundreds of billions of dollars in damage (e.g., Donald 2021). Poor and marginalized populations are often the hardest hit by these disasters (Ahmadalipour et al. 2019). As the effects of climate change accelerate and global migration increases for cultural, humanitarian, and environmental reasons, there is a critical need to better understand human adaptation, acclimatization, and biocultural resilience. This knowledge is crucial for current and future human health and well-being as we continue to face unprecedented challenges imposed by climate change.

Here I review and update our current understanding of human bodies in the classic three extreme environments: hot, cold, and high altitude. Adaptations among Indigenous populations are the main focus of this review, while acclimatizations are briefly summarized in the sidebars. I then argue that the intersecting vulnerabilities of structural inequality and climate change have an outsized impact on populations living in environmental extremes. However, these populations are not passive and powerless; they have demonstrated breathtaking resilience. Finally, I discuss the ways in which the theoretical frameworks of local/situated biologies and biological normalcy need to be employed to better assess how humans live in and adapt to extreme conditions in a rapidly changing world.

THE BIG THREE: HOT, COLD, AND HIGH ALTITUDE

Human adaptability has deep roots within the field of anthropology, formalized with the publication of *The Biology of Human Adaptability* in 1966 (Baker & Weiner 1966). We understand human adaptability and acclimatization better now, particularly in terms of the genetics behind adaptations, but we still have a poor understanding of some topics, such as the different thermoregulatory mechanisms that humans employ between hot-humid and hot-arid environments. Here I focus on recent developments and future directions in hot, cold, and high-altitude environments (**Table 1**), whereas the more well-known adaptations and acclimatizations are summarized using figures and tables.

Table 1 Summary of the classic three extreme environments (heat, cold, high altitude), their defining metrics, environmental dangers, and health concerns (Burt 2007)

Environment	Defining extreme	Environmental dangers	Health concerns
Hot-dry	Temperature: >35°C Humidity: <15%	Heat Sun exposure High parasitic burden Water and food insecurity	Hyperthermia Heat stroke Dehydration Parasites and infectious disease
Hot-humid	Temperature: >35°C Humidity: >85%	Heat Sun exposure High parasitic burden Water and food insecurity	Hyperthermia Heat stroke Dehydration Parasites and infectious disease
Cold	Temperature: <5°C or Latitude: >76.25°N	Extreme cold Low bioavailability	Hypothermia Frostbite Increased blood viscosity → cardiovascular issues Environmental injury from slippery conditions Respiratory issue exacerbation
High altitude	Altitude: >2,500 m	Hypoxia High UV radiation exposure Low bioavailability	Acute mountain sickness Chronic mountain sickness

Hot

Much of the work on hot climate adaptations and acclimatizations (see the sidebar titled Hot Climate Acclimatizations) is inconclusive, with only a handful of known patterns, a high degree of interindividual and interpopulational variation, a great deal of contradictory results, and few new advances in our understanding. Hot climates can be categorized as hot-arid or hot-humid. The key challenge in these environments is thermoregulatory in nature; however, the difference in air water vapor content places different stresses on the human body, which result in a variety of anatomical and physiological responses to avoid hyperthermia (**Figure 1**).

Hyperthermia: condition in which body temperature is ≥40°C, which can have drastic impacts on normal physiology and can be deadly

Evidence suggests that basal metabolic rate (BMR, in kcal per day) responds more to humidity than to heat alone. Laboratory studies find that BMR increases in replicated hot-humid conditions but not in hot-arid conditions (Shapiro et al. 1980, Hori 1995, Chinevere et al. 2008, Sun & Zhu 2012). A higher BMR may be the result of greater body heat storage in hot-humid environments. However, it is also possible that the higher BMR encourages greater heat loss

HOT CLIMATE ACCLIMATIZATION

Sojourners to hot climates undergo a number of acclimatizations. When someone enters a hot-arid environment, over the course of 1–2 weeks they will experience a reduction in surface and core body temperatures, rapid onset of sweating that reduces over time to become more efficient, reduced heart rates, and a reduced BMR (Hori 1995, Moran 2008). Sojourners to hot-humid environments increase sweat rates as well, but they will also experience an increase in heart rate and metabolic rate to increase the body's core temperature and eventually the water vapor pressure at the skin to increase evaporative heat loss despite the environmental humidity. Sweat rates also appear to change across body regions such that sweat production increases at the forearms more than at the thigh, for example (Périard et al. 2015).

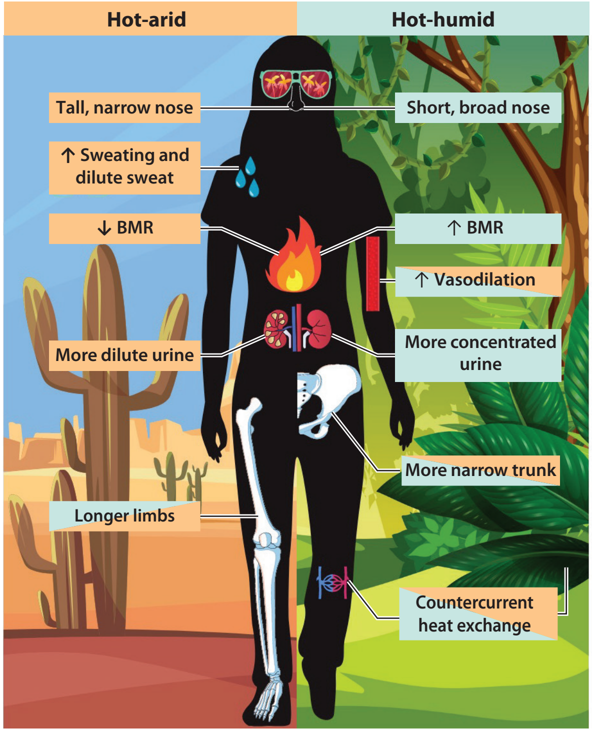

Figure 1

A comparative summary of the key adaptations among Indigenous hot-arid (*orange*) and hot-humid (*green*) populations. Adaptations in orange-green mixed boxes mean that they are present in both hot-arid and hot-humid populations. Abbreviation: BMR, basal metabolic rate.

through radiation and convection as heat travels from a warm-to-cool gradient, from core to skin (Tochihara et al. 2022). A high BMR would also lead to greater water vapor pressure at the skin relative to the environment, encouraging greater evaporative heat loss despite high environmental humidity (Périard et al. 2015). Among cold climate populations, an increase in BMR is correlated with higher thyroid hormone levels (Pääkkönen 2010). However, no modern studies have examined if the increase in BMR associated with hot-humid climates is also related to alterations in thyroid hormone dynamics.

Sweating is a crucial physiological mechanism for maintaining core body temperature in hot climates through evaporative heat loss (Hori 1995). However, it is effective only in hot-arid environments because sweat will not evaporate in humid environments. Indigenous tropical populations tend to have higher concentrations of sweat glands but higher skin temperatures, which work to increase radiative and convective heat loss while simultaneously delaying the onset of sweating. Sweat in these populations is typically more dilute—containing less salt—which also helps them to maintain electrolyte balance in the face of water loss (Yanovich et al. 2020).

Basal metabolic rate (BMR): metabolic cost of maintenance; calories the body needs to perform regular functions, not including activity, thermoregulation, reproduction, or immune costs

To maintain core body temperatures, Indigenous hot-arid populations tend to increase sweating, a rather dilute sweat, particularly from the limbs where there is the greatest surface area (Adolph 1938, Cramer & Jay 2016). These populations also increase limb vasodilation so more heat is lost through radiation and convection from increased blood flow in peripheral vessels along high surface area limbs.

Humans appear to follow Bergmann's, Allen's, and Thomson's rules with longer limbs and higher surface area–to–body mass ratios in hot environments (Katzmarzyk & Leonard 1998, Foster & Collard 2013, Cramer & Jay 2016) and tall, narrow noses in hot-arid environments and short, broad noses in humid environments (Thomson & Buxton 1923). Body composition also plays a thermoregulatory role, though a seemingly negative one in hot climates. Research has examined the thermoregulatory properties of fat and muscle in hopes of determining whether fat or muscle provides greater insulation. Both tissues are currently thought to be insulative, but the heat-saving/heat-producing contributions of each within hot climates are unknown. Those with greater body fat percentages, relative to body mass–similar individuals with lower body fat, show a greater increase in core body temperature, despite similar levels of sweating and heat dissipation, putting them at greater risk for heat injury (Koppe et al. 2004, Dervis et al. 2016). Muscle, though we rely on it to move about the world, is incredibly inefficient: 30–70% of the energy used by muscle is released as heat. This inefficiency and excess heat can be detrimental, contributing to an increase in core body temperature and risk for heat-related injuries, particularly during rigorous exercise (González-Alonso 2012).

Bergmann's rule: high body mass/surface area in high latitudes for greater heat production and less heat loss with the inverse at low latitudes

Allen's rule: shortened extremities at high latitudes to reduce surface area, with the inverse at low latitudes

Thomson's rule: observation that climate affects nose shape and size. Tall, narrow noses occur in cold and hot-arid environments

Due to a greater density of parasitic vectors and reservoirs, humans in hot-humid environments have to cope with a high parasitic load and subsequently higher immune costs (Short et al. 2017). For example, the Shuar, horticulturalists in Ecuador, experience elevated immune costs, which has resulted in greater total energy expenditure than temperate populations (Urlacher et al. 2018, Christopher et al. 2019). This higher immune burden has resulted in a trade-off, with Shuar children exhibiting reduced growth (Urlacher et al. 2018, 2019). This finding may be an example of constrained total energy expenditure budgets, such that in a limited energy budget, more calories devoted to immune costs result in fewer calories allocated to growth (Westerterp 2001b, Pontzer et al. 2016, Urlacher et al. 2019).

A wide range of cooling behaviors have been identified globally. Low-tech ways to cool down include, but are not limited to, timing physical activity during cooler portions of the day, wearing light-colored clothing, wearing multiple thin layers of cloth to trap cooling/insulating air and protect the skin from UV radiation, wetting clothing to increase evaporative cooling, consuming more water, and increasing the consumption of spicy/stimulating foods to induce a cooling sensation. In locations with infrastructure and resources, cooling technologies such as air conditioners, fans, and cooling centers are used to cope with extreme heat. However, these technologies are not currently sustainable, and a great deal more effort will be needed to make cooling technologies more efficient and/or to increase knowledge of how to behaviorally cope with heat (Khosla et al. 2022).

There is a lack of recent robust research examining different adaptations and acclimatizations in hot-humid and hot-arid environments. This is not to say recent work in hot climates has not been conducted; rather, it has, but the focus has shifted to one of growth and development (Urlacher et al. 2019), immune burden (Gildner et al. 2020), total energy expenditure (Pontzer et al. 2012, Urlacher et al. 2021), and water insecurity and thirst (Rosinger 2023, this volume), with thermoregulatory adaptation/acclimatization work falling by the wayside.

When studying humans in extreme heat, anthropology would benefit from collaborating with exercise physiologists. Sports science is extremely interested in determining how to improve performance and increase safety among athletes competing in extreme hot environments (González-Alonso 2012). A recent study examined the impact of heat and humidity on performance among elite Dutch athletes to simulate what the athletes would experience during the 2021 Olympics in Tokyo, Japan. Investigators found that athletes fatigued 26% faster, had a 16% reduction in peak power, and saw a significant increase in core body temperature in the simulated

Tokyo condition, demonstrating the negative impact that heat and humidity can have on athletic performance (de Korte et al. 2021).

Research has explored methods for improving athlete performance in hot conditions, which could be coopted for nonathletes. These methods include preacclimatization, exposing individuals to simulated hot conditions prior to their experiencing the actual environment; precooling an individual for a short period (~30 min); taking short breaks from the heat; consuming water or ice slurries; and/or placing ice cold towels on the body (Sanderson 2022). In particular, pre- and per-cooling (before and during bouts of exercise) seem to be effective means of mitigating performance declines and of preventing steep increases in core body temperature (Bongers et al. 2015). Cooling vests, ice towels, and cold-water immersion may become necessary for individuals who cannot avoid extreme heat exposure; however, this step must be done with care so that the cooling does not negatively impact enzyme kinetics. As temperatures rise to dangerous levels globally, anthropologists should work with exercise physiologists and local populations to find accessible, sustainable, and culturally appropriate methods for mitigating the dangers of extreme heat.

Hypothermia: condition in which body temperature is ≤35°C, which can have drastic impacts on normal physiology and lead to injury and death

Countercurrent heat exchange: shunting blood to deep arteries and veins to reduce heat lost from peripheral blood vessels in cold; the inverse occurs in heat

Cold

Some may think cold adaptation/acclimatization research will be unnecessary, given the concerning climate change–induced warming trends. However, cold, through extreme day-night temperature fluctuations or extreme cold weather events, as was seen in the December 2022 bomb cyclone that plunged much of the United States into a deep freeze, will likely always be a stress that humans need to face. Much like the research for hot climates, human biology cold climate research has focused on vascular and metabolic adaptations (**Figure 2**) and acclimatizations (see the sidebar titled Cold Climate Acclimatizations) to cold stress that work in concert to reduce the risk of sustaining a cold-related injury or hypothermia.

BMR among Indigenous cold climate populations can be ~20–40% higher than expected and likely driven by high thyroid hormone levels (Galloway et al. 2000, Leonard et al. 2002, Leonard et al. 2005, Snodgrass et al. 2005, Cepon et al. 2011). However, a great deal of inter- and intrapopulational variation could be the result of differences in lifestyle or genetics (Rode & Shephard 1995). For example, among a small sample of reindeer herders from subarctic Finland, females, but not males, had higher BMRs than predicted. This unusual result may be due to the study's small sample size or perhaps to the dual role of thyroid hormone for maintaining BMR as well as pregnancy (Ocobock et al. 2020). Cold climate populations also experience countercurrent heat exchange as well as oscillating vasoconstriction and vasodilation in order to reduce heat lost while still maintaining tissue viability (Stocks et al. 2004, Steegmann 2007).

Nonshivering thermogenesis, particularly brown adipose tissue (BAT), has recently received a great deal of scientific attention for its thermoregulatory and antiobesogenic therapeutic potentials. BAT is a mitochondria-dense tissue that, in response to mild cold (~10–15°C), short-circuits the electron transport chain, via the action of uncoupling protein-1 (UCP-1), to produce heat rather than energy for work. Among human adults, BAT can be found in the supraclavicular and paracervical regions as well as along major deep core blood vessels (Heaton 1972, Tanuma et al. 1976, Huttunen et al. 1981, Lean 1989, van der Lans 2016, Levy et al. 2018, Levy 2019). There are a number of potential BAT-associated gene candidates. *Myf5* (myogenic regulatory gene) is found in BAT and could explain why the developmental origin and pathway of this tissue is similar to that of muscle. *PRDM16* and *FoxC2* have also been identified as genes that induce white adipose tissue to beige, meaning the white adipose tissue will behave more like BAT (Lidell et al. 2014, Cannon et al. 2020). *MTUS1*, *EVA1*, and *KCNK3* are positively associated with high BAT volume, whereas *ZIC1* is associated with a low BAT volume phenotype (Nascimento et al. 2018).

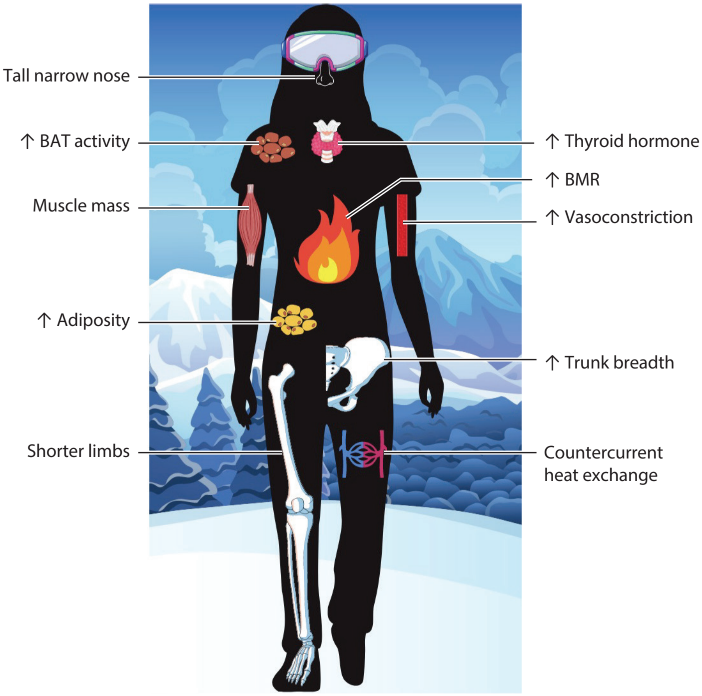

Figure 2

A summary of the key adaptations among Indigenous cold climate populations. Abbreviations: BAT, brown adipose tissue; BMR, basal metabolic rate.

BAT, long considered a purely cold climate adaptation, has been found among cold (Levy et al. 2022, Ocobock et al. 2022a), temperate (Levy et al. 2016, Niclou & Ocobock 2022), and hot climate populations (Oyama et al. 2021, Niclou et al. 2022), suggesting that BAT may be a pan-human adaptation. BAT could have been evolutionarily significant as nighttime temperatures even in hot climates can be cold enough to elicit a thermoregulatory response (Scholander et al. 1958).

When activated, BAT can significantly increase metabolic rate by as much as ∼9%, as seen among the reindeer herders in Finland (Ocobock et al. 2022a) and among Samoans (Niclou et al. 2022). However, some Sakha males from Siberia experienced no change or even a decrease in metabolic rate (Levy et al. 2018). Populational BAT variation also extends to substrate utilization; some populations use more glucose to fuel BAT (Vallerand & Jacobs 1989, Levy et al. 2018),

COLD CLIMATE ACCLIMATIZATIONS

Many of the acclimatizations we see among cold climate populations are incredibly similar to the adaptations discussed in this review. Those acclimatizing to cold experience an increase in BMR and shivering as well as the cycling between vasoconstriction and vasodilation to preserve both body heat and tissue viability (Castellani & Young 2016). We do not currently have much data with regards to brown adipose tissue (BAT) activity and acclimatization. One study among an Albany, New York, population found that BAT activity produced higher skin temperatures but no difference in metabolic rate in winter relative to the summer, suggesting BAT acclimatization as well as improved efficiency (Niclou & Ocobock 2022). BAT acclimatization in cold climates needs to be more thoroughly explored.

others metabolize more fatty acids (Chondronikola et al. 2014, Ocobock et al. 2022a), and others still utilize a mixed substrate metabolism (Niclou et al. 2022). This high degree of variation could be due to differential environmental exposure during key periods of childhood development (Levy et al. 2021) or other factors, such as differing evolutionary trajectories or dietary traditions.

Constrained theory for total energy expenditure: contends that animals operate within a narrow range of total energy expenditure

The ability of BAT to remove glucose and fatty acids from the blood as well as to potentially increase metabolism makes this tissue an intriguing tool in the fight against the obesity epidemic. However, BAT activity has been measured or inferred among only a small number of populations. A much stronger grasp of the initiation and variation of BAT activity in terms of population, development, age, sex, and diet is needed before we can even begin to assess BAT's therapeutic potential.

Beyond metabolism, body proportions and composition also play a role in cold climate adaptations. Larger bodies with shorter limbs have been observed among Indigenous cold climate populations, though there is a recent trend of increasing leg length (Ruff 1994, Katzmarzyk & Leonard 1998, Steudel-Numbers & Tilkens 2004, Churchill 2006, Foster & Collard 2013, Savell et al. 2016). Such morphology should increase heat production while minimizing the surface area through which heat is lost to the environment. Taller, more narrow noses also work to warm and humidify cold air before it reaches the delicate lung tissue (Thomson & Buxton 1923). Cold climate populations also tend to have greater body adiposity and muscle mass. Both tissues can contribute to heat retention and production, respectively. Body fat serves as an insulator (McArdle et al. 1984, Tikuisis et al. 2000), though it is inversely related with BAT volume (Cypess et al. 2009, Drubach et al. 2011), and muscle mass can serve as both an insulator and a heat producer through both shivering and physical activity (Payne et al. 2018). As mentioned above, the natural inefficiency of muscle can provide an important heat benefit in cold climates, such that greater physical activity in the cold can help reduce thermoregulatory costs (Ocobock 2016).

Behaviorally, wearing traditional clothing made of animal furs as well as modern highly insulative clothing, scheduling outdoor work during favorable conditions, alternating passive and active outdoor efforts, consuming warm foods, consuming high-protein and high-fat foods, being aware of weather conditions, and applying traditional ecological knowledge are all key actions for mitigating the risk of cold-related injury (Rintamäki & Rissanen 2006, Anttonen et al. 2009, Turunen et al. 2021). Recent data among cold climate populations reveal high levels of physical activity and total energy expenditure (Ocobock et al. 2021, Sellers et al. 2022), which contribute to thermoregulatory heat production but also contradict the constrained theory for total energy expenditure (Ocobock 2020).

High Altitude

High altitude presents an interesting extreme because, unlike extreme heat and cold, the main stressor, low oxygen, cannot be mitigated behaviorally (Moore 2017). Work among high-altitude populations (**Table 2**) and sojourners (see the sidebar titled High-Altitude Acclimatizations) represents some of our most extensive knowledge of comparative human biology. Populations in the Andes, Tibet, and highland Ethiopia, who have inhabited these high-altitude regions for millennia, represent three different evolutionary routes to high-altitude physiological and anatomical adaptation (Beall 2007, 2014; Moore 2017).

High-altitude adaptations, such as modifying lung capacity, ventilation rate, hemoglobin and nitric oxide levels, pulmonary pressure, mitochondrial density, and capillary network extensiveness, improve oxygen delivery and utilization in a hypoxic environment over both evolutionary and life span timescales. A recent assessment found that measures of hemoglobin concentration and blood oxygen saturation are highly reliable and repeatable measures at high altitude, making

Table 2 Summary of the three high-altitude populations who have been studied most extensively. Each population has evolved a unique suite of adaptations to their hypoxic environments

Potential for adaptation	Tibetan	Andean	Ethiopian
Energy expenditure	BMR and VO_2 max similar	BMR and VO_2 max similar	Unknown
Ventilation	Increased rate	No increase, actually lower Larger, more barrel-shaped chests	Unknown
O_2 concentration	↓ O_2 ↓ hemoglobin, but more efficient	↑ hemoglobin and erythropoietin, which help ↑ O_2	↑ hemoglobin, even relative to Andean populations
Blood flow	↑ blood flow to brain ↑ nitric oxide	↑ blood flow to brain ↑ pulmonary vasoconstriction	↑ pulmonary artery pressure Intermediate nitric oxide levels
Capillary network	More extensive	No difference	Unknown
Mitochondria	Fewer?	Fewer?	Greater number

Abbreviations: BMR, basal metabolic rate; VO_2 max, maximal oxygen consumption.

these key data points for future and comparative work (Beall et al. 2022). Each of the above populations has "mixed and matched," through an impressive range of phenotypic variation, these potential points of hypoxia adaptation (**Table 2**). A thorough review of these adaptations has already been done (Beall 2014) and discussed in great detail elsewhere (Frisancho 1975, 2013; Moran 2008; Bigham et al. 2010; Beall 2013; Vitzthum 2013); therefore, this topic is not covered in as much depth as the previous two extremes.

The Tibetan and Andean populations are the most thoroughly studied to date. More recent work has aimed at linking particular physiologies to specific genes to detect natural selection among high-altitude populations (Moore 2017); more than 60 candidate genes have been identified. Among these 60 candidates, one-third are shared among both populations, one-third are found only among Tibetans, and one-third are found only among Andeans. For example, *EGLN1* and *EPAS1* are loci associated with the production of hypoxia-inducible factors (HIFs) that alter gene transcription in response to low levels of cellular oxygen. HIFs, particularly HIF-alpha, initiate transcription of genes related to angiogenesis, production of erythropoietin, cell death, glucose

Hypoxia: though there is no official cutoff, a blood oxygen saturation ≤95% is considered hypoxic for adults

HIGH-ALTITUDE ACCLIMATIZATIONS

Sojourners to high altitudes undergo a number of acclimatizations to improve oxygen delivery throughout the body. During the acclimatization period, sojourners will experience increases in BMR, ventilation rates, red blood cell production, and capillarization (Beall 2007, Imray et al. 2010). However, even with acclimatizations, sojourners are at high risk for acute and chronic mountain sickness as well as an increased risk of pulmonary disease (Westerterp 2001a). Those with chronic mountain sickness from extended periods at high altitude may experience breathlessness, heart palpitations, disturbed sleep, cyanosis, vasodilation, burning or prickling sensations across the body, headaches, tinnitus, and increased hemoglobin levels (Villafuerte & Corante 2016). Acute mountain sickness can occur during rapid ascent to >3000 m above sea level. Symptoms include headache, insomnia, fatigue, shortness of breath, dizziness, reduced mental capacity, nausea, reduced appetite, and reduced urine output. If an individual displaying signs and symptoms of acute mountain sickness does not quickly descend, they can develop cerebral and/or pulmonary edema, both of which can be life-threatening (Imray et al. 2010).

metabolism, inflammation, and other functions associated with oxygen transport and utilization (Moore 2017).

Studies have found evidence to support positive selection for *EGLIN1* among Tibetan and Andean populations and positive selection for *EPAS1* among the Tibetan population. The major Tibetan alleles of *EGLIN1* and *EPAS1* appear to be associated with the Tibetan phenotype of reduced hemoglobin levels and a dampening of the HIF response (Beall 2014). Among Andeans, the *PRKAA1* gene region is associated with uterine artery size, such that those with *PRKAA1* had greater maternal blood flow to the developing embryo/fetus, which has resulted in higher birth weights.

Recent work has also examined how high altitude may alter breast milk macronutrient and hormone content. A study of breast milk content was recently conducted among Tibetans living in high- and low-altitude villages in the Nubri Valley of Nepal as well as at low-altitude Kathmandu, Nepal. Investigators found no association of milk fat, sugar, and protein composition with altitude; however, fat content was associated with maternal adiposity. Fat content was also higher when compared with reference populations (Quinn et al. 2016). Leptin and adiponectin levels showed no altitude-correlated differences among these populations (Quinn & Childs 2017). However, these studies were cross-sectional in nature and may capture neither the differential stress experienced at different developmental periods nor how high altitude exacerbates these stresses. Furthermore, research recently reported that females from the same valley had decreased levels of cortisol and testosterone. These two hormones increase somatic costs and utilization of stored energy; reducing their levels could be an adaptive response to the high energy demands of living in a high-altitude environment (Sarma et al. 2018).

INTERSECTING VULNERABILITIES OF STRUCTURAL INEQUALITY AND CLIMATE CHANGE: THE PRESENT AND FUTURE EXTREME

Extreme structural inequality resulting from racist and classist policies is and will continue to be an issue with which humanity needs to contend, and contend with it we must because it has lasting, generational impacts on health and well-being (Young 1996, Young et al. 2007, Snodgrass 2013, Valeggia & Snodgrass 2015, Godfrey et al. 2022). Furthermore, many of the populations inhabiting the environments discussed above experience structural inequalities, inequalities that are being exacerbated by the damaging effects of climate change.

Inadequate health care access, due to the intersecting factors of structural racism and poverty, exist globally with dire consequences (Brockerhoff & Hewett 2000, Cutter et al. 2001, Nazroo et al. 2007). Structural racism is the result of cultural practices, public policies, and institutional policies that create and perpetuate racial inequity (Taylor 2020). Research has shown again and again that discrimination and poverty can become embodied, leading to overall worse health, and that embodiment can even be passed along intergenerationally through epigenetic mechanisms (Seeman et al. 2008, Crimmins et al. 2009, Gravlee 2009, Conroy et al. 2010, Williams et al. 2010, Rej et al. 2020, Fuller et al. 2021, Mulligan 2021). Populations in extreme environments are particularly vulnerable to this embodiment, as many have experienced the historical trauma of colonialism.

For example, a significant, documented increase in cardiovascular disease and risks among Indigenous circumpolar populations can be linked to the ensuing racism, assimilation, damaging policies, and inequities brought about by European colonialism (Young 1996, Young et al. 2007, Snodgrass 2013, Valeggia & Snodgrass 2015, Godfrey et al. 2022). These populations have been forced to abandon their traditional lifeways, their diet, their physical activity levels, and even their land while being exposed to greater pollution and a lack of access to healthy food and health care

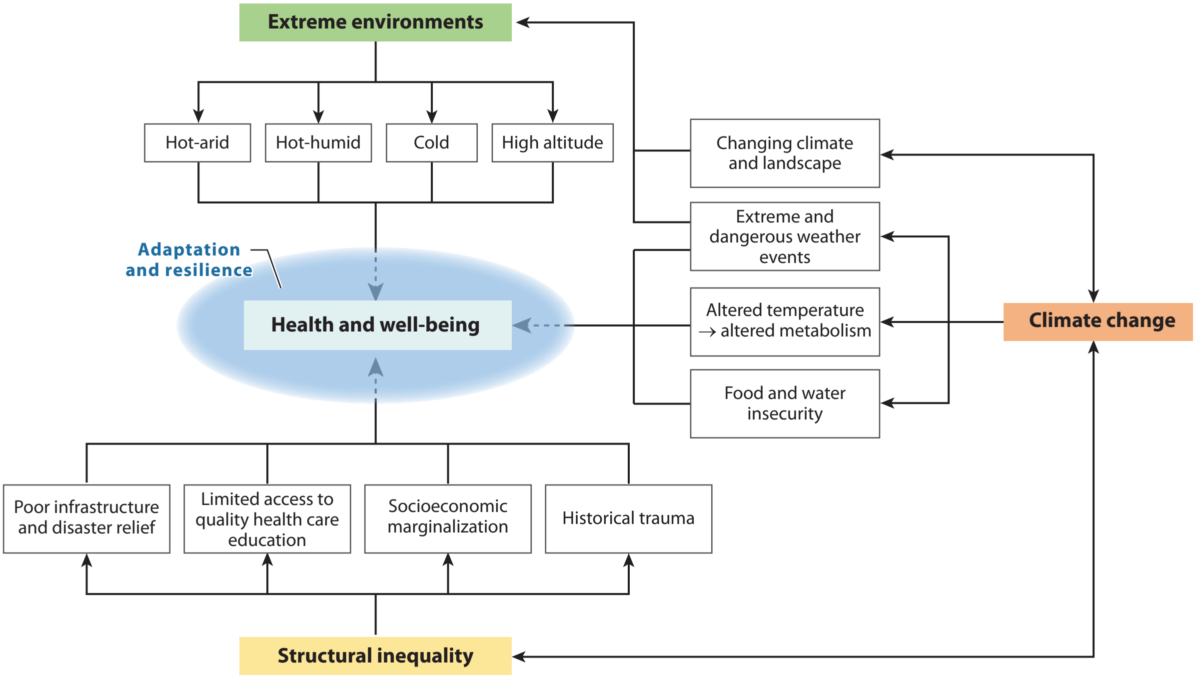

Figure 3

Concept map of the intersecting vulnerabilities of extreme environments, climate change, and structural inequality. Each of these stresses produces different mechanisms (*white boxes*) that have various negative effects (*solid black lines with arrows*) on the health and well-being of populations living in these environments. However, adaptations and resilient behavior (*blue oval*) can mitigate (*indicated by dashed arrows*) the harmful effects.

services (Godfrey et al. 2022). Infectious diseases are still an ever-present threat among Indigenous populations who are also now experiencing a greater incidence of cardiometabolic diseases, substance abuse, and poor mental health (Valeggia & Snodgrass 2015). For example, due to the loss of traditional language, culture, and lifeways, Indigenous Sami of Finland are at a 2.3 times greater risk of suicide relative to their Finnish counterparts (Young et al. 2015), and Canadian Inuit are 6–11 times more likely to commit suicide than are their non-Indigenous Canadian counterparts (Valeggia & Snodgrass 2015). The lasting effects of this historical trauma make these populations more vulnerable to their extreme conditions, to the impacts of climate change, and to worse physical and mental health (**Figure 3**).

The intersecting vulnerabilities of historical trauma, extreme environments, and climate change impacts can be observed among hot climate and high-altitude populations as well. Food and water insecurity are of particular concern in hot climates, even hot-humid ones, as access to clean drinking water is unreliable (Rosinger & Young 2020). For example, the Tsimane horticulturalists of Bolivia experienced a historic flood in 2014, for whom longitudinal data were collected comparing food and water insecurity, nutritional status, blood pressure, and diarrheal and respiratory disease before and after the flood. Investigators found that though water insecurity improved in the two months after the flood, food insecurity persisted. Furthermore, adults, but not children, experienced a significant decline in body mass index, indicating that Tsimane adults were preferentially providing resources to their children. Rates of respiratory illness increased while diarrheal illness declined, though not significantly (Rosinger 2018, Rosinger et al. 2022). With extreme events such as flooding becoming more frequent, with little infrastructure in place to mitigate the accompanying dangers or provide disaster relief, hot climates (arid and humid) will be increasingly vulnerable to conditions that harm health and well-being on short and long timescales.

High-altitude populations are also increasingly vulnerable to the effects of climate change and poor infrastructure (Kaltenborn et al. 2010). Given the remote location and low environmental production, food insecurity is high and medical care difficult to access. Low birth weights are typical among high-altitude populations (Beall 2001, López Camelo et al. 2006, Dang et al. 2007, Niermeyer et al. 2009, Wehbya et al. 2010); however, high-altitude-related hypoxia is not the only reason for low birth weights. In a study examining birth weights of lowland and high-altitude populations in South America, investigators found that altitude did indeed have a negative correlation with birth weight, but maternal health and socioeconomic status also had significant, negative effects on birth weight (Wehbya et al. 2010). Similarly, poor nutritional status among the high-altitude population of Nuñoa, Peru, also led to a reduction in childhood growth, but this pattern was more prevalent among low-socioeconomic-status children (Leonard 1989). Climate change will exacerbate food and water security vulnerabilities among high-altitude populations, particularly through the loss of mountain glaciers. The rapid melting of these glaciers can lead to flash flooding, a loss of what was a previously reliable freshwater source, and a drastic change in the biodiversity that relies on seasonal glacial waters (Kaltenborn et al. 2010).

Extreme environments are only becoming more extreme. The intersecting pressures of a harsh habitat, the rapid and damaging effects of climate change, and historical trauma are creating an environment that increases the risk of poor health. However, this dangerous combination is different for each population and will manifest just as differently. The high degree of variation, from before and after these relatively new pressures, means that we need to approach each context differently and question what we have previously regarded as biologically "normal."

SITUATING THE "NORMAL"

A new analytical framework has been developed to interrogate what we as biological anthropologists and human biologists mean by "normal" (Cullin et al. 2021; Wiley 2021, 2023, in this volume). In many ways, our work requires us to operate within statistical distributions with discussions of variation around the mean. That in and of itself is not inherently bad; however, the human tendency to apply meaning and judgment to statistically defined norms creates hierarchical relationships that often lead to bias and harm (Graves 2021). Furthermore, reference values are typically defined by data collected among Western, educated, industrialized, rich, and democratic (WEIRD) populations and, therefore, are unlikely to be broadly applicable, especially to those in extreme climates. Even more, populations in similar environments may not have similar physiologies, anatomies, or behaviors (e.g., adaptive variation across high-altitude populations). Finally, with the intersecting pressures of structural inequality and climate change resulting in relatively rapid alterations to the environmental landscape, physical and mental health profiles, and behavior, what is normal becomes less meaningful.

For example, researchers recently proposed that climate change and obesity reinforce one another and may lead to overall worse health due to drastic changes in diet, reduced physical activity levels, increased mechanization, and reduced exposure to cold (Young 1996, Mäkinen et al. 2006, Kozlov et al. 2007, Young et al. 2007, Levy et al. 2018, Gildner & Levy 2021). Although cold climate populations have traditionally had relatively healthy metabolic profiles (Young et al. 1993, Young 1996, Ocobock et al. 2022b), these same populations, in some circumstances due to climatic warming, may be undergoing a transition and experiencing an evolutionary mismatch that leads to worse health (Chateau-Degat et al. 2010a,b, 2011; Ocobock & Niclou 2022). In other words, what previously was may no longer be normal.

The framework of situated or local biologies is also highly relevant to this discussion because it theorizes that differences between populations are due to the population-specific interactions of biology, culture, history, and socioeconomic and political landscapes. Biocultural responses to each of these conditions vary depending on the local context (Lock 2017, Leatherman & Goodman 2020). Returning to the reindeer herders from subarctic Finland, the increasing local temperature due to climate change has reduced cold stress. Larger body sizes and greater adiposity, though helpful for thermoregulatory purposes, may become problematic in a warmer environment in conjunction with behavioral shifts due to Western and colonialist influences that alter diet (by consuming more processed foods) and reduce activity levels (Young 1996, Young et al. 2007, Snodgrass 2013, Valeggia & Snodgrass 2015, Godfrey et al. 2022). Furthermore, with warmer ambient temperatures, the environmental signal for maintaining a high BMR is weakened, which could lead to a slow accumulation of additional body fat over time and worsening cardiometabolic health (Gildner & Levy 2021, Ocobock & Niclou 2022, Ocobock et al. 2022c).

Among the herders in particular, this situation is compounded by the dual pressures of land use competition with forestry and mining interests as well as the direct effects of climate change on the landscape. With their livelihoods under threat and reindeer herding becoming more physically demanding and dangerous as well as more expensive due to an increase in the number of extreme weather events, herders experience greater financial strain, risk for injury, stress, and worsening mental health (Tervo & Nikkonen 2010, Jaakkola et al. 2018). A key area of future research will be to gain a better understanding of how humans embody climate change, and circumpolar regions that experience these changes faster and more acutely than do other areas of the world while also contending with the lasting impacts of colonialism would be a good place to start.

However, it is also important to explore how populations have demonstrated resilience in the face of these pressures, resilience that can, to some degree, help mitigate the intersecting pressures of extreme environments, climate change, and structural inequality (**Figure 3**). Resilience is the capacity of a population to respond to changes in ways that maintain its relationship with the environment (Holling 1973, Barrios 2016). Among the Tsimane, adults consumed ~50% of their daily water intake from foods, fruit in particular, which may help them in times of water scarcity but also provide an uncontaminated water source (Rosinger & Tanner 2015). The reindeer herders have displayed resilience in the face of climate change as well. Herders rely heavily on their traditional ecological knowledge, skills, and technology to navigate the difficult landscape and rapidly changing weather conditions (Vuojala-Magga 2009, Rasmus et al. 2022, Salmi et al. 2022). As climate change is drastically altering the once highly recognizable landscape, herders have incorporated modern technology and knowledge to complement their traditional skill set (Rasmus et al. 2022). This flexibility, which is being passed from generation to generation, has helped herders maintain their livelihood in less-than-optimal conditions.

These frameworks are going to be critically important as we work to better understand human biology at the extremes and how humans bioculturally display resilience. Assessing the local environment, with all its various inputs, will aid us as we put biological data within the proper context for analysis and broader applicability.

CONCLUSION

The history of studying humans in extreme conditions leaves us with a deep record to guide future research among populations in hot, cold, and high-altitude environments. This research is critically necessary, especially now in the face of climate change. As we become more aware of the biological signatures of climate change and historical trauma, we need to interrogate the significance of biological normalcy in inter- and intrapopulational comparative studies and better appreciate how human populations have adapted, acclimatized, and demonstrated resilience to their local conditions. The biological and cultural ways that these extreme-environment populations have adapted to survive and thrive in harsh conditions are incredibly informative as we explore new means to cope with a warming and increasingly unpredictable global climate. These efforts will not only give us a stronger grasp of human variation and biocultural flexibility, but also help build a tool kit that we will need to rely on as we learn to navigate our rapidly changing world.

SUMMARY POINTS

1. Humans have inhabited, adapted to, and acclimatized to the extreme environments of heat, cold, and high altitude for millennia.
2. Populations in hot-arid and hot-humid environments share some adaptations; however, differences in humidity have also led to adaptive differences. The variation and range of adaptations in these environments are still relatively understudied.
3. Cold climate populations demonstrate a number of metabolic adaptations to their harsh environments. There has been renewed focus, particularly for brown adipose tissue (BAT) studies. BAT and basal metabolic rate show a great deal of variation that requires further research across different cold climate populations.
4. High-altitude research among Tibetan, Andean, and Ethiopian populations represents the most comprehensive extreme environment dataset and most recent work tying genes to adaptive phenotypes, providing a model for researchers of hot and cold climate populations to follow.
5. Populations in extreme environments are often members of historically excluded groups, particularly Indigenous populations, who face poor health and low socioeconomic status due to structural inequalities.
6. Climate change is affecting these extreme environments more drastically and rapidly than in other parts of the world, putting greater pressure on already vulnerable populations and environments, leading to worsening health and well-being while also revealing resilience strategies.
7. The frameworks of local biologies, biological normalcy, and resilience are being applied more regularly to research among extreme environment populations.

FUTURE ISSUES

1. A great deal more observational and empirical work is needed to better understand biocultural adaptations to hot-arid and hot-humid environments, including experimentally testing the physiological fitness of Bergmann's, Allen's, and Thomson's rules.
2. Cold climate research has a deep history; however, it suffered a lack of interest until recently. As with high altitude, a great deal more comparative work needs to be done among a variety of cold climate populations to determine the range and variation in cold climate adaptations.

3. More research is needed across populations to understand the variation in BAT volume, activity, associated genes, and environmental cue thresholds for activating this heat-producing tissue. Current work has revealed few associations, and, given the ability of BAT to increase metabolic rate and clear glucose and/or lipids from the blood, such research could have major implications for the obesity epidemic.
4. The excellent work tying together genotype and phenotype for high-altitude adaptations needs to continue and expand to cover more adaptive features and candidate genes.
5. Anthropologists need to intentionally undertake research, using the frameworks of local biologies and biological normalcy, to examine how the intersecting stresses of climate change and structural inequalities become embodied, particularly in extreme environments, which are typically home to vulnerable populations.
6. Anthropologists, also using the frameworks of local biologies and biological normalcy, need to identify and quantify resilience strategies among extreme climate populations to not only better understand limits to human adaptability, but also build a tool kit for researchers to employ in a rapidly change world.

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