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RESEARCH ARTICLE

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Human energy expenditure, allocation, and interactions in natural temperate, hot, and cold environments

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Abstract

Objective: The aim of this research is to analyze how energy is allocated differently in temperate, hot, and cold environments among National Outdoor Leadership School students.

Method: Basal metabolic rate, physical activity, thermoregulation, and the thermic effect of food were estimated to determine the total energy expenditure and energy allocation differences among a group of healthy, highly active adults ($N = 59$) participating in National Outdoor Leadership School courses in the western United States. Two of these courses took place in both hot and temperate climates ($N = 22$) and the other two in both temperate and cold climates ($N = 28$). Data from a pilot study ($N = 6$) in a temperate climate were also included. Each climate regime lasted for one month.

Results: Total energy expenditure values were statistically equivalent in temperate and hot climates ($p = .97$). However, subjects experienced significantly higher total energy expenditures in cold climates ($p < .0001$), expending an additional ~1550 kcal day^{-1}. There is a significant interaction between physical activity and thermoregulation, such that physical activity reduces thermoregulatory costs in cold climates, but increases it in hot climates.

Conclusions: Dissection of the energy budget revealed that total energy expenditure is significantly higher in cold climates. This is due to a combination of high levels of physical activity and high thermoregulatory costs. High levels of physical activity may substantially lower the cost of thermoregulation in cold climates, and this interaction should be taken into account when estimating TEE.

KEYWORDS
activity, energetics, extreme climates, flex-heart rate method, basal metabolic rate, thermic effect of food, thermoregulation, total energy expenditure

1 | INTRODUCTION

Much of the information on the impact environmental factors such as climate and altitude have on human total energy expenditure (TEE kcal day^{-1}) comes from laboratory and fieldwork among indigenous populations (Leonard et al., 2002, 2005, McArdle et al., 1984a, b; Moran 2008; Sloan & Keatinge 1973; Snodgrass et al., 2005, 2006, 2008; StrØmme et al., 1963). This has provided detailed knowledge of the different components of TEE, such as basal metabolic rate (BMR), physical activity, and thermoregulation. However, how these components interact with one another, and how humans adjust energy allocation under different climatic conditions outside of the laboratory is still poorly understood. The work here presents a within-subjects analysis of TEE among a group of highly physically active humans living in hot, cold, and temperate environments of the western United States. Their energy budgets are dissected into four main components: BMR, thermoregulation, physical activity, and the thermic effect of food (TEF). Finally, the energy expenditure and energy allocation differences are analyzed for each climate.

Laboratory studies and fieldwork among indigenous circumpolar populations such as the Inuit and Yakut have found an increased BMR in response to cold temperatures (Leonard et al., 2002, 2014; McArdle

Abbreviations: TEE, total energy expenditure; BMR, basal metabolic rate; Flex-HR, Flex-Heart Rate; NOLS, National Outdoor Leadership School; AIM, Allocation and Interaction Model; TEF, thermic effect of food; EAA, Energy and Activity assessment.

TABLE 1 NOLS course location summary

Course	*N*	Climate	EAA location	Duration of EAA (days)
NS1	14	Temperate	Absaroka Mountain Range, WY	11
		Hot	City of Rocks, ID	6
NS2	11	Temperate	Absaroka Mountain Range, WY	11
		Hot	Devil's Tower, WY	6
FS5	14	Temperate	Wind River Range, WY	7
		Cold	Absaroka Mountain Range, WY	7
FS8	14	Temperate	Wind River Range, WY	8
		Cold	Absaroka Mountain Range, WY	7
Pilot	6	Temperate	Wind River Range, WY	6

et al., 1984a,b; Moran, 2008; Sloan & Keatinge, 1973; Snodgrass et al., 2005, 2006, 2008; StrØmme et al., 1963; Tilkens et al., 2007). Peripheral vasoconstriction, nonshivering thermogenesis, and behavioral responses (shelter, clothing, and external heat sources) also help maintain core body temperature despite low environmental temperatures (Moran, 2008; Stocks et al., 2004). In hot conditions sweating, vasodilation, and changes in BMR help to maintain core body temperature (Chinevere et al., 2008; Hori, 1995; Osiba, 1957; Shapiro et al., 1980). BMR has been documented to increase in hot, humid environments but decrease in hot, dry environments (Chinevere et al., 2008; Hori, 1995; Osiba, 1957; Shapiro et al., 1980).

The importance of the contribution physical activity makes to total energy expenditure has recently come into question. Work among the Hadza and a meta-analysis comparison of adults from industrialized and developing countries present the possibility of an upper bound to adult human energy expenditure in the face of high levels of physical activity. It also highlights the important of that physical activity for health and successful weight loss (Dugas et al., 2011; Pontzer et al., 2012, 2016).

Although its contribution to total energy expenditure may be questionable, laboratory evidence suggests that physical activity may be important for maintaining core body temperature during extreme temperature exposure (McArdle et al., 1984a,b; StrØmme et al., 1963; Tikuisis et al., 2000; Toner et al., 1986). In hot climates, the risk of hyperthermia associated with exercise is relatively well studied compared to cold climate studies (Montain et al., 1994; Raynaud et al., 1976; Rivera-Brown et al., 2007). Investigation of the interaction between thermoregulation and physical activity in cold climates has been limited to the laboratory. When Tikuisis et al. (2000) immersed men and women in cold water they found a decrease in body temperature despite a three-fold increase in metabolic rate. However, exercising while still immersed seemed to mitigate that drop in body temperature (Tikuisis et al., 2000; Toner et al. 1986). Active muscle, whether through physical activity or shivering, can add to heat production, helping to combat cold conditions (McArdle et al., 1984a,b). However, to date no work has been done to assess this interaction between physical activity and thermoregulation among people living for extended periods in natural conditions in cold or hot climates.

The work here presents data on TEE and its components among highly active people living in natural temperate, hot, and cold environments. The TEE budget as a whole is analyzed and dissected it into its various components: BMR, physical activity, thermoregulation, and the TEF. This analysis is used to test two hypotheses:

1. Inhabiting a cold climate is more expensive, after taking into account differences in physical activity, than inhabiting temperate or hot climates.
2. Physical activity decreases thermoregulatory costs in cold climates but increases it in hot climates.

2 | SUBJECTS AND METHODS

2.1 | Subjects

Participants included 59 healthy, unacclimated volunteers (40 males, 19 females, 18–44 years old) from the United States. Subjects were taking part in 12–16 week courses with the National Outdoor Leadership School (NOLS) in Wyoming, Utah, and Idaho, U.S., in 2010 and 2011. NOLS provided logistical support for field data collection. Two of the courses, NS1 and NS2, lasted 12 weeks and took place during the spring and summer ($n = 25$). The other two courses, FS5 and FS8, lasted 16 weeks in the fall and winter ($n = 28$). NS1 and NS2 experienced temperate and hot climates. FS5 and FS8 experienced temperate and cold climates. Six subjects were part of a pilot study (named Pilot) that took place in summer of 2010 (Table 1). There was no overlap between subjects across the different courses; each course is an independent sample. The Institutional Review Board of Washington University, St. Louis, approved this study and subjects gave informed consent prior to participation (IRB Protocol 201104106).

2.2 | Field settings

NOLS is a US-based, not-for-profit outdoor education program that offers its students a chance to live in the wilderness for an extended period of time. The core curriculum includes outdoor survival skills, leadership, risk management, and environmental studies. The majority of individuals who took part in the NOLS courses included in this study were college students looking to either improve their backcountry expedition skills or earn college credit.

Subjects took part in two types of data collection. The first, Calibration, consisted of BMR, heart rate calibration, weight, height, and bioelectrical impedance measurements. These data were collected three times throughout each course. The second type of data collection, the Energy and Activity Assessment (EAA), consisted of in-field heart rate, body weight, food diary, activity diary, and daily temperature data collection. The EAA data were collected twice during each course for 6–11 days, once during the temperate regime and once during the extreme, either hot or cold, regime (Table 1).

The typical schedule for a NOLS course began with students arriving in Lander, WY before they embarked on their backcountry experience. Students prepared their gear and rations at this time as well as met their course-mates and instructors. It was during this time that the first Calibration was performed. Students then left for the temperate section of their course. All four courses, as well as the Pilot, took part in a temperate climate. During this time, subjects took part in extensive daily hiking and beginner mountaineering. Subjects carried all of their equipment and food in backpacks during this section, camping at a new location almost daily. After they had spent two weeks in this condition, the EAA data collection was performed over 6–11 days.

Students finished the first section of their course and returned to Lander, WY, changed gear for a different climate, and replenished rations. During this time the second Calibration was performed. Subjects left for the second section of their course, in either a hot or cold climate. Hot climates, courses NS1 and NS2, consisted of hiking, top rope climbing, lead climbing, multi-pitch climbing, and bouldering. These subjects stayed camped at the same location. Cold climates, courses FS5 and FS8, consisted of cross-country skiing or snow shoeing with their gear and food, shoveling snow, and downhill skiing. Similar to the temperate climates, subjects frequently camped in different locations. Once the courses had been in their respective climates for two weeks, the second EAA for six-to-eight days was performed. Upon finishing their courses, subjects returned to Lander, WY where the third Calibration was performed. Each course also took part in additional NOLS curriculum including river rafting and kayaking; however, for the sake of non-water-proof equipment, data were only collected for the sections described above. The Pilot took place only in the temperate climate and consisted of daily hiking and mountaineering. They would camp in the same location for a few nights at a time. A summary of the courses, subjects, and locations can be found in Table 1.

2.3 | Metabolic measurements

2.3.1 | Basal metabolic rate

BMR was collected from each subject using a portable respirometry unit (Cosmed K4b2, Chicago, IL) following standard practice (Gayda et al., 2010). This system measures oxygen consumption and carbon dioxide production using a breath-by-breath analysis. BMR measurements were taken, as part of the Calibrations, in the morning before subjects had their first meal. Subjects were in a supine position on foam pads placed on the floor, in a temperature controlled room, and rested 15–20 min before measurements were taken. Measurements were taken for 6–8 min. Once steady state was observed by monitoring the live data collection with the Cosmed software, the last 4 min of that measurement were averaged to determine BMR.

2.3.2 | Flex-HR measurements

Heart rate was measured using a chest-strap monitor worn continuously for two weeks; data were logged using ActiTrainer devices (Actigraph, Pensacola, FL) worn on the hip. To convert heart rate to energy expenditure, a set of calibration measurements were collected for each subject. For the calibration, subjects were asked to stand, walk (1, 1.5, and 2 m s^{-1}), and run (2, 2.5, and 3 m s^{-1}) on a treadmill for 5 min at each speed. Heart rate and metabolic rate were simultaneously collected during this calibration. The Flex-HR flex-point for each subject was calculated as the mean of the highest heart rate at rest and the lowest heart rate during exercise following Leonard (2003). The relationship between heart rate and energy expenditure was calculated as the least-squares regression line for heart rate and energy expenditure. Heart rate was converted to metabolic rate using the equations generated from the calibration following Leonard (2003). In previous research it was found that the Flex-HR method overestimates TEEs above 3000 kcal day^{-1} by 17% among the NOLS population (Ocobock, 2016). This 17% corrected Flex-HR values were used for analysis in this study.

2.4 | Anthropometrics, activity, food, and clothing diaries

Height measurements were collected following standard procedures using a cloth tape in millimeters (Lohman et al., 1988). Body mass, muscle mass, and percent body fat were measured using a Tanita BC-558 Ironman Segmental Body Composition Monitor bioelectrical impedance scale (Tanita Corporation, Arington Heights, IL). The athletic setting was chosen for these measurements due to the increased fitness achieved throughout courses and to maintain measurement consistency. The Tanita equations are unpublished.

Subjects were asked to keep activity and food diaries for the duration of the EAA. Subjects reported activity type (hiking, walking, climbing, cross country skiing, shoveling snow), distance or duration of activity, and estimated backpack weight during activity. Activity logs were compared to course instructor official travel logs, official course maps, and NOLS curricula travel schedules to ensure accuracy. Subjects also reported type and quantity of food eaten. Data from the food logs were transcribed into Microsoft© Excel© for Mac 2010, and calories were calculated (Ocobock, 2016). In the temperate climate, subjects ate mostly dried goods such as pasta and lentils. During the early portions of the temperate climate, they also consumed cheese and summer sausage. In the hot climates, subjects had access to coolers, ice, and gas station markets; they were able to consume more meat and dairy products. Similarly, in the cold climates, with access to abundant snow and ice, subjects kept and consumed more meat and dairy. Subjects also documented the clothing they took with them including the brand and garment name.

TABLE 2 EAA temperatures

Course	Climate	Minimum (°C)	Maximum (°C)	Mean (°C)
NS1	Temperate	1.2	42.1	15.6
	Hot	15.1	45.1	23.3
NS2	Temperate	0.3	39.2	13.5
	Hot	15.4	46.7	23.5
FS5	Temperate	−2.1	30.3	6.2
	Cold	−17.5	17.0	−4.9
FS8	Temperate	0	41.1	14.0
	Cold	−26.8	14.8	−9.4
Pilot	Temperate	−3.3	25	12.8

2.5 | Temperature data

Environmental temperature was measured using an Extech RHT10 Humidity and Temperature USB Data-logger (Extech Industries, Nashua, NH) carried by the course instructors. This device measured and recorded temperature and humidity on a minute-by-minute basis. Temperature data were downloaded using the Extech software (Extech Industries, Nashua, NH). High, low, and mean temperatures were calculated for each day as well as averaged across the EAA for each climate (Table 2).

2.6 | Allocation and interaction model TEE estimates

The Allocation and Interaction Model (AIM) was previously validated using the doubly labeled water and flex-heart rate methods (Ocobock, 2016). AIM takes the general form of:

$$\mathrm{TEE} = \mathrm{BMR} + E_{\mathrm{activity}} + E_{\mathrm{therm}} + \mathrm{TEF}$$

BMR measurements were taken, as described above, and used in this equation. E_{activity} was estimated using specific equations for walking, running, climbing, hiking, cross country skiing, downhill skiing, shoveling snow, swimming, yoga, and light calisthenics from the literature (Ocobock, 2016). Activity type and duration were determined from subjects' daily activity logs activity. Thermoregulation, E_{therm}, was calculated using the COMFA Thermal Outdoor Comfort Model (Kenny et al., 2009). Activity and thermoregulation estimates included body mass in their calculations; the body mass collected during each climate EAA was used to estimate these variables. TEF was estimated to be 10% of caloric intake (Kinabo & Durnin, 1990). TEE and each of its components were estimated for each subject in the temperate and extreme environments.

2.7 | Total energy expenditure and thermoregulation without physical activity costs

To analyze the impact physical activity had on the total energy expenditure budget thermoregulatory costs were estimated with zero activity assumed so that there was no benefit from heat produced from physical activity. If core body temperatures were maintained through only physiological thermoregulatory mechanisms, then a significant difference between climates would be expected. However, if a combination of thermoregulation and heat produced through physical activity maintained core body temperature, as suggested by Tikuisis et al. (2000), then no significant difference would be expected between climates once physical activity costs were removed from TEE.

2.8 | Statistical analysis

Plots were generated using Microsoft© Excel© for Mac 2010 and RStudio, ©RStudio 2009–2012. Linear regressions controlling for age, sex, fat free mass, and height followed by Tukey's pair-wise comparisons with Bonferroni corrections were used to compare total energy expenditures between climates. Paired student's T-tests were used to analyze total energy expenditure between climates within each subject. The differences in the energy allocation between climates were analyzed using a repeated measures ANOVA. Mauchly's Test for Sphericity was performed and revealed that the differences between the variances were not equal ($p < .001$). The adjusted within subjects test, Greenhouse-Geisser, was performed and revealed a significant interaction between the component of TEE and climate; the impact of climate depends on the component being analyzed ($p < .001$).

To determine how climate impacts each component two analyses were performed. A One-way ANOVA was performed for the TEE components that meet the assumptions of Levene's Test for Homogeneity. The variables that meet these assumptions were the proportion of TEE comprised by TEF and the absolute cost values for TEF. The remaining TEE components (proportion of TEE comprised of activity, thermoregulation, and BMR; and the absolute cost values of activity and thermoregulation) failed Levene's Test for Homogeneity, and were analyzed using non-parametric analyses. Kruskal-Wallis tests were completed first, and for those components with significant results, the post-hoc Dunn-Bonferroni test was performed. A One-way ANOVA was performed to determine if there was a difference in thermoregulation costs with and without the heat of activity included. All statistical analyses using IBM© SPSS© Version 21 were used. Results were considered significant at $p < .05$.

3 | RESULTS

3.1 | Flex-HR TEE measurements and BMR

3.1.1 | Total energy expenditure

As measured by the Flex-HR Method, subjects expended a mean daily TEE of 3563 ± 804 kcal day^{-1} for temperate climates, 3633 ± 765 kcal day^{-1} for hot climates and 4780 ± 1647 kcal day^{-1} for cold climates. Figure 1 shows the range of TEE values for temperate, hot, and cold climates. The TEE values from the Flex-HR method were similar to those measured by the doubly labeled water method (Ocobock, 2016). A multiple regression controlling for age, sex, mass, and height for the corrected Flex-HR TEE values was performed with Tukey's pair-wise comparisons ($F = 10.882$, $p < .001$). There was no significant difference between subject TEEs in temperate and hot climates ($p = .97$), but subjects experienced significantly higher TEEs in cold climates ($p < .01$ for

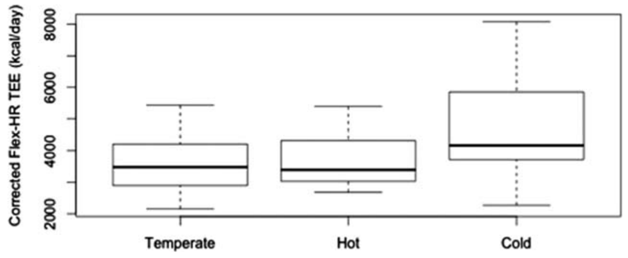

FIGURE 1 Corrected flex-HR measured mean total energy expenditure (kcal day^{-1}) for each subject in temperate, hot, and cold climates during the data collection period

both temperate and hot climates, Bonferroni corrected $\alpha = 0.017$). Subjects expended an additional ~1550 kcal day^{-1} in cold climates.

3.1.2 | Basal metabolic rate

BMRs had a mean of 2176 ± 550 kcal day^{-1} for temperate climates, 2251 ± 460 kcal day^{-1} for hot climates, and 2898 ± 855 kcal day^{-1} for cold climates (Figure 2). Multiple regression analysis was performed controlling for age, sex, mass, and height for BMRs with Tukey's pair-wise comparisons ($F = 11.570$ $p < .001$). There was no significant difference between BMR in temperate climates and hot climates ($p = .790$), but subjects in cold climates had significantly higher BMRs ($p < .001$, Bonferroni corrected $\alpha = 0.017$).

3.2 | Total energy expenditure allocation

The mean daily breakdown of energy expenditure between BMR, activity, thermoregulation, and TEF in the three different climates are discussed below and can be seen in Figure 3A–C. Table 3 summarizes the mean metabolic cost (kcal day^{-1}) for each component of the TEE budget for the three different climates.

3.2.1 | Thermic effect of food

TEF costs, which are estimated as 10% of total caloric intake, had a mean of 254 ± 70 kcal day^{-1} for temperate climates, 250 ± 75 kcal day^{-1} for hot climates, and 282 ± 77 kcal day^{-1} for cold climates (Figure 4**A**). A multiple regressions analysis controlling for age, sex, mass, and height was performed for TEF with Tukey's pair-wise comparisons was performed ($F = 1.294$, $p = .279$). There was no significant difference between any of the climates (One-way ANOVA, $p = .256$).

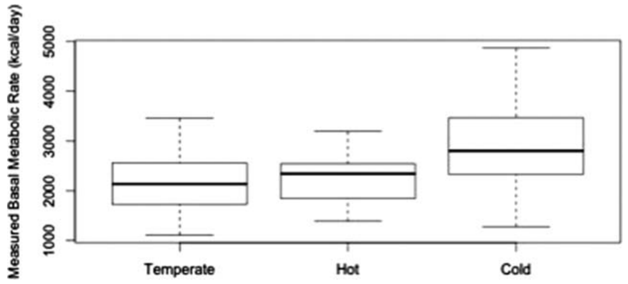

FIGURE 2 Basal metabolic rates (kcal day^{-1}) for the three climates

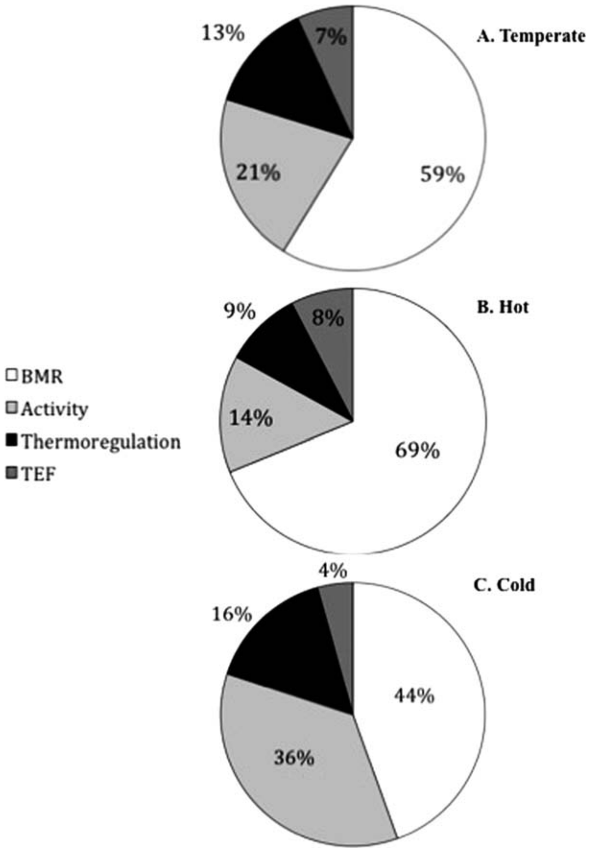

FIGURE 3 Energy allocation (kcal day^{-1}) in (A) temperate, (B) hot, and (C) cold climates

3.2.2 | Physical activity

Mean estimated physical activity costs were 780 ± 261 kcal day^{-1} for temperate climates, 465 ± 176 kcal day^{-1} for hot climates, and 2316 ± 502 kcal day^{-1} for cold climates (Figure 4B). Activity levels were significantly different between all the climates. Cold climate activity was significantly higher than the temperate climate, which was significantly higher than in the hot climate (Kruskal-Wallis with post-hoc Dunn-Bonferroni, $p < .001$). The proportion of energy allocated to physical activity was significantly different in each climate. Physical activity made up a significantly higher proportion of TEE in the cold climate (Kruskal-Wallis with post-hoc Dunn-Bonferroni, $p < .001$).

3.2.3 | Thermoregulation

Estimated heat gained from physical activity was sufficient to have a substantial effect on estimated thermoregulatory costs. When the heat gained from physical activity is included in thermoregulatory burden following the AIM model (Ocobock, 2016), estimated costs were 494 ± 173 kcal day^{-1} for temperate climates, 306 ± 38 kcal day^{-1} for hot climates, and 1018 ± 310 kcal day^{-1} for cold climates (Figure 4C). When heat gain from physical activity is ignored, estimated thermoregulatory costs are 23% greater for temperate climates (585 ± 106 kcal day^{-1}) and 29% greater for cold climates (1428 ± 432 kcal day^{-1}) but 30% lower for hot climates (237 ± 27 kcal day^{-1}; Figure 5, Table 4).

TABLE 3 TEE component summary, mean metabolic cost of the four TEE components BMR, activity (E_{act}), thermoregulation (E_{therm}), and TEF included in this study

Climate	Temperature (°C)	*N*	Mass (kg)	BMR (kcal day^{-1})	E_{Act} (kcal day^{-1})	E_{Therm} (kcal day^{-1})	TEF (kcal day^{-1})
Temperate	12.3 ± 1.8	59	73.4 ± 11.3	2176 ± 550	780 ± 261	494 ± 173	254 ± 70
Hot	23.7 ± 2.0	22	73.5 ± 9.9	2251 ± 460	465 ± 176	306 ± 38	250 ± 75
Cold	−7.6 ± 4.2	23	75.8 ± 10.6	2898 ± 855	2316 ± 502	1018 ± 310	282 ± 77

A summary of the thermoregulatory costs with (Figure 4C) and without activity (Figure 5) can be found in Table 4.

Regardless of the approach used to estimate thermoregulatory costs, cold climate thermoregulation was significantly more costly than in the temperate climate condition, which in turn was significantly higher than thermoregulation cost in the hot climate (Kruskal-Wallis with post-hoc Dunn-Bonferroni, $p < .001$). Thermoregulation comprised significantly more of TEE in the cold climate than the temperate climate, and the temperate climate significantly more than in the hot climate (Kruskal-Wallis with post-hoc Dunn-Bonferroni, $p < .001$).

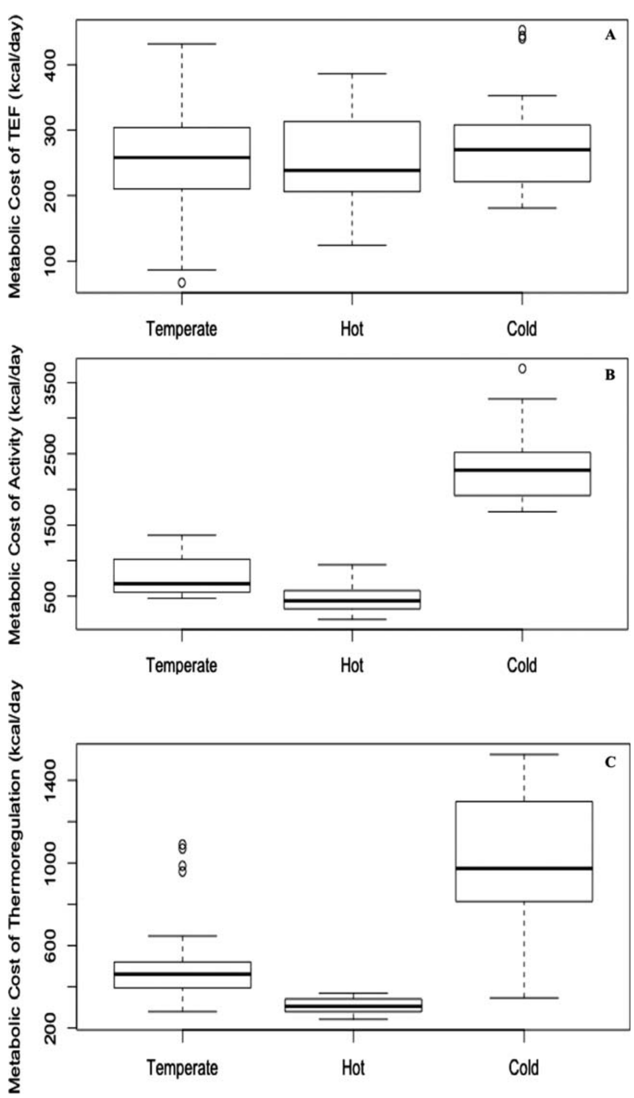

FIGURE 4 Estimated activity (A) thermic effect of food (kcal day^{-1}), (B) physical activity (kcal day^{-1}), and (C) thermoregulation costs (kcal day^{-1})

4 | DISCUSSION

Humans exposed to extreme hot or cold environments incur greater metabolic costs. Generally, increases in BMR and thermoregulatory costs are the driving force behind this (Leonard et al., 2002, 2005; McArdle et al., 1984a,b; Moran, 2008; Sloan & Keatinge, 1973; Snodgrass et al., 2005, 2006, 2008; StrØmme et al., 1963). However, the interaction of the other components of TEE in extreme temperatures is relatively unknown. In this study, high levels of physical activity lead to high TEE. Furthermore, this high level of physical activity impacts thermoregulatory costs in hot and cold climates, increasing them in the former and decreasing them in the latter. This important interaction should be taken into account when estimating TEE.

4.1 | Energy allocation in different climates

NOLS subjects were able to act as their own control by inhabiting temperate climates before entering hot or cold climates. This allowed for an analysis of how TEE budgets and energy allocation differed in the three different climates (Figure 3A–C). Overall, subjects experienced significantly higher metabolic costs in cold climates for each of the four components. BMR and TEF made up a significantly greater proportion of the energy budget in the hot climate, but that is due to an overall smaller budget in the hot climate relative to the other climates.

BMR values were about 20% higher than that would be expected from predictive equations (Henry, 2005). It is possible the high observed BMRs were due to short measurement durations, or subjects consuming food before measurements. Altitude could also be a factor

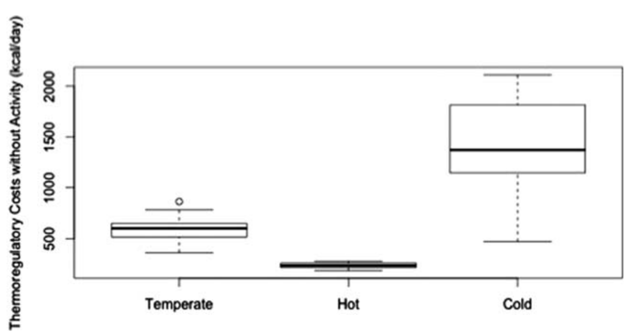

FIGURE 5 Thermoregulatory costs (kcal day^{-1}) estimated using AIM with zero activity assumed. Please refer to Figure 4C for thermoregulatory costs estimated including heat produced from physical activity

TABLE 4 Summary of estimated thermoregulatory costs (kcal day^{-1}) with and without the added heat from physical activity

Climate	Temperature (°C)	N	Mass (kg)	E_{Therm} with physical activity (kcal day^{-1})	E_{Therm} without physical activity (kcal day^{-1})
Temperate	12.3 ± 1.8	59	71.4 ± 9.5	494 ± 173	585 ± 106
Hot	23.7 ± 2.0	22	75.8 ± 8.7	306 ± 38	237 ± 27
Cold	−7.6 ± 4.2	23	73.6 ± 10.1	1018 ± 310	1428 ± 432

in the high BMRs. Measurements were taken at ~1500m, and there is a known increase in BMR with increasing altitude (Frisancho, 1993; Moran, 2008). However, all BMR measurements were taken at the same altitude, and BMR remained high well after the typical high altitude acclimatization period (Frisancho, 1993) Furthermore, cold temperatures have been shown to increase BMR by as much as 30% (Leonard et al., 2002, 2014; McArdle et al., 1984a,b; Moran, 2008; Sloan & Keatinge, 1973; Snodgrass et al., 2005, 2006, 2008; StrØmme et al., 1963; Tilkens et al., 2007). Another consideration is that an increase in BMR could be a response to tissue damage incurred during the course. Dolezal et al (2000) demonstrated that resting metabolic rate increases in the 48 hr following intense exercise, a cost associated with tissue repair. Since the NOLS students were taking part in continuous extreme physical activity, the observed increase in BMR is a typical response to exercise induced tissue damage. The increase in BMR due to environmental temperature and tissue repair is not taken into account in BMR predictive equations. Furthermore, individuals planning wilderness expeditions should be aware of BMR underestimations, particularly in extreme conditions, when calculating rations.

Activity levels were also significantly higher in the cold climate than in temperate or hot climates. Physical activity comprised more than a third of the TEE budget in cold climates, whereas it was only one fifth and one sixth of the temperate and hot energy budgets respectively. This greater level of physical activity in the cold climate is likely the result of navigating the difficult winter environment.

The Rocky Mountains in the winter are not an easy place to survive. Traveling without motorized technology requires cross-country skiing or snow shoeing. Both of these activities are more metabolically demanding than locomotion in non-snow covered landscapes. Even once NOLS subjects reached their destinations, their environment demanded a great deal of physical activity. In order to set up camp for the night, subjects had to shovel snow for several hours to protect their tents and gear from high winds and snowfall. Shoveling snow is also an extremely metabolically demanding activity (Ainsworth et al., 2000). This suggests that the high activity levels experienced by the NOLS subjects were not merely an artifact of the course curriculum, but a representation of the demanding lifestyle of cold climate inhabitation.

4.2 | Interaction between thermoregulation and physical activity

This study indicates that heat production from physical activity can have a large impact on estimated thermoregulatory costs. This impact is evident by predicted TEE more closely matching observed TEE when the heat from physical activity is incorporated into the TEE predictive models. Alternatively, when heat from physical activity is not included, predicted TEE is ~10% higher in cold climates. High levels of physical activity under cold conditions have been implicated in laboratory studies as a mechanism for reducing physiological heat production (Tikuisis et al., 2000; Toner et al., 1986). Work here suggests that heat produced through physical activity can be an effective means of maintaining core body temperature, reducing the potential metabolic cost of thermoregulation in natural cold conditions (Tikuisis et al., 2000; Toner et al., 1986). In hot climates, physical activity had the opposite effect; it increased the thermoregulatory burden, and risk of hyperthermia, by producing more heat the body needed to dissipate to maintain core body temperature (Moran, 2008; Shapiro et al., 1980).

4.3 | Health implications for high levels of total energy expenditure

Recent work has questioned the importance of physical activity levels for total energy expenditure and weight loss programs. For example, a recent meta-analysis revealed that though adults in developing countries exhibited a lower body mass index than those from industrialized countries, total energy expenditure did not differ (Dugas et al., 2011). Work among the Hadza observed that despite high levels of physical activity, Hadza total energy expenditure was not significantly different from more sedentary Western populations (Pontzer et al., 2012). These studies have lead to the development of a constrained model of total energy expenditure among adult humans. This model posits that as energy expenditure increases with increasing levels of physical activity, adults will adapt to keep total energy expenditure within a restricted range, thus lowering their total energy expenditure (Pontzer et al., 2016).

This model has gained support from a recent, popular study among former "The Biggest Loser" contestants (Fothergill et al., 2016). This study demonstrated that contestants experienced a reduced resting metabolic rate in response to an extremely restrictive diet, high levels of physical activity, and significant weight loss. Despite regaining much of the weight they had lost, participants still experienced the reduced resting metabolic rate six years after they participated on "The Biggest Loser" (Fothergill et al., 2016). This suggests the persistence of a metabolic adaptation and exemplifies how the narrow range of total energy expenditure can be down-shifted in response to extreme diet and exercise, but struggle to recover. The data collected among the NOLS population indicated a sustained level of physical activity and total energy expenditure; energy expenditure did not plateau as the constrained model for TEE would suggest, but increased in cold climates. At face value, these data do not support this new model. However, the participants in this study were living in ever changing environments, which required different types and intensities of physical activity; perhaps providing the exception that supports the constrained total energy expenditure rule. This suggests that a possible way to avoid a metabolic adaptation and downward shift in total energy expenditure range is to increase the variation in physical activity levels and conditions to which the body is exposed. . .in other words, keep the body guessing. The concept and benefit of altering exercise routines and diet at regular intervals is well known and frequently practiced in resistance training (Kraemer & Ratamess, 2004). However, it will take longitudinal studies focused on altering comprehensive diet and exercise programs to determine if this an effective means of achieving sustained weight loss without a metabolic adaptation.

5 | LIMITATIONS

First, the Cosmed k4b2 has been known to overestimate BMR (Duffield et al., 2004). This overestimation would affect both the BMR measurements and heart rate calibrations. Second, the three climates had different levels of physical activity. For example, the hot climates were relatively inactive compared to the temperate and cold climates. It would be better to have a standard level of activity; however, this study had to fit within the confines of the NOLS curricula.

6 | CONCLUSION

This work attempts to address some of the gaps in our current understanding of human total energy expenditure and explore the impact environmental factors can have on total energy budget and energy allocation. Living in a cold climate is physically demanding and metabolically expensive. The NOLS population not only experienced an increased BMR and thermoregulatory costs, but also took part in high levels of physical activity. These high levels of physical activity can reduce thermoregulatory costs in cold climates and increase thermoregulatory costs in hot climates. Without physical activity, thermoregulatory costs would be detrimentally high in cold climates. This is the first demonstration of this important interaction among humans living in natural cold environments. Furthermore, this shows the utility of the Allocation and Interaction Model to not only dissect total energy expenditure into its component parts, but to also estimate energy expenditure within different hypothetical parameters. AIM enables analysis of the interaction between these different components and can be used to assess how different populations in different environments use their energy.

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