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Original Research Article

The Allocation and Interaction Model: A New Model for Predicting Total Energy Expenditure of Highly Active Humans in Natural Environments

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Objective: The purpose of this study was to develop a new model, the Allocation and Interaction Model (AIM), to better predict human total energy expenditure (TEE) among a group of highly active humans living in a variety of natural environments. AIM estimates were tested to determine if it produces more accurate TEE predictions than the Factorial Method.

Methods: AIM includes metabolic cost terms for basal metabolic rate, thermoregulation, and the thermic effect of food, as well as more accurate activity cost estimations. AIM was tested using doubly labeled water and Flex-Heart Rate (Flex-HR)-measured TEEs of healthy, highly active adults ($N = 59$) participating in National Outdoor Leadership School semester-long courses. Data from a month-long pilot study ($N = 6$) were also included.

Results: AIM produced TEE estimates that were not significantly different from measured energy expenditure values. Overall, AIM came within 4.1% of measured values; the Factorial Method underestimated by over 25%. At TEEs greater than 3,000 kcal day^{-1}, AIM underestimated TEE by 11% compared to 31.6% by the Factorial Method. Also, at TEEs greater than 3,000 kcal day^{-1}, the Flex-HR method overestimated TEE by 17%.

Conclusions: This analysis demonstrated that AIM is more accurate than the Factorial Method for predicting TEE across a range of climates and physical activity levels. This suggests that AIM should be used in place of the Factorial Method for estimating human TEE. Am. J. Hum. Biol. 28:372–380, 2016.

INTRODUCTION

Models that predict human total energy expenditure (TEE, kcal day^{-1}) are used to develop energy and nutrition standards as well as estimate TEE among industrialized and nonindustrialized populations (Aiello and Wheeler, 2003, Dufour and Piperata, 2008; FAO/WHO/UNU, 2001; Katzmarzyk et al., 1996; Leonard et al., 1995, 1997; Spurr et al., 1996). They have also been applied to produce energy expenditure estimates for past populations (Froehle and Churchill, 2009; Leonard and Robertson, 1997, Steudel-Numbers and Tilkens, 2004). The currently recommended, and most frequently used, model for predicting TEE without physiological measurements is the Factorial Method (FAO/WHO/UNU, 1985, 2001). However, the Factorial Method consistently underestimates TEE (Durnin, 1990; Haggarty et al., 1994, Leonard et al., 1995, 1997; Roberts et al., 1991; Spurr et al., 1996).

The Factorial Method estimates TEE by summing the energetic cost of basal metabolic rate (BMR) and activity throughout the day. Each activity cost is estimated as a multiple of BMR based on activity intensity (FAO/WHO/UNU, 1985, 2001). Comparisons with TEE measurements using the doubly labeled water (DLW) and Flex-Heart Rate (Flex-HR) methods have found that the Factorial Method underestimates TEE by 16–22% (Leonard et al., 1995, 1997; Roberts et al., 1991). These underestimations can be as great as 30% among highly active populations. It has been suggested that discrepancies in BMR and physical activity cost estimations are the root of this underestimation (Leonard et al., 1997). Furthermore, the Factorial Method does not include cost estimates for thermoregulation nor the thermic effect of food (TEF), both of which can comprise a significant proportion of TEE. Thermoregulatory demands are known to increase BMR among indigenous cold populations by as much as 20% (Leonard et al., 2005; Snodgrass et al., 2005, 2006, 2008). TEF compromises roughly 10% of the overall TEE budget of a person in energy balance (Kinabo and Durnin, 1990).

Although these are well-established concerns, little effort has gone into producing a new model that better represents TEE and its multiple interacting components. The primary goal of the work presented here is to produce an accurate model for predicting human TEE over a range of climates and physical activity levels (PALs). The new model presented here, the Allocation and Interaction Model (AIM), improves upon current methods by including interacting cost terms for BMR, physical activity, thermoregulation, and the TEF. The general form of this model is:

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

where BMR is basal metabolic rate, E_{activity} is the metabolic cost of physical activity, E_{therm} is the metabolic cost of thermoregulation, and TEF is the thermic effect of food. Although AIM is a factorial type of model, it allows for interactions among its components, which have been shown to significantly impact TEE in extreme conditions such as cold climates (Steegmann, 2007).

Here, I present AIM. I then test it using a population of highly active adults living outdoors in temperate, hot, and cold climates taking part in National Outdoor Leadership

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TABLE 1. A summary of the total number of subjects, the number of subjects taking part in the different measurements

Course	N	Course duration	Climate	Mean temp. (°C)	Flex-HR participants	DLW participants	EAA location	Duration of EAA
NS1[a]	14	6/2/11–8/10/11	Temperate	15.6	14	1	Absaroka Mountain Range, WY	11
			Hot	23.3	14	1	City of Rocks, ID	6
NS2[a]	11	6/4/11–8/12/11	Temperate	13.5	11	1	Absaroka Mountain Range, WY	11
			Hot	23.5	11	1	Devil's Tower, WY	6
FS5	14	9/4/11–12/3/11	Temperate	13.8	14	1	Wind River Range, WY	7
			Cold	−4.9	12	1	Absaroka Mountain Range, WY	7
FS8[a]	14	9/8/11–12/10/11	Temperate	14.2	14	1	Wind River Range, WY	8
			Cold	−9.4	14	1	Absaroka Mountain Range, WY	7
Pilot	6	7/1/10–8/4/10	Temperate	12.8	6	3	Wind River Range, WY	6

[a]Indicates courses for which the same subject participated in the DLW measurements for both the temperate and extreme climate.

School (NOLS) courses. I used the Flex-HR and DLW methods to measure TEE. First, I compare TEE of the NOLS population to Western and indigenous populations to ensure that they are more physically active, to better test the accuracy of AIM at high levels of TEE where the Factorial Method traditionally fails. Second, as the Flex-HR method has not been validated at high levels of TEE, I compare Flex-HR measurements to DLW measurements. Finally, I compare AIM and the Factorial Method TEE predictions to DLW and Flex-HR method TEE measurements. I demonstrate that the Flex-HR method needs further evaluation at high levels of activity, and that AIM is an accurate new tool for predicting human TEE.

SUBJECTS AND METHODS

Subjects

Participants included 59 healthy volunteers (40 males, 19 females, aged 18–44 years) from four 12- to 16-week courses and one 5-week outdoor education course in the western United States in 2010 and 2011. The Institutional Review Board of Washington University, St. Louis, (IRB protocol 201104106) approved this study and subjects gave informed consent prior to participating.

NOLS operated these courses and provided logistical support for field data collection. Two of the courses ($N = 25$) were in the spring and summer, course names NS1 and NS2, that lasted 12 weeks, and two ($N = 28$) were in the fall and winter that lasted 16 weeks, course names FS5 and FS8. An additional six subjects took part in a shorter (5 weeks) pilot study that I conducted during the summer of 2010. This resulted in five separate courses taking place in three different conditions. The NS1 and NS2 course participants experienced temperate (mean 14.6°C) and hot (mean 23.4°C) climates, FS5 and FS8 participants experienced temperate (mean 14.0°C) and cold (mean −7.2°C) climates, and the Pilot study took place solely in a temperate climate (mean 12.8°C).

Data collection

All subjects ($N = 59$) took part in two types of data collection. The first consisted of BMR, heart rate calibration, anthropometric, and bioelectrical impedance measurements; this is referred to as Calibration. I collected these data three times throughout the semester long course: before the course began (Calibration 1), in between temperate and extreme climate (hot or cold) regimes (Calibration 2), and at the end of the course (Calibration 3). The second type of data collection consisted of in-field heart rate, DLW, food diary, activity diary, and daily temperature data collection. I collected these data twice during each semester course, once during the temperate regime and once during the extreme, either hot or cold, regime. This data collection is referred to as the Energy and Activity Assessment (EAA) (Table 1).

Data collection settings

The 12- to 16-week courses, Pilot study excluded, followed a similar schedule. Subjects arrived at the NOLS headquarters in Lander, WY, and spent several days there to meet their course mates and instructors as well as prepare gear and rations for the first of the three sections of their semester. NS1 and NS2 ($N = 25$) arrived in Lander in late May 2011. During this time, I performed Calibration 1 with NS1 and NS2. They embarked on the temperate climate portion of their course in early June in the Absaroka Mountain Range, WY, which consisted of hiking. After subjects had been in the field for 2 weeks, I met them to conduct the EAA for 11 days. After another 2 weeks, the NOLS students finished the hiking portion of their semester and returned to Lander, WY to change and refurbish their gear and rations. During this time, I conducted Calibration 2.

The second portion of the semester consisted of rock climbing at the City of Rocks, ID (NS1) and Devils Tower, WY (NS2) in late July 2011, this comprised the hot climate portion of the study. Similarly, I conducted the EAA for 6 days after subjects had been at these new locations for 2 weeks. Once the remainder of the hot climate course was complete, subjects returned to Lander, WY for one final gear change and ration replenishment, during which time I conducted Calibration 3. The third portion of the semester involved kayaking and river rafting based out of Vernal, UT. I did not perform the EAA during this portion given the extremely high risk of nonwater proof equipment being fully submerged in river water.

FS5 and FS8 ($N = 28$) followed a similar schedule, however, their courses consisted of a 2-month long temperate climate hiking section and ended with a cold climate cross-country skiing section. Both courses arrived in Lander, WY in early September 2011 during which time they prepared for their course and I performed Calibration 1. They embarked on their temperate climate, hiking section in the Wind River Mountain Range, WY. After 2 weeks in the field, I met each course and performed the EAA for 7 days with FS5 and 8 days with FS8. Once they completed this section of their course, they returned to Lander, WY in mid-November 2011, and I performed Calibration 2. The NOLS students then began the cold climate, cross-country skiing portion of their course in the Absaroka Mountain Range, WY. Once the subjects had been in the field for 2 weeks, I met them to perform the EAA. The students finished their course, and I performed Calibration 3 in early- to mid-December 2011 in Lander, WY.

The Pilot study ($N = 6$) consisted of a five weeklong course, which took place entirely in the Wind River Mountain Range, WY in July and August of 2010. This course consisted of hiking and moderate mountaineering in a temperate climate. Subjects from the Pilot study arrived in Lander, WY in late June for several days of course preparation during which time I performed Calibration 1. Once subjects were in the Wind River Mountain Range, WY for 2 weeks, I met them to perform the EAA for 6 days. Subjects finished the rest of their course and returned to Lander, WY where I performed Calibration 2 before subjects left for their respective homes (Table 1).

Metabolic measurements

Basal metabolic rate. BMRs were 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. I took BMR measurements 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 I took measurements. I took measurements for 6–8 min with the last 4 min of the measurement averaged to determine BMR.

Flex-HR measurements. I calculated TEE for each subject from heart-rate data using the Flex-HR method (Leonard, 2003). I measured heart rate using a chest-strap monitor worn continuously for 2 weeks; data were logged using an ActiTrainer device (Actigraph, Pensacola, FL) worn on the hip. To convert heart rate to energy expenditure, I collected calibration measurements for each subject following their BMR measurement. I asked subjects to stand, walk (1, 1.5, and 2 m s^{-1}), and run (2, 2.5, and 3 m s^{-1}) for 5 min at each speed on a treadmill while I recorded heart rate (bpm) and respirometry (kcal min^{-1}) data simultaneously. I determined the Flex-HR flex-point for each subject as the mean of the highest heart rate at rest and the lowest heart rate during exercise following Leonard (2003). I then determined the relationship between heart rate and energy expenditure as the least-squares regression line for heart rate and energy expenditure. Expenditure during sleeping hours was calculated using their BMR value. I filled in missing heart rate values using averaged values (beats/min) calculated from the available data for each day to calculate 24 h Flex-HR TEE predictions. The Flex-HR calibration that took place closest in time to in-field heart rate measurements was used to calculate TEE to take into account changes in body composition and cardiovascular fitness.

Doubly labeled water method. For $N = 8$ subjects, I measured TEE using the DLW method for 6–11 days (Table 1). I measured three subjects twice, once in the temperate climate and once in the extreme hot or cold climate. I measured two subjects from the same course, FS5, only once, one in the temperate climate and one in the cold climate. The subject who participated in the temperate climate DLW measurement opted to not participate during the cold climate DLW measurement. Three subjects from the pilot study took part in one set of DLW measurements. This resulted in 8 total subjects, but 11 DLW measurements.

I gave subjects an oral dose of DLW (116.08–122.62 g; 10% $H_2^{18}O$, 6% ^2H_2O). I rinsed dose bottles with bottled water twice which was also consumed by subjects to ensure the full dose was administered. I collected urine samples prior to the DLW dose, 6–8 h after the dose, and then every other day for the duration of the EAA. I collected urine in clean, dry wax coated paper cups. I filled four 2-ml cryovials (Sarstedt) at each urine sample collection and placed vials in waterproof plastic bags, kept cold in a small soft-pack cooler using pack snow, ice, or mountain river water.

The three DLW samples from the 2010 Pilot study were analyzed with gas-isotope mass spectrometry at the Baylor College of Medicine, under the direction of Dr. William Wong. I analyzed the DLW samples from the five subjects from the full 2011 study using the Cavity Ring-Down Spectrometry system (Picarro, Sunnyvale, CA) at Hunter College in New York. Standard equations for determining CO_2 production and TEE were used and are described elsewhere (International Atomic Energy Agency, 2009). Analyzing samples in two laboratories presents the possibility of variation between the results from the two laboratories. An interlaboratory variation protocol was not performed.

Activity, food, and clothing diaries

I asked subjects to keep activity and food diaries for the duration of the EAA; the duration of this assessment for each course can be found in Table 1. Subjects reported activity type, distance or duration of activity, and backpack weight. Activity logs were compared to course instructor official travel logs, official course maps, and NOLS curricula travel schedules to ensure accuracy. The typical NOLS course schedule consisted of a mix of strenuous activity days and rest days filled with wilderness education curriculum. Activities consisted of hiking and mountaineering in temperate climates; rock climbing and hiking in hot climates; and cross country skiing and snow shoveling in cold climates.

Subjects also reported type and quantity of food eaten. Data from the food logs were transcribed into a Microsoft© Excel© spreadsheet using the *NOLS Cookery* (Pearson, 2004), *NOLS Backcountry Cooking* (Pearson and Kuntz, 2008), and *NOLS Backcountry Nutrition* (Howley Ryan, 2008) to breakdown typical backcountry recipes. The official USDA National Nutrient Database for Standard Reference was used to assign nutritional values and calories to the foods consumed (U.S. Department of Agriculture, Agricultural Research Service, 2012). Calories were summed for each day. I provided collapsible measuring cups to aid measuring accuracy. Subjects also documented the clothing they took with them including the brand and garment name.

Temperature data

I measured temperature using an Extech RHT10 Humidity and Temperature USB Data-logger (Extech

TABLE 2. Activity specific equations for determining the total metabolic cost of activity

Activity	Equation	Unit	Physical activity level[a]
Walking[b]	$4.1M^{-0.449}$	kcal km^{-1} kg^{-1}	3.2
Running[c]	$30.55 + 1.595(M) - 0.9(L_L)$	kcal km^{-1}	4.4
Climbing[d]	$0.1352M + 1.7853$	kcal min^{-1}	5.1
Hiking[e]	$0.14[1.5M + (2.0(M + B)(BM^{-1})^2 + \eta(M + B)[1.5v^2 + 0.35vg]$	kcal min^{-1}	5.1
Cross-country skiing[f]	$0.274Mt$	kcal min^{-1}	5.1
Downhill skiing[g]	$0.162Mt$	kcal min^{-1}	3.8
Digging snow[h]	$6.0Mt$	kcal min^{-1}	5.1
Light swimming[i]	$0.1Mt$	kcal min^{-1}	3.8
Push-ups and sit-ups[f]	$0.08Mt$	kcal min^{-1}	2.8
Yoga[f]	$0.1Mt$	kcal min^{-1}	2.8

M = body mass (kg), L_L = lower limb length, B = backpack weight (kg), η = terrain factor estimated to be 1.20 (26), v = speed (m s^{-1}), g = percent grade of terrain, and t = time (h). Climbing speed estimated at 3.2 m min^{-1} (Booth et al. 1999). Percent grade of the terrain was determined using distance and elevation traveled documented in the activity logs. Hiking speed (m s^{-1}) was determined following Pandolf et al. (1977), and B is the backpack weight (kg). Sources are as follows: [a]FAO/WHO/UNU (2001); [b]Rubenson et al. (2007), [c]Steudel-Numbers and Tilkens, (2004); [d]Booth et al. (1999); [e]Pandolf et al. (1977); [f]McArdle et al. (2001); [g]Audet (1994); [h]Ainsworth et al. (2000); [i]Capelli et al. (1998).

Industries, Nashua, NH) carried by the course instructors. This device measured and recorded temperature and humidity on a minute-by-minute basis. I downloaded temperature data using the Extech software (Extech Industries, Nashua, NH). I calculated high, low, and mean temperatures for each day as well as averaged across the EAA.

Predictive models for daily energy expenditure

Factorial model. I predicted TEE for each subject in each climate using the Factorial Method (FAO/WHO/UNU, 1985). The general form of the Factorial Method is:

$$\mathrm{TEE} = \mathrm{BMR} + \mathrm{Activity}$$

BMR was calculated using existing equations that incorporate age, sex, and body mass (Henry, 2005).

For males: $16.0M + 545$

For females: $13.1M + 558$where M is mass (kg). These equations were chosen for their generalizability, which is ideal for application of this model to multiple populations. I calculated activity costs as PAL values (i.e., a multiple of BMR) based on the intensity of the activity, using a standardized list of activity-specific values (FAO/WHO/UNU, 2001). These values can be found in Table 2. Subjects' activity logs were used to determine type and duration of activities.

The Allocation and Interaction model. I predicted TEE for each subject in each climate using AIM. This model takes the general form of:

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

I calculated BMR following equations from Henry (2005) listed above. E_{activity} was determined by activity-specific cost equations (Table 2). I calculated E_{therm} following the COMFA outdoor thermal comfort model (Kenny et al., 2009). This model is based on first principles of metabolic heat production, convection, radiation, and evaporation. Derivation of this equation and its details are described elsewhere (Kenny et al., 2009). I was able to measure all the necessary variables for using the COMFA outdoor thermal comfort model. The general form of this model is:

$$E_{\mathrm{therm}} = M + R_{RT} - C - E - L$$

Where M is the metabolic heat generated by a person calculated using BMR and the metabolic cost of activity. R_{RT} is radiation absorbed by a person calculated following Kenny et al. (2008) using body temperature and ambient temperature. C is the convective heat loss calculated using body temperature, ambient temperature, and clothing resistance. E is the evaporative heat loss calculated using body temperature, ambient temperature, exposed skin area, clothing resistance, atmospheric pressure, and known constants for skin tissue resistance to vapor transfer (Kenny et al., 2009). L is the long-wave radiation heat loss calculated using known constants for the emissivity of human skin and clothing as well as body temperature, exposed skin area, and ambient temperature. A constant body temperature of 37°C was used, and I measured ambient temperature using the Extech RHT10 Humidity and Temperature USB Data-logger. In temperate climates, I used an estimate of 25% exposed skin surface area, 10% for cold climates, and 60% for hot climates following International Standards Organization (2007) guidelines. I estimated TEF, the metabolic cost incurred from digesting food, to be 10% of caloric intake (Kinabo and Durnin, 1990).

Anthropometrics and body composition

I collected several external anatomical measurements including height, lower limb length, and bi-iliac breadth following standard procedures (Lohman et al., 1988). I collected these measurements using a standard cloth measuring tape and large calipers. I collected data on body mass, percent body fat, and muscle mass using a bioelectrical impedance scale, Tanita BC-558 Ironman Segmental Body Composition Monitor, the Tanita equations are unpublished (Tanita Corporation, Arlington Heights, IL).

Statistical analysis

I generated plots using Microsoft© Excel© for Mac 2010 and RStudio, ©RStudio, Inc. 2009-2012. I performed all statistical analyses including linear regressions, multiple regressions, and Tukey's pairwise comparisons using IBM© SPSS© Version 21. I considered results significant at $P < 0.05$. I used multiple regressions controlling for age, sex, fat free mass, and height followed by a Tukey's pair-wise comparisons to compare the NOLS population to

TABLE 3. TEE (kcal day^{-1}) measurements and predictions

Subject	Sex	Mass (kg)	Climate	DLW	Flex-HR	AIM	Factorial
NS1-12	M	89.9	Temperate	4,264	5,427	3,280	3,156
NS2-1	F	64.5	Temperate	2,837	2,814	3,217	2,591
FS5-12	F	65.8	Temperate	2,593	3,949	2,595	2,196
FS8-10	M	72.7	Temperate	3,597	3,138	3,118	2,839
Pilot 1	F	68.7	Temperate	3,340	3,729	3,675	2,286
Pilot 3	M	70.0	Temperate	3,641	4,031	3,537	2,644
Pilot 4	M	69.7	Temperate	4,313	4,889	4,276	2,839
NS1-12	M	95.0	Hot	3,790	5,668	3,629	3,093
NS2-1	F	65.5	Hot	2,838	3,651	2,154	2,027
FS5-1	M	73.8	Cold	4,517	9,155	5,090	3,031
FS8-10	M	71.9	Cold	4,137	4,678	5,687	3,261

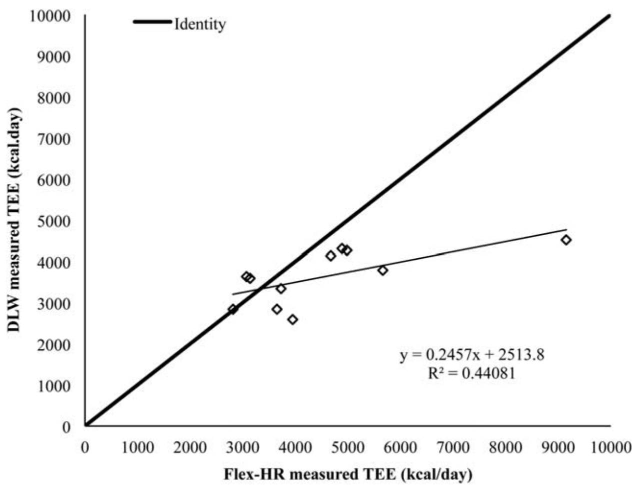

Fig. 1. The relationship between DLW measured TEE and Flex-HR measured TEE for the NOLS subjects ($N = 11$) who took part in DLW measurements.

TEE values for indigenous and nonindigenous populations collected from the literature. I used Bonferroni adjusted Student's t-tests to compare TEE measured through different methods (DLW, Flex-HR, the Factorial Method, and AIM) within subjects. I performed Bland-Altman analyses using Microsoft© Excel© for Mac 2010 to determine bias within the Factorial Method and AIM.

RESULTS

TEE measurements

TEE, as measured by the DLW method ($N = 11$ measurements from eight subjects), ranged from 2,593 to 4,517 kcal day^{-1} and had a mean of 3,624 ± 660 kcal day^{-1}. TEE, as measured by the Flex-HR Method ($N = 59$), ranged from 2,150 to 9,730 kcal day^{-1} and had a mean of 4,586 ± 1,499 kcal day^{-1}. A summary of the different TEE measurement results can be found in Table 3. Comparison with other populations confirmed that the subjects in this study had relatively high TEE. A linear regression controlling for age, sex, fat free mass, and height followed by a Tukey's pair-wise comparison ($F = 11.036$, $P < 0.001$) revealed that the NOLS sample had a significantly higher TEE than traditional Hadza hunter-gatherers ($N = 30$) (Pontzer et al., 2012), subsistence-agricultural Bolivians ($N = 24$) (Kashiwazaki et al., 2009), U.S. and European

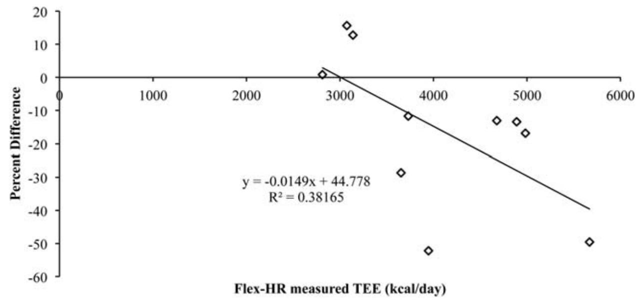

Fig. 2. The Flex-HR TEE measurements compared to their percent difference from DLW measurements for the NOLS subjects ($N = 11$) who took part in DLW measurements.

populations ($N = 51$) (Davidson et al., 1997; Prentice et al., 1986; Schulz et al., 1989; Seale et al., 1990; Welle et al., 1992), rural Yakut Siberians ($N = 27$) (Snodgrass et al., 2006), and urban Guatemalans ($N = 14$) Stein et al., 1988) ($P < 0.001$ for all cases).

Flex-HR method vs. DLW method

Flex-HR TEE measurements tended to be lower than DLW measurements at lower levels of TEE, but this difference did not meet the criterion for significance after Bonferroni correction (Bonferroni adjusted $\alpha = 0.008$, $P = 0.026$ paired t-test). However, at high levels of energy expenditure, the Flex-HR method tended to overestimate TEE. Figure 1 shows the relationship between DLW measured TEE and Flex-HR TEE. The percent difference between Flex-HR TEE and DLW TEE ranged from −15.6 to 102.7% with a mean of 24 ± 34.1% (Table 3). Subject FS5-1 had an exceptionally large Flex-HR measurement of greater than 9,000 kcal day^{-1}. When subject FS5-1 was removed from the analysis (Fig. 2) Flex-HR discrepancies were greatest above 3,000 kcal day^{-1}, after this point, Flex-HR overestimated DLW measured TEEs by a mean of 17%. Although this difference did not reach statistical significance, for comparisons with modeled TEE within the NOLS population, a 17% correction factor was applied to Flex-HR TEE measurements greater than 3,000 kcal day^{-1}. After this correction, Flex-HR TEE ranged from 2,150 to 8,076 kcal day^{-1} and had a mean of 3,867 ± 1,176 kcal day^{-1}.

Modeled TEE compared to measured TEE

AIM produced daily TEEs with a range of 1,947–7,080 kcal day^{-1} and a mean of 3,548 ± 1,090 kcal day^{-1}. The Factorial Method produced daily TEEs with a range of 1,894–4,156 kcal day^{-1} and a mean of 2,775 ± 423 kcal day^{-1}. Figure 3 shows TEE as measured by the DLW method and Flex-HR method as well as TEE predicted by AIM and Factorial Method. A full summary of AIM and Factorial Method calculated mean daily TEEs for each course is found in Table 3.

The Bland–Altman method was applied to the data to determine if there was any bias in the Factorial Method and AIM (Fig. 4). The Factorial Method tended to underestimate TEE at greater levels of energy expenditure in comparison to both DLW and Flex-HR measurements. AIM did not present this bias. AIM had the tendency to produce worse predictions at higher levels of TEE;

however, the inaccuracy did not bias toward overestimation or underestimation.

AIM compared to the factorial method

A linear regression drawn through the origin of AIM with DLW measured TEEs produced a slope of 0.97 (95% CI: 0.84–1.07), $r^2 = 0.48$. A linear regression drawn through the origin of the Factorial Method with the DLW TEE values for daily TEE produced a slope of 1.31 (95% CI: 1.24–1.42), $r^2 = 0.70$. The slope from the Factorial Method was significantly different from a slope of one, but the slope from AIM was not (Fig. 5), and the slopes from the two models differed (AIM: $F = 328.98$, $P < 0.001$; Factorial Method: $F = 1{,}126.688$, $P < 0.001$). Forcing these slopes through the origin gave similar results (Fig. 6). AIM produced a slope of 1.04 (95% CI: 0.99–1.1) $r^2 = 0.37$,

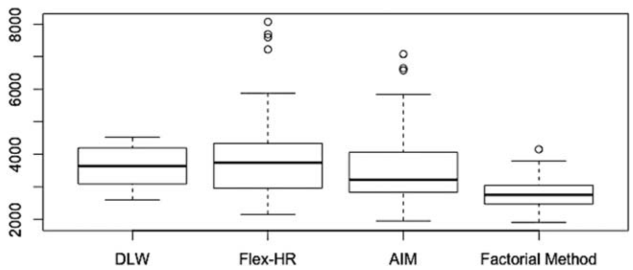

Fig. 3. Summary of TEE as measured by the doubly labeled water and Flex-HR methods as well as TEEs predicted by AIM and Factorial Method for the $N = 11$ NOLS subjects who took part in DLW measurements.

and the Factorial Method produced a slope of 1.40 (95% CI: 1.33–1.47) $r^2 = 0.35$ (AIM: $F = 1{,}364.5$, $P < 0.001$; Factorial Method $F = 1{,}626.834$, $P < 0.001$).

For the entire dataset, AIM overestimated TEE by 4.1%, a smaller absolute difference ($P < 0.001$, paired t-test) than the 25.3% underestimation produced by the Factorial Method. At TEEs > 3,000 kcal day^{-1}, the Factorial Method underestimated TEE by 31.6%, which was significantly higher than the AIM underestimation of TEE by only 10.7% ($P < 0.001$, paired samples t-test).

As a final test of the models' effectiveness, a within-subjects analysis was performed for a subsample of 12 subjects, three from each semester course, with high quality Flex-HR calibrations and in-field data collection. The predictions and measurements were compared on a day-to-day basis for the temperate climate. AIM produced a mean slope across subjects of 1.15 ± 0.27 with a range of 0.73–1.62 and a mean $r^2 = 0.36 \pm 0.24$ with a range of 0.01–0.67. When pooled, the confidence intervals were 1.0–1.2, $\alpha = 0.05$ ($F = 936.3$, $P < 0.001$) and not significantly different from a slope of one. The Factorial Method produced a mean slope of 1.33 ± 0.29 with a range of 0.87–1.8 and a mean $r^2 = 0.29 \pm 0.19$ with a range of 0.02–0.71. When pooled, the Factorial Method confidence intervals were 1.1–1.3, $\alpha = 0.05$ ($F = 762.8$, $P < 0.001$), and significantly different from a slope of one.

DISCUSSION

This study presented a new model, AIM, for predicting human TEE. AIM includes specific terms for BMR, thermoregulation, activity, and TEF, and allows for interactions

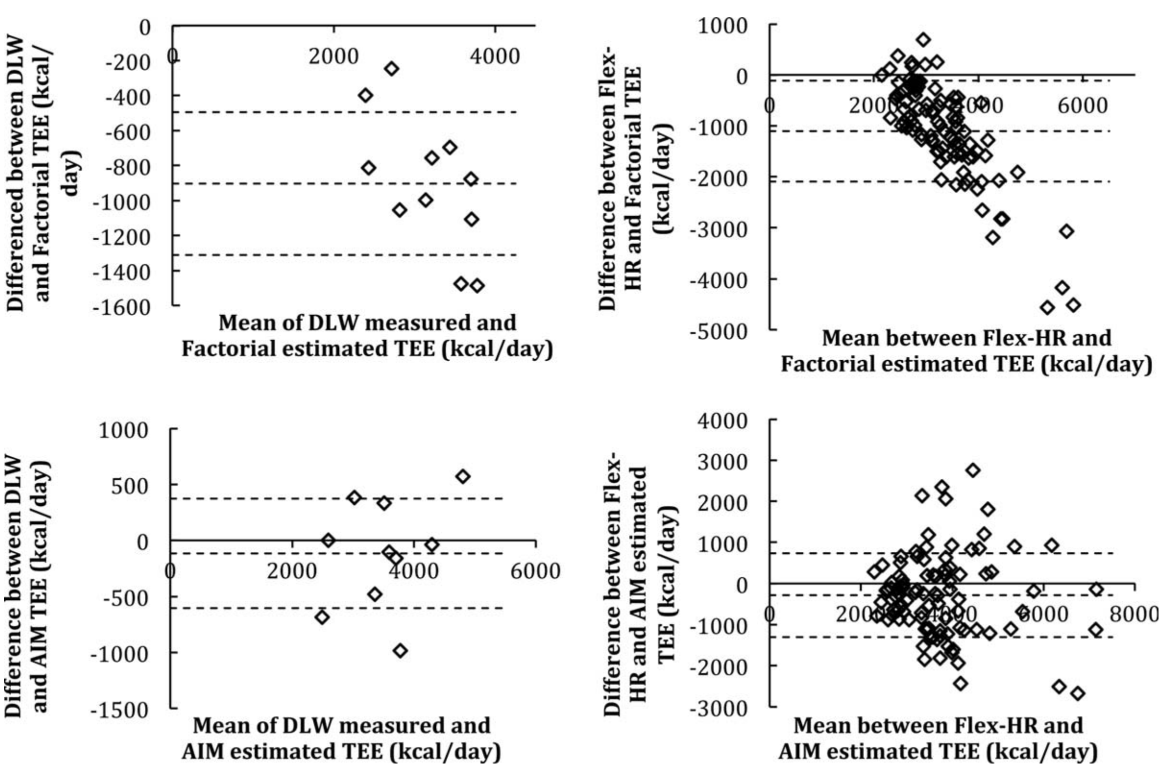

Fig. 4. Bland–Altman analysis of the Factorial Method and AIM compared to DLW TEE for the $N = 11$, and compared to Flex-HR TEE for $N = 59$.

among these variables. AIM and Factorial Method TEE estimates were compared to DLW and Flex-HR TEE measurements among healthy, highly active participants of NOLS courses. The Flex-HR method overestimates TEE at high levels of energy expenditure, and AIM produces more accurate TEE estimates than the Factorial Method.

Limitations to this study

First, the Cosmed k4b2 has been known to overestimate BMR (Duffield et al., 2004). This would impact the BMR measurements along with heart rate calibrations. Second, this study does not take into account psychological stress, which can increase heart rate and metabolic rate. This could account for some of the unusually high Flex-HR measurements observed. Third, two laboratories were used to analyze the DLW results from this study. No protocol was used to determine if there was significant variation between the two laboratories, introducing the possibility of DLW measured TEE error. Fourth, the NOLS subjects in this study are not representative of all populations. AIM needs to be validated among a variety of populations before it can broadly applied.

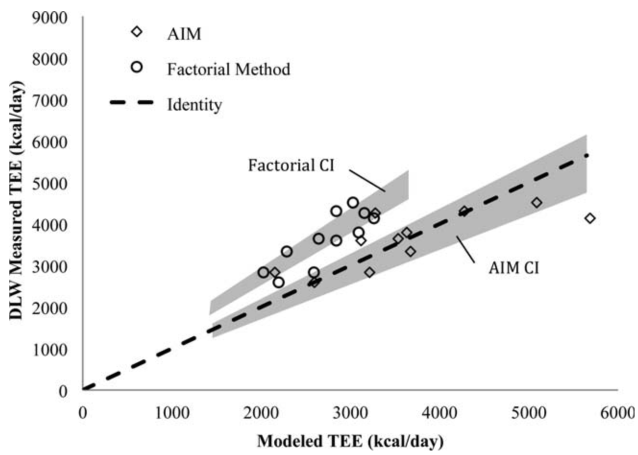

Fig. 5. Linear regression of the AIM and the Factorial Method TEE data against the observed DLW TEE data for NOLS subjects ($N = 11$, measurements for eight subjects) who took part in DLW measurements.

Flex-HR discrepancies

In this study, the Flex-HR method produced TEE estimates of greater than 9,000 kcal day^{-1}. This measurement is substantially higher than the highest DLW measured human TEE of roughly 7,000 kcal day^{-1} among Tour de France cyclists (Westerterp et al., 1986). However, this is not uncommon. Flex-HR discrepancies have been reported to range from −22.2 to 52.1% of DLW measurements at the individual level (Livingstone et al., 1990, Leonard, 2003), and 10% at the group level (Leonard, 2003).

There are a number of reasons for the divergence between DLW and Flex-HR measurements among the NOLS sample. The ActiTrainer devices used to collect HR data were used for extended periods of time without recharging, used for eight different 6–11 days of data collection over 7 months, exposed to the elements in the backcountry, and exposed to possible interference from satellite phones and avalanche beacons. As there is currently no research of ActiTrainer data degradation over repeated use and abuse or interference from other devices, it is difficult to confirm that any of the above reasons are possible causes for the large difference between the DLW and Flex-HR results.

Recent work has also suggested that climatic extremes can impact heart rate, disrupting the traditionally held relationship between heart rate and metabolic rate upon which the Flex-HR method depends. The Frank–Starling law of the heart relates heart stroke volume to the volume of blood filling the heart, such that a change in blood pressure accompanies a change in heart rate (Wilson et al.,

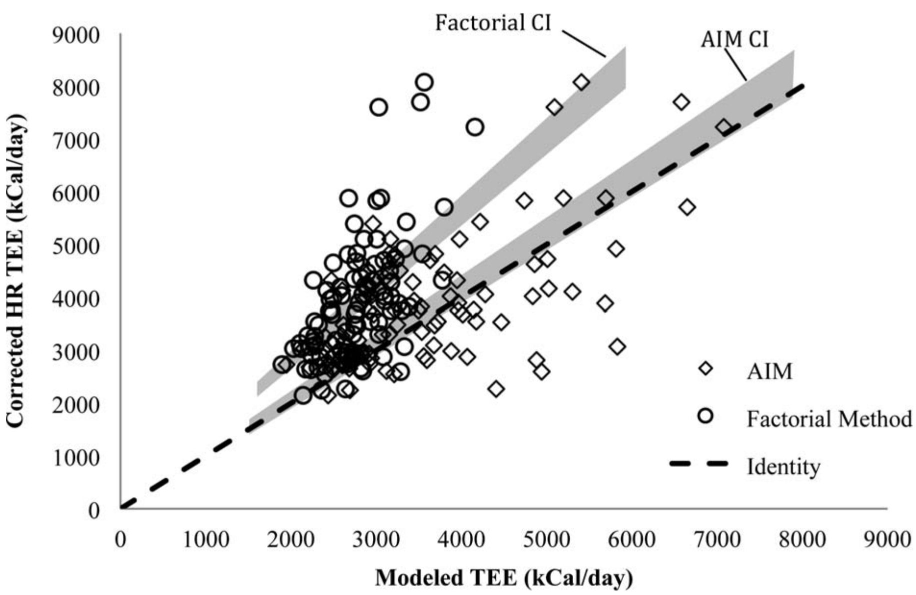

Fig. 6. Linear regression of the AIM and the Factorial Method TEE data against the corrected Flex-HR TEE data for all $N = 59$ NOLS subjects.

2009). In cold climates, humans experience cutaneous arterial vasoconstriction, which increases blood pressure thereby reducing heart rate. In hot conditions, humans experience vasodilation, which increases heart rate (Wilson et al., 2009). These changes in heart rate do not correspond to complementary changes in metabolic rate. All heart rate calibrations for this study were performed under thermoneutral conditions. This suggests that under cold conditions subjects would experience depressed heart rates, and thermoneutral calibrated TEE estimates would be lower than actual TEE. The converse is true in hot climates, TEE estimates would be greater than actual energy expenditure. This environmental impact on heart rate makes the use of the Flex-HR method in extreme temperatures difficult. Making models that do not rely on heart rate, such as AIM, preferable.

The AIM outperforms the factorial method

AIM was designed to produce more accurate estimates of human TEE across a range of climates and PALs. The NOLS population was used because of its high level of physical activity, which allowed for AIM to be tested where the Factorial Method fails, at high levels of TEE (Leonard et al., 1997). The results show that AIM is more accurate at both low and high levels of physical activity, making it a superior method for predicting TEE. This was achieved by including more specific metabolic cost terms and allowing for interaction among them, which has been shown to be an important factor particularly in cold climates (Steegmann, 2007).

AIM performs particularly well at high TEEs. This is likely due to the ability of AIM to produce TEE estimates greater than 4,000 kcal day^{-1} (Fig. 6). The Factorial Method is unable to account for possible internal tradeoffs when energy expenditures are high. AIM appears to avoid this issue. However, both models have low r^2-values. Given the high level of individual variation in metabolic rate, this is not wholly unexpected.

Once more broadly validated, AIM can be used to analyze energy expenditure within and between populations. Furthermore, as AIM is a more explicit model, it can be used to assess energy allocation differences among populations inhabiting different climates. A better understanding of how humans allocate energy to costly activities such as thermoregulation, physical activity, and reproduction can help us explore the subtle, and possibly adaptive, differences in life history strategies.

This analysis demonstrates that AIM is more accurate at predicting human TEE than the Factorial Method, and possibly even the Flex-HR method, across a range of PALs and climates. Furthermore, AIM succeeds where the Factorial Method has traditionally failed—at high levels of energy expenditure. The results presented here suggest that AIM should be used in place of the Factorial Method for estimating human TEE.

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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

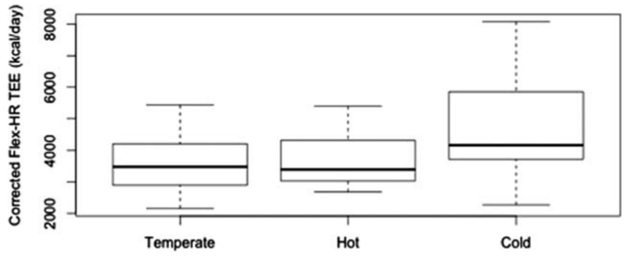

FIGURE 1 Corrected flex-HR measured mean total energy expenditure (kcal day^{-1}) for each subject in temperate, hot, and cold climates during the data collection period

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, $p = .256$).

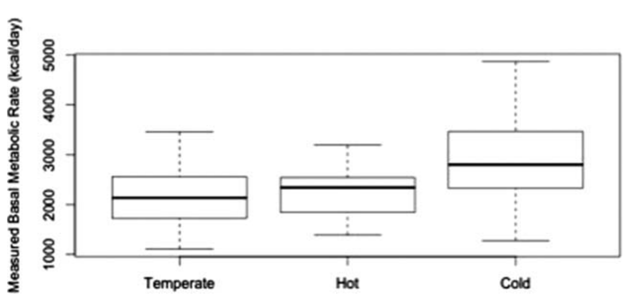

FIGURE 2 Basal metabolic rates (kcal day^{-1}) for the three climates

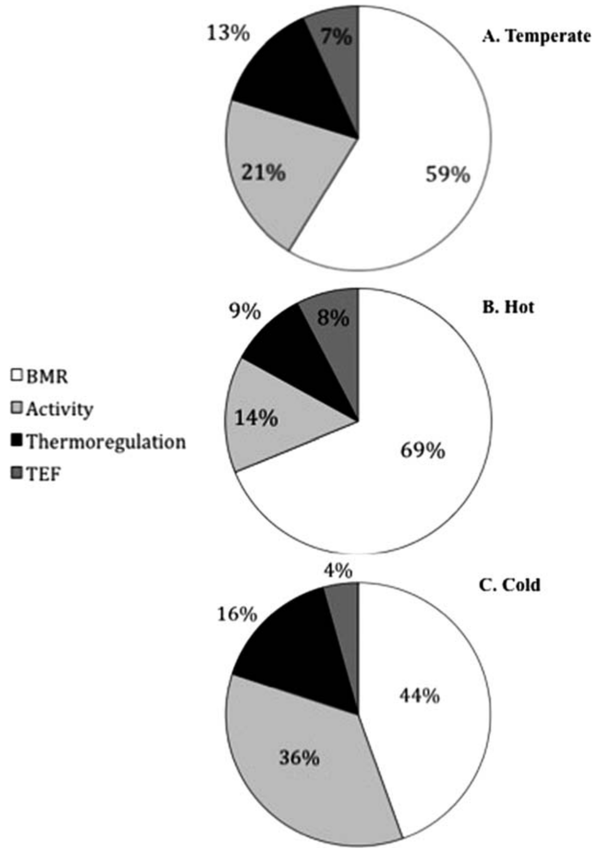

FIGURE 3 Energy allocation (kcal day^{-1}) in (A) temperate, (B) hot, and (C) cold climates

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, $p < .001$).

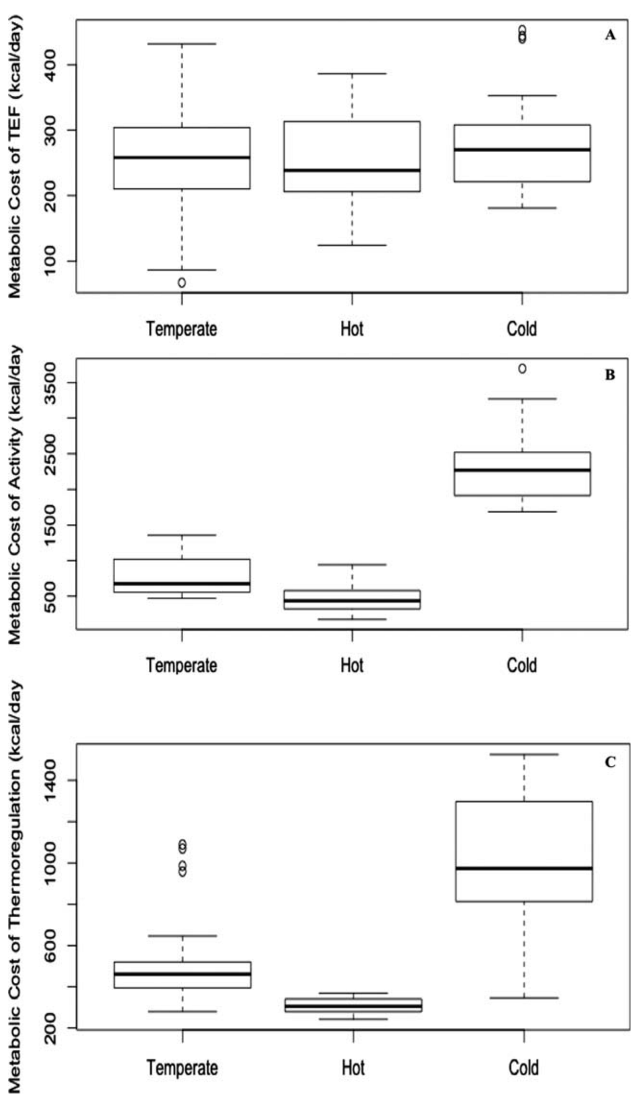

FIGURE 4 Estimated activity (A) thermic effect of food (kcal day^{-1}), (B) physical activity (kcal day^{-1}), and (C) thermoregulation costs (kcal day^{-1})

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

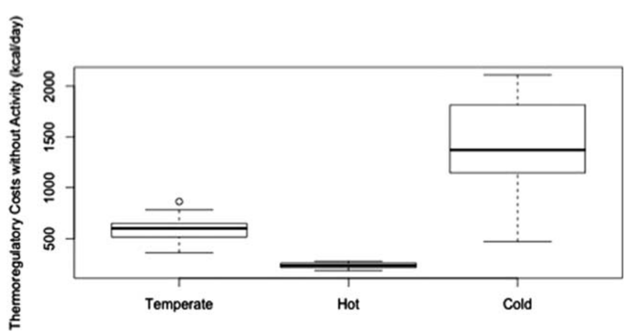

FIGURE 5 Thermoregulatory costs (kcal day^{-1}) estimated using AIM with zero activity assumed. Please refer to Figure 4C for thermoregulatory costs estimated including heat produced from physical activity

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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ORIGINAL RESEARCH ARTICLE

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Body fat attenuates muscle mass catabolism among physically active humans in temperate and cold high altitude environments

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Abstract

Objective: Typical diet plans are based on an individual's body mass; however, body composition may be important to consider when an individual is in a negative energy balance. This study examines if high initial body fat and dietary macronutrient content reduce muscle mass catabolism during excursions in temperate and cold high altitude environments.

Methods: Subjects—53 healthy, un-acclimated volunteers (37 males and 16 females)—took part in 12-16 week-long outdoor education courses in moderately high altitude temperate and cold climates in the western United States. Body mass, body fat percentage, fat mass, and muscle mass were measured before and after each excursion. Total energy expenditure and dietary intake were also measured.

Results: In temperate and cold environments, both sexes lost significant amounts of body mass. In temperate climates both sexes lost a significant amount of fat mass, but not muscle mass. In cold climates, there was no significant change in fat mass for either sex; however, females gained muscle mass while males lost muscle mass. In both climates subjects with lower initial body fat percentages lost significantly more muscle mass than subjects with higher initial body fat percentages. There was no significant relationship between macronutrient intake and muscle mass loss for either sex.

Conclusion: These results suggests that during a negative energy balance dietary macronutrient content cannot abate the loss of muscle mass, but body fat may have a protective effect. This information should be used to improve individualized diets based on body composition, not body mass.

KEYWORDS
body composition, energetics, high altitude, nutrition

1 | INTRODUCTION

Body mass is the key variable used to estimate dietary needs and ration plans; however, these body mass based estimates do not take into account an individual's risk of body composition changes while in a negative energy balance, where energy expenditure exceeds energy intake. High levels of physical activity and stressful environments can contribute to creating this negative energy balance (Zaccagni, Barbieri, Cogo, & Gualdi-Russo, 2014). Currently, much of the work examining body composition changes in extreme conditions focuses on high altitude environments. Acclimatization to hypoxia and altitude related illness increases energy expenditure, which can lead to a 17-27% increase in basal metabolic rate (Boyer & Blume, 1984; Butterfield et al., 1992; Rose et al., 1988; Wagner, 2010; Wee & Climstein, 2015; West,

Abbreviations: BM, body mass; FM, fat mass; Flex-HR, flex-heart rate method; IEA, in-field energy assessment; MM, muscle mass; NOLS, National outdoor leadership school; RMR, resting metabolic rate; TEE, total energy expenditure.

2010; Westerterp, Kayser, Brouns, Herry, & Saris, 1992; Westerterp, Kayser, Wouters, Le Trong, & Richalet, 1994; Westerterp, Meijer, Rubbens, Robach, & Richalet, 2000; Tschop, Strasburger, Hartmann, Biollaz, & Bartsch, 1998; Zaccagni et al., 2014). A similar increase in basal metabolic rate is also seen among individuals in cold climates in order to maintain core body temperature (Moran, 2008; Steegmann, 2007). The increased metabolic costs due to cold climate and high altitude, in conjunction with high levels of activity, create a negative energy balance that leads to a reduction in body mass from fat and muscle mass. Many researchers have focused on these changes and how nutrition can be used to abate them; however, few have investigated how initial body composition affects body composition outcome. The work presented here investigates the importance of initial body composition and dietary macronutrient content to body composition changes incurred during physically demanding excursions in high altitude temperate and cold climates.

When in a negative energy balance, energy stores within the body, which come from glycogen, fat, and skeletal muscle protein, must meet metabolic demands. Glycogen is the most readily available source of energy during exercise. Once glycogen stores have been depleted, which can happen in less than four hours of strenuous exercise, fat is then used as an energy source (Edwards, Margaria, & Dill, 1934; McArdle, Katch, & Katch, 2013). However, fat stores cannot be fully depleted during a sustained negative energy balance. Humans require a minimum amount of fat, 4–8% in males and 8–19% in females, to maintain basic health and physiological functions (Achten, Gleeson, & Jeukendrup, 2002; Achten & Jeukendrup, 2004; FAO, 1998; Friedl et al., 1994; Gallagher et al., 2000; Venables, Achten, & Jeukendrup, 2005). Once this lower limit of essential fat has been reached, the body relies on protein stores to meet energetic needs (Carbone, McClung, & Pasiakos, 2012; Friedl et al., 1994; Horton, Pagliassotti, Hobbs, & Hill, 1998; Kayser, 1994; Wagenmakers, 1998).

How and when the body catabolizes skeletal muscle during a negative balance is still poorly understood (Kumar, Atherton, Smith, & Rennie, 2009). However, limited evidence suggests that after endurance exercise there is immediate protein breakdown, the rate of which can remain elevated for 24 h (Koopman et al., 2004; Kumar et al., 2009; Tipton, Ferrando, William, & Wolfe, 1996). This protein breakdown normally comes from dietary protein. However, in a negative energy balance, the protein is catabolized from skeletal muscle, which can result in muscle damage not only from catabolism but also from a lack of repair (Belcastro, Shewchuk, & Raj, 1998; Tipton & Wolfe, 2001). A diet with protein levels exceeding the recommended daily allowance has been shown to mitigate this potential muscle mass loss (Carbone et al., 2012; Farnsworth et al., 2003; Layman et al., 2003; Rodriguez & Garlick, 2008; Skov, Toubro, Ronn, Holm, & Astrup, 1999).

Having a greater reservoir of fat is another possible way to limit muscle mass catabolism, suggesting that those with higher body fat percentages experience reduced muscle mass loss. A number of studies have demonstrated the loss of fat and muscle mass during high altitude excursions, but these changes have not been related to initial body composition. For instance, Reynolds et al. (1999) found that Mt. Everest climbers and base camp workers lost fat mass while experiencing a negative energy balance. Among nonacclimatized individuals of European descent taking part in a Himalayan expedition, those with lower initial fat mass experienced greater muscle mass loss than those with a higher initial fat mass (Zaccagni et al., 2014). Two separate American Medical Research Expeditions to Mt. Everest found that expedition members experienced significant fat and muscle mass loss in the face of the high altitude and high levels of physical activity, but the relationship to initial body composition was not established (Boyer & Blume, 1984; West, 2010).

Further research is needed among individuals taking part in high levels of physical activity at high altitudes to determine the impact of initial body composition on final body composition outcome during a negative energy balance. Students taking part in a month-long National Outdoor Leadership School (NOLS) course experienced significant changes in body composition (Ocobock, Gookin, & Baynes, 2011). To expand upon that, total energy expenditure (TEE), energy balance and body composition changes were measured among NOLS students who took part in 12–16-week-long courses in the western U.S. backcountry in high altitude temperate and cold climates. TEE, energy intake, and macronutrient content were assessed to determine if NOLS students experienced a negative energy balance. Body mass, body fat percentage, and muscle mass were measured among these students before and after each climate regime to test two hypotheses that subjects with high initial body fat percentages experience (1) a greater fat mass loss and (2) reduced muscle mass catabolism. Macronutrient content was estimated to test the hypothesis that consuming greater amounts of dietary protein reduces muscle mass catabolism. Results from this study can be used to inform more individualized dietary plans and food ration preparation for physically demanding excursions.

2 | SUBJECTS AND METHODS

2.1 | Subjects

In this study 53 healthy volunteers (37 males and 16 females, aged 18–31 years) took part in four 12–16 week-long outdoor education courses operated by NOLS. They were US citizens, all of whom were un-acclimatized to high-altitude at the start of their course. Individual ancestry data were not collected. The Institutional Review Board of Washington University, St. Louis (IRB protocol 201104106) approved this study, and subjects gave informed consent prior to participating.

2.2 | Field settings

NOLS is a US-based nonprofit outdoor education program that offers its students the opportunity to live in the wilderness for an extended period of time. The core curriculum includes outdoor survival skills, leadership, risk management, and environmental studies. Two of the courses in this study, course names NS1 and NS2, took place during spring and summer for 12 weeks. The other two courses, course names FS5 and FS8, were in fall and winter for 16 weeks (Table 1). Students in NS1 and NS2 experienced temperate and hot climates. The hot climate portion was not included in this analysis since it did not take place at high altitude. Students in FS5 and FS8 experienced temperate and cold climates. NS1, NS2, FS5, and FS8 are four separate courses; there was no subject overlap from one course to another. Temperate climate exposures lasted five weeks, and cold climate exposures lasted four weeks. The locations and altitudes for the temperate and cold climates are provided in Table 1.

Body composition measurements were collected before (1st Measurement) and after (2nd Measurement) exposure to each climate. These measurements were taken at the NOLS headquarters in Lander, WY (1633 m altitude). The In-Field Energy Assessment (IEA) was performed while subjects were in the field for each climate. During the IEA, total energy expenditure (TEE), and dietary intake were measured.

The typical schedule for a NOLS course begins with students arriving in Lander, WY, several days before they embark on their backcountry experience. Students use this time to prepare gear and rations and meet their course-mates and instructors. It was during this time that the 1st Measurement of body composition was performed. Students then left for the first section of their course. Subjects were exposed to their in-field conditions for 2 weeks to allow for acclimatization. After this 2-week period, the IEA was performed and lasted 6–11 days (Table 1). Once the IEA was complete, subjects finished the first section of their course and returned to Lander, WY, for 2 days to change gear and replenish rations. During this time the 2nd Measurement of body composition was performed. This procedure schedule was followed for each of the climates.

During these courses, subjects took part in rigorous physical activities in which laborious days were followed by rest days. Subjects carried 2 weeks' worth of rations during their courses, and NOLS provided planned re-rations at two-week intervals. During the temperate climate sections of all four courses, subjects took part in extensive daily hiking and beginner mountaineering. Subjects would hike a mean of 7.3 ± 4.0 km day^{-1}. They carried all of their equipment and food during these hikes, often ending each day setting up a new campsite. During the cold climate sections of FS5 and FS8, subjects would cross-country ski or snow-shoe with their equipment and food for a mean of 5.7 ± 4.2 km day^{-1}, frequently ending each day camping at a new location. Subjects had to shovel snow a mean of 1.0 ± 1.7 h day^{-1} in order to set up camp.

2.3 | Anthropometric and body composition measurements

Body mass, muscle mass, fat 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.

TABLE 1 NOLS course summary including number of subjects, mean temperature, location, altitude, and duration of IEA (in-field energy assessment)

Course	*N*	Climate	Mean temp. (°C)	IEA location	Altitude (m)	IEA duration (days)
NS1	14	Temperate	15.6	Absaroka Mountain Range, WY	3205	11
NS2	11	Temperate	13.5	Absaroka Mountain Range, WY	3205	11
FS5	14	Temperate	13.8	Wind River Range, WY	3658	7
		Cold	−4.9	Absaroka Mountain Range, WY	3205	7
FS8	14	Temperate	14.2	Wind River Range, WY	3658	8
		Cold	−9.4	Absaroka Mountain Range, WY	3205	7

Measurements were taken on subjects in the morning before they consumed their first meal of the day.

2.4 | Temperature measurements

Temperature was measured using an Extech RHT10 Humidity and Temperature USB Data-logger (Extech Industries, Nashua, NH, USA) carried by the course instructors, attached to the outside of their backpacks. The device was brought into the tents with the backpacks each night. 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, USA). High, low, and mean temperatures were calculated for each day as well as averaged across the IEA (Table 1).

2.5 | Energy expenditure measurements

Resting metabolic rates (RMR) were collected from each subject using a portable respirometry unit (Cosmed K4b2, Chicago, IL, USA) following standard practice (Gayda et al., 2010). This system measures oxygen consumption and carbon dioxide production using a breath-by-breath analysis. RMR measurements were performed 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. They rested 15–20 min before measurements were taken. Measurements lasted 6–8 min with the last four minutes of the measurement averaged to determine RMR.

TEE was measured among subjects using the Flex-Heart Rate method (Flex-HR) based on in-field heart-rate data collected using an ActiTrainer (Actigraph, Pensacola, FL, USA) heart rate monitor. This device was worn continuously during the IEA. Equations were calculated from a set of calibration measurements performed for each subject to convert heart rate to metabolic rate. For the calibration measurements, heart rate (bpm) and metabolic rate (kcal min^{-1}) were recorded simultaneously using a portable respirometry unit (Cosmed K4b2, Chicago, IL, USA) while subjects stood, walked (1, 1.5, 2 m s^{-1}), and ran (2, 2.5, 3 m s^{-1}) for 5 min at each speed on a treadmill. Calibration measurements were conducted before and after climate exposure.

To calculate the Flex-HR equations, the Flex-HR flex-point was determined for each subject as the mean of the highest heart rate at rest and the lowest heart rate during exercise following Leonard (2003). All in-field HR measurements below this flex-point were assigned the RMR. TEE for all in-field HR measurements above this flex-point, indicating activity, were calculated as the least-squares regression line for heart rate and energy expenditure. Missing in-field heart rate data were filled in using averaged heart rate values calculated from the available data for each day. A mean of 5.6 ± 1.9% heart rate data points was missing per subject per day. To account for changes in fitness throughout the course, only equations calculated from the calibration closest in time to the relevant IEA (temperate or cold) were used to implement the Flex-HR method. For example, the calibration measurements conducted at the end, not the beginning, of the temperate climate were used to estimate temperate climate TEE.

2.6 | Dietary intake

Subjects kept a daily diet log recording type and amount of food–collapsible measuring cups were provided to aid measuring accuracy. These logs were transcribed into Microsoft© Excel© for Mac 2010. Typical backcountry recipes were broken down into separate ingredients using *NOLS Cookery* (Pearson, 2004), *NOLS Backcountry Cooking* (Pearson & Kuntz, 2008), and *NOLS Backcountry Nutrition* (Howley, 2008). The official USDA National Nutrient Database for Standard Reference was used to assign nutritional values and protein, carbohydrate, and fat content for the foods consumed (USDA, 2012). Calories and macronutrients were summed for each subject for each day during the IEA. Subjects with blank or incomplete diet logs ($N = 9$) were removed, resulting in 44 subjects included in the macronutrient analysis.

2.7 | Statistical analysis

Figures were generated using Microsoft© Excel© for Mac 2010. Linear regressions and Students' t tests were performed using IBM© SPSS© Version 21. Males and females were analyzed separately and together for all analyses. Linear regressions were used to determine the relationship between initial body composition and the change in composition experienced while subjects were in the field. Repeated t tests were used to analyze composition differences within each subject. One sample binomial Clopper–Pearson and Jeffreys tests were used to determine the relationship between macronutrient (carbohydrates, protein, and fat) intake and muscle mass catabolism. Results were considered significant at the $p = .05$ level.

3 | RESULTS

For this study, it was hypothesized that initial body composition would influence body composition changes experienced by individuals participating in high levels of physical activity in high altitude temperate and cold climates. Specifically, it was expected that individuals with greater body fat

TABLE 2 Summary of female subjects' measurements

Climate	N	TEE (kcal day^{-1})	Dietary intake (kcal day^{-1})	Protein intake (g day^{-1})	Carbohydrate intake (g day^{-1})	Fat intake (g day^{-1})	Variables	1st measure	2nd measure	p values
Temperate	16	2884 ± 496	2238 ± 240	75.2 ± 11.5	290.7 ± 34.8	108.0 ± 19.1				
							HT (cm)	168.2 ± 0.1	–	
							BM (kg)	68.8 ± 9.3	67.7 ± 8.9	0.03
							Fat%	23.7 ± 6.0	21.7 ± 6.5	0.08
							FM (kg)	16.8 ± 6.4	15.2 ± 6.4	0.04
							MM (kg)	49.4 ± 3.5	49.9 ± 3.4	0.48
Cold	6	3837 ± 1176	2439 ± 384	74.0 ± 9.2	268.5 ± 15.0	96.3 ± 14.3				
							HT (cm)	170.0 ± 0.04	–	
							BM (kg)	70.1 ± 7.1	68.0 ± 8.7	0.04
							Fat%	24.9 ± 5.3	21.8 ± 5.7	0.02
							FM (kg)	17.8 ± 5.6	15.2 ± 6.1	0.48
							MM (kg)	49.7 ± 2.8	50.3 ± 3.3	0.01

The six subjects that took part in the cold climate also took part in the temperate climate. Results were considered significant at $p < .05$. TEE is total energy expenditure, HT is height, BM is body mass, FM is fat mass, and MM is muscle mass.

percentages would experience greater fat mass loss but reduced muscle mass loss compared to individuals with a lower initial body fat percentage. Furthermore, the effect of dietary macronutrient content on body composition changed was analyzed.

3.1 | Total energy expenditure and dietary intake

As measured by the Flex-HR Method in temperate climates, females expended a mean daily TEE of 2884 ± 496 kcal day^{-1} and a mean dietary intake of 2238 ± 240 kcal day^{-1} while males expended 3848 ± 783 kcal day^{-1} and consumed 2525 ± 119 kcal day^{-1}. In cold climates, females expended 3837 ± 1176 kcal day^{-1} and consumed 2439± kcal day^{-1} while males expended 5113 ± 1660 kcal day^{-1} and consumed 3095 ± 319 kcal day^{-1}. Subjects consumed roughly 1000 kcal day^{-1} fewer than they expended in temperate climates and consumed almost 2000 kcal day^{-1} fewer than they expended in cold climates.

3.2 | Body mass

In temperate climates males lost 2.8 ± 2.9 kg ($p < .001$) and females lost 1.1 ± 1.7 kg ($p = .027$). Similarly, males and females both lost body mass in the cold climate, 2.3 ± 1.1 kg ($p < .001$) and 2.1 ± 1.7 kg ($p = .04$), respectively. The mean values for anthropometrics and body composition data are in Table 2 for females and Table 3 for males.

3.3 | Body fat percentage and fat mass

In temperate climates, males lost 1.9 ± 2.4 kg ($p < .001$) and females lost 1.6 ± 2.7 kg of their fat mass ($p = .04$); 6 of 16 females (37.5%) and 18 of the 37 males (48.6%) reached a body fat percentage within the essential fat range. In cold climates, females tended to lose more than males, 2.6 ± 1.5 and 0.8 ± 1.9 kg, respectively; however, neither were significant ($p > .08$). Three of six female subjects (50%) and eight of 22 male subjects (42.1%) reached a body fat percentage within the essential fat range.

Individuals with a greater 1st measurement of body fat lost significantly more fat mass in both temperate ($p = .02$, $r^2 = 0.10$) (Figure 1A) and cold climates ($p = .029$, $r^2 = 0.19$) (Figure 1B). There was no significant relationship between initial body fat and fat mass lost among females ($p > .52$) for either climate. However, males with a high initial body fat lost significantly more body fat in the temperate climate ($p < .001$). There was not a similarly significant relationship in the cold climate ($p = .62$).

3.4 | Muscle mass

In temperate climates, females tended to gain muscle mass, 0.5 ± 2.54 kg, though not to a significant degree ($p = .48$).

TABLE 3 Summary of male subjects' measurements

Climate	N	TEE (kcal day^{-1})	Dietary intake (kcal day^{-1})	Protein intake (g day^{-1})	Carbohydrate intake (g day^{-1})	Fat intake (g day^{-1})	Variables	1st measure	2nd measure	p values
Temperate	37	3848 ± 783	2525 ± 119	86.6 ± 10.3	323.3 ± 43.0	122.7 ± 16.3				
							HT (cm)	181.8 ± 0.1	–	
							BM (kg)	77.4 ± 12.9	74.6 ± 11.5	<0.001
							Fat%	10.0 ± 5.3	9.0 ± 4.1	<0.001
							FM (kg)	8.9 ± 6.1	7.1 ± 4.6	<0.001
							MM (kg)	65.0 ± 7.8	64.1 ± 6.6	0.06
Cold	22	5113 ± 1660	3095 ± 319	94.6 ± 16.2	330.5 ± 57.5	131.1 ± 23.8				
							HT (cm)	181.1 ± 0.1	–	
							BM (kg)	77.6 ± 10.9	75.3 ± 10.2	<0.001
							Fat%	10.4 ± 3.9	9.6 ± 4.0	0.22
							FM (kg)	8.3 ± 4.3	7.5 ± 4.0	0.08
							MM (kg)	65.9 ± 7.5	64.4 ± 7.4	0.003

The 22 subjects that took part in the cold climate also took part in the temperate climate. Results were considered significant $p < .05$. TEE is total energy expenditure, HT is height, BM is body mass, FM is fat mass, and MM is muscle mass

Males tended to lose muscle mass, 0.9 ± 2.8 kg, which approached significance ($p = .06$). However, subjects with a low 1st Measurement of body fat percentage lost significantly more muscle mass than those with a higher initial body fat percentage (Figure 2A) ($p = .019$, $r^2 = 0.105$). In cold climates, females gained a significant amount of muscle mass, 0.6 ± 1.7 kg ($p = .01$), and males lost a significant amount of muscle mass, 1.5 ± 1.8 ($p = .003$). Subjects with a low 1st Measurement of body fat percentage lost significantly more muscle mass than those with high initial body fat percentages ($p = .013$, $r^2 = 0.241$) (Figure 2B). There is no significant relationship between initial body fat and muscle mass loss for either climate when the sexes are analyzed separately ($p > .1$).

3.5 | Macronutrient content and effect on body composition

Overall, in the temperate climate the dietary composition was 47% carbohydrates, 12% protein, and 41% fat. In the cold climate the dietary composition was 46% carbohydrate, 13% protein, and 41% fat (Table 4). There was no significant difference in macronutrient content between climates among males or females (Paired t test, $p > .3$ for all cases). There was no significant relationship between protein intake, which has been shown to reduce muscle catabolism, and changes in muscle mass in either climate for either sex ($p > .25$) (Figure 3A,B). The same was also true for carbohydrate and fat intake (carbohydrates: $p > .41$; fat: $p > .39$).

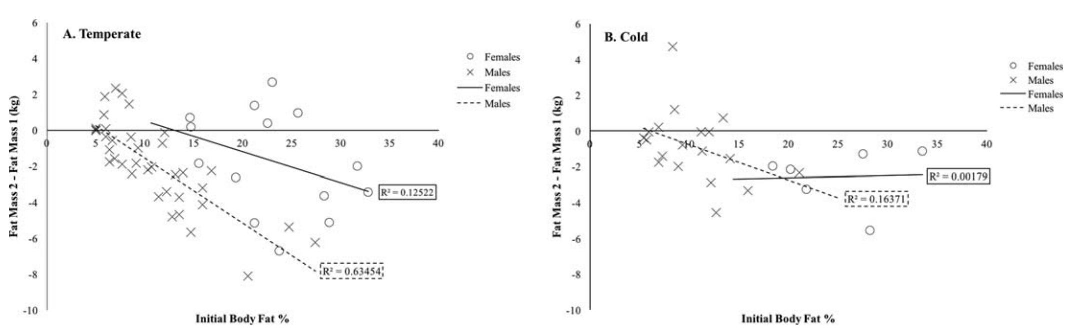

FIGURE 1 **A, B** Relationship between initial body fat percentage and fat mass lost in (**A**) temperate and (**B**) cold climates. Individuals with greater initial body fat percentage lost significantly more fat mass during their high altitude excursions in both climates. Females: ○ and Males: ×.

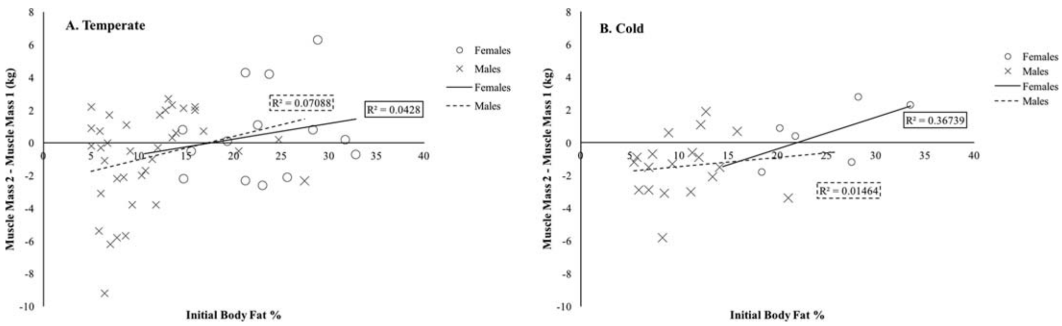

FIGURE 2 **A**, **B** Relationship between initial body fat percentage and muscle mass lost in (**A**) temperate and (**B**) cold climates. Individuals with higher initial body fat percentage lost significantly less muscle mass during their high altitude excursions. Females: ○ and Males: ×

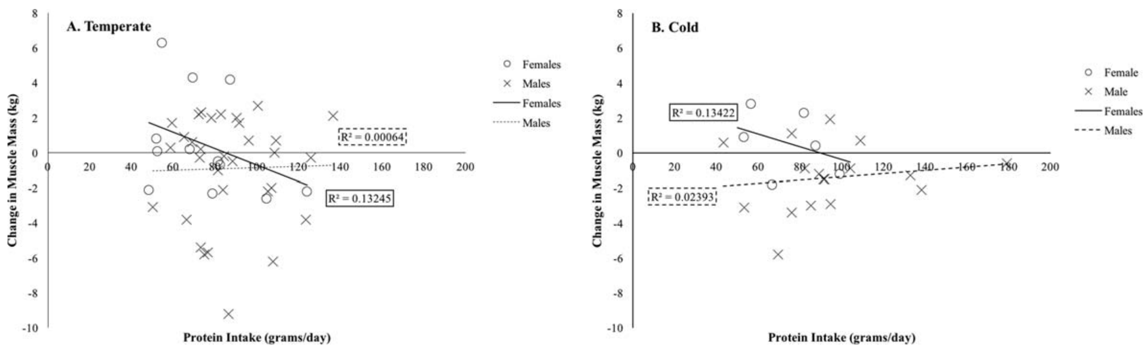

FIGURE 3 **A**, **B** Relationship between protein intake and muscle mass loss in (**A**) temperate and (**B**) cold climates. Females: ○ and Males: ×. Individuals who consumed more dietary protein did not experience reduced muscle mass catabolism, $p > .25$ in temperate and $p > .48$ in cold for both males and females

4 | DISCUSSION

This study analyzed how initial body composition influenced body composition changes during a period of a negative energy balance due to high activity levels in high altitude temperate and cold climates. NOLS subjects took part in prolonged endurance activities almost daily for several weeks. Given the known increase in protein catabolism within 24 h of endurance exercise (Koopman et al., 2004; Kumar et al., 2009; Tipton et al., 1996), these subjects were at a greater risk of catabolizing muscle mass. Subjects experienced an energy deficit of more than 1000 kcal day^{-1} in the temperate climates, and 2000 kcal day^{-1} in cold climates. Deficits of this magnitude required the NOLS students to utilize their own bodily energy stores to maintain their high levels of energy expenditure. At least 37% of NOLS students reached essential fat levels, requiring them to utilize stored protein for energy.

Overall, females tended to gain muscle mass but lose fat mass in both climates, whereas males tended to lose both. Furthermore, individuals with low initial body fat percentages lost significantly more muscle mass than those with high initial body fat percentages. These results suggest that possessing a higher body fat percentage might spare muscle mass catabolism during long periods of negative energy balance at high altitudes, which supports previous research that indicated a possible protective effect of body fat (Reynolds et al., 1999; Zaccagni et al., 2014).

TABLE 4 Summary of the body mass, total energy expenditure (TEE), caloric intake, and macronutrient content results for female and male subjects in temperate and cold high altitude environments

Climate	Sex	*N*	Body mass (kg)	TEE (kcal day^{-1})	Caloric intake (kcal day^{-1})	Carbohydrates (g day^{-1})	Protein (g day^{-1})	Fat (g day^{-1})
Temperate	Male	32	75.7	3822	2695	323.3	86.6	122.7
	Female	12	67.9	3081	2388	290.7	75.2	108.0
Cold	Male	17	75.7	4787	2880	330.5	94.6	131.1
	Female	6	67.7	3880	2287	268.5	74.0	96.3

Nutrition in a negative energy balance can play a critical role. In cold climates, subjects had the ability to carry perishable items such as meat, cheese, and eggs and preserve them in the snow. Access to a regular supply of fresh food with higher protein content, as opposed to the typical dry rations consumed during the temperate climate, vastly alters the macronutrient profile. A diet with protein levels exceeding the recommended daily allowance has been shown to mitigate muscle loss and promote muscle repair in individuals experiencing a negative energy balance (Carbone et al., 2012; Farnsworth et al., 2003; Fisher, Yagaloff, & Burn, 1999; Kayser, 1992; Koopman et al., 2004; Layman et al., 2003; Rodriguez & Garlick, 2007; Skov et al., 1999). However, even with potential greater access to a diet higher in protein, subjects did not eat significantly more protein and still experienced muscle mass loss in cold climates.

High altitude impacts metabolism and appetite beyond just higher energy expenditure, it can also lead to a decreased appetite (Westerterp et al., 2000; Westerterp-Plantenga, Westerterp, Rubbens, Verwegen, Richelet, & Gardette, 1999). One explanation for this is the broken link between hunger and the desire to eat, thought to be due to the elevated concentration of leptin observed at high altitudes (Westerterp, 2001; Westerterp et al., 1992). High levels of leptin, a satiety mediator, would reduce the feeling of hunger in an individual even if his or her body were in need of sustenance, perpetuating the negative energy balance (Tschop et al., 1998; Westerterp, 2001). Furthermore, there was no relationship between any of the dietary macronutrient levels and fat-free mass loss, suggesting that, in the face of such a large negative energy balance, macronutrient content, even protein levels, cannot protect against muscle mass loss.

These results demonstrate the need to assess initial body composition, an important factor that is often overlooked when planning diet rations for long-term backcountry forays. Traditional ration planning focuses on the number of individuals and each individual's body mass (Howley, 2008). However, one ration plan does not fit all. Individuals with a low body fat percentage are at greater risk for muscle mass catabolism as they will more quickly reach the lower limit of healthy body fat levels, and their physical performance will suffer (Carbone et al., 2012; Kayser, 1994). However, few ration plans take into account this individual variation in initial body composition, and, therefore, variation in nutritional needs. Ration plans should address this issue and provide recommended provisions based on body composition.

The present study has limitations. First, the use of a bioelectrical impedance scale is not the ideal method for measuring body composition due to changes in whole body hydration, particularly at high altitudes (Fulco et al., 1992). Steps were taken to reduce the impact of whole body hydration on measurements, such as collecting data in the morning before subjects ate or drank. Furthermore, all body composition measurements were taken at the same altitude (1633 m) in Lander, WY. Second, the two altitudes covered in this study were not the exact same, there was a difference of 400 m, which makes it difficult to assess the direct effect climate had on body composition changes. Finally, the sample of females in this study was much smaller than that of males. It is likely that with a greater sample size of women some of the trends seen in this study would have approached statistical significance. But, given the constraints of the NOLS curriculum and tendency for NOLS to have a higher male enrollment, these issues could not be avoided.

5 | CONCLUSION

This study reinforces the observed patterns of body mass loss at high altitude through fat and muscle mass loss. This study also establishes the relationship between initial body fat percentage and muscle mass loss, demonstrating the need for more individualized provision planning to mitigate potential muscle mass catabolism during high altitude excursions. Finally, changes in dietary macronutrient content, though high levels of protein have been shown to mitigate muscle mass loss, will not impact body composition changes in the face of a significant negative energy balance.

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