



ORIGINAL RESEARCH ARTICLE

Elevated resting metabolic rates among female, but not male, reindeer herders from subarctic Finland

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Abstract

Objective: Elevated resting metabolic rates (RMR, kcal/day) are a well-established mechanism for maintaining core body temperature among cold climate populations. A high degree of interindividual variation has recently been noted among circumpolar populations. To further examine RMR variability, we investigated anthropometric and metabolic differences among reindeer herders from subarctic Finland.

Methods: Resting metabolic rates, body mass, body composition, height, age, and sex were measured among 20 reindeer herders (5 females, 15 males, 20–64 years) from seven herding districts surrounding the Arctic Circle of Finland in January of 2019.

Results: Females had a mean RMR of 1798 ± 216 kcal/day and males 1753 ± 503 kcal/day. When controlling for body mass and fat-free mass, females had significantly higher RMRs relative to males ($P < .01$). Contrary to previous cold climate population studies, measured RMR among males was not significantly different from predictive equation estimates ($P > .05$). However, predictive equations significantly underestimated female RMR by a mean of $25.2\% \pm 5.9\%$ ($P < .01$).

Conclusion: These results mirror earlier findings, though in ways previously unseen. In this population: (a) There is a high degree of RMR interindividual variability, but only among males, and (b) there is evidence for elevated RMR, but only among females. Though the sample size is small, preliminary results suggest the presence of sex-based differences in metabolic adaptations to cold climates within this population subset. Potential reasons for this sex-based difference are discussed including a presentation of a hypothesis about the dual role of thyroid hormone in both reproductive and metabolic processes.

1 | INTRODUCTION

The inverse relationship between resting metabolic rate (RMR, kcal/day) and mean annual temperature is a well-established pattern among cold climate populations (Folk Jr., 1966; Galloway, Leonard, & Ivakine, 2000;

Abbreviations: RMR, resting metabolic rate; TH, thyroid hormone; RMA, reindeer management area; HD, herding district; FFM, fat-free mass; FM, fat mass; BMI, body mass index; SoS, sum of skinfolds.

Hammel, 1964; Heinbecker, 1928, 1931; Katzmarzyk, Leonard, Crawford, & Sukernik, 1994; W. T. Leonard, Snodgrass, & Sorensen, 2005; W. R. Leonard et al., 2002; Little & Hochner, 1973; Moran, 2008; Snodgrass, Leonard, Tarskaia, Alekseev, & Krivoschapkin, 2005). This higher rate of baseline metabolism is a potential adaptation for maintaining core body temperature despite severe environmental cold stress, whether that stress be due to high latitude or high altitude (Leonard et al., 2002). Though these relationships are broadly accepted, recent work using modern techniques reveals a great deal of inter- and intrapopulation variation (Galloway et al., 2000; Rode & Shephard, 1995). Furthermore, circumpolar populations still remain relatively underrepresented in metabolic studies when considering the preponderance of RMR data among temperate and tropical populations (Snodgrass et al., 2005). The pattern of increasing RMR with decreasing mean annual temperature is far from universal, and requires greater exploration incorporating a wider swath of circumpolar populations.

Over 60% of the variation seen in RMR among humans is attributed to differences in body mass, fat-free mass (FFM) in particular (Johnstone, Murison, Duncan, Rance, & Speakman, 2005). However, age, sex, fat mass (FM), ambient temperature, and height also contribute to this variation, though to a lesser degree. This means that in the absence of direct measurements, RMR can be estimated with data-driven equations that include some combination of the variables listed above (Froehle, 2008; Harris & Benedict, 1919; Henry, 2005; Mifflin et al., 1990; Nelson, Weinsier, Long, & Schutz, 1992; Owen et al., 1986, 1987; Schofield, Schofield, & James, 1985). These equations are also used to generate predictions to which actual measurements can be compared. Such comparisons have become a foundation of cold climate population metabolic studies. For example, W. R. Leonard et al. (2002) performed an analysis on all existing records of circumpolar resting metabolic rates among indigenous and nonindigenous peoples. Investigators found that male and female indigenous participants had RMRs that were +7% to +19% and +3% to +17% higher than predictive values respectively, whereas male and female nonindigenous participants had RMRs that deviated from predictive values by +3% to +14% and -7% to +5%, respectively. More recently, Snodgrass et al. (2005) measured RMRs among the Yakut of Siberia and compared the results to predictive standards cited above. Similar to previous findings, males and females had significantly elevated RMRs, +7% to +18% and +7% to +23%, respectively. These studies not only reaffirm that there is a trend of elevated RMR among cold climate populations, but that there is also a large range of variation within that elevation.

When measurements significantly deviate from predictions or there are unexpected intrapopulation differences, physiological, anatomical, and behavioral explanations for those deviations are sought. From a behavioral perspective, Rode and Shephard (1995) observed a high degree of interindividual RMR variation among Igloolik Inuit, though they noted that older individuals living more traditional life styles tended to have higher RMRs than younger individuals. The impact of life style on interpopulation variation has also been documented elsewhere. For example, Katzmarzyk et al. (1994) worked among male and female Evenki, indigenous reindeer herders from Siberia, comparing the RMRs of individuals who lived in town to those who lived in brigades—camp style living—while tending to reindeer herds. When controlling for differences in body mass, investigators found that individuals in brigades had significantly higher RMRs compared to town residents.

Similarly, RMRs were compared among Evenki reindeer herders living in two different villages—Surinda and Poligus, with Surinda being the more traditional and remote of the two villages (Galloway et al., 2000). When controlling for body mass within this sample, male and female Evenki living in Surinda had RMRs more than 26% and 19% higher, respectively, than their counterparts in Poligus. Investigators credited the RMR difference between the two villages to the more nomadic lifestyle among the Surinda herders, which would mean they were more regularly exposed to harsh, cold conditions. Physiologically, increases in RMR among cold climate populations are positively correlated with increases in thyroid hormone (TH) (Leonard et al., 1999; W. R. Leonard et al., 2002).

Previous work on circumpolar populations has confirmed the well-established pattern of increased RMR with decreased mean annual temperature while also highlighting the high degree of variation within and between circumpolar populations. In an effort to broaden the view and data set on potential cold climate adaptations, we collected anthropometric and resting metabolic rate (RMR) data among male and female reindeer herders from herding districts (HD) in Lapland, the northern province of Finland, on and around the Arctic Circle (Figure 1) during January 2019. We then compared the RMR measurements to predictive standards. We hypothesized that these highly active individuals, who are regularly exposed to the harsh, cold climate, would have elevated resting metabolic rates relative to predictive standards similar to previous work among other circumpolar populations. Results from this study further inform our understanding of cold climate metabolic adaptations and the observed variation within cold climate populations.



FIGURE 1 Map of the study region. Rovaniemi served as a base of operations for the majority of the data collection. The herding districts included in this study are labeled in the lower right inset

2 | METHODS

2.1 | Participant population and reindeer management

The development of reindeer herding in Finland is based on western and eastern traditions. The western tradition developed from or in contact with nomadic Sámi (the Indigenous population of Fenno-Scandinavia) herding, which spread to western Lapland from central parts of Scandinavia during the 16th and 17th centuries (Heikkinen, 2006). In nomadic Sámi herding, Fell Sámi families migrated hundreds of kilometers with their reindeer herds from summer to winter pastures and back again. They used reindeer mainly as a source of meat and milk. The eastern herding tradition, which originated in practices used by Forest, Inari, and Skolt Sámi and later by Finnish peasants was based on small-scale herding,

and combined with hunting, fishing, and farming (Heikkinen, 2006). Forest Sámi did not adopt the yearly nomadic herding cycle or milk reindeer; their animals grazed freely until the round-ups in early winter. They used reindeer mainly as draught animals for transport. When settlements spread from south to north around the turn of the 19th century, Finnish peasants adopted herding practices from the Forest Sámi (Itkonen, 1948; Kortessalmi, 2007; Paulaharju, 1927).

The present reindeer management area (RMA) covers 36% of Finland's surface area and is divided into 54 reindeer HDs (Figure 1). In Finland, all Finnish citizens may practice reindeer husbandry in contrast to Norway and Sweden where the livelihood is mainly an exclusive right of the Sámi. Altogether, 40% of reindeer in Finland are owned by Sámi herders. In the reindeer herding year 2019-2020, there were 188 190 reindeer and 4354 reindeer owners within the RMA. HDs included in this study

ranged from 1104 to 3652 km² in size with 1448 to 5594 reindeer per district (Table 1). Among the herders, 69.7% are male and 30.3% are female (RHA, 2020). In addition to meat production, reindeer husbandry creates employment in the meat processing industry, handicraft production, and tourism. It also has an important position in the cultural and social discourse of the residents in northern Finland (Soppela & Turunen, 2017). In the Sámi home area (13 northernmost HDs) reindeer herds are generally larger, and herding is more commonly the main source of livelihood; whereas in the southern HDs herding is more often combined with other livelihoods, particularly forestry (Jaakkola, Juntunen, & Näkkäläjärvi, 2018). In the southern and central parts of the RMA, boreal forest is largely used as a pastureland for reindeer husbandry, whereas in the northern part of the RMA the pastures are characterized by subarctic mountain birch woodland and fells.

Reindeer herding has experienced fundamental changes since the mid-20th century, including the shift from a subsistence economy to a financial economy and a transition to permanent housing, as well as the introduction of snowmobiles, terrestrial vehicles, and other new technology such as mobile phones and global positioning system collars (Kortesalmi, 2007; Peltto, Linkola, & Sammallahti, 1968). Winter reindeer pastures have become fragmented and have declined in number and quality for several reasons: Finland's cession of territory to the Soviet Union after the Second World War; other competing land use modes including forest and energy industries, mining, and agriculture; and the construction of transportation networks (Soppela & Turunen, 2017; Turunen & Vuojala-Magga, 2014). Competing land use activities and global climate change are among the most serious threats to reindeer management (Soppela &

Turunen, 2017; Turunen, Rasmus, Bavay, Ruosteenoja, & Heiskanen, 2016).

The reindeer herding year starts in May with calving (Helle, 2015; Turunen et al., 2016). In free-ranging calving, reindeer give birth to their calves in their natural calving regions, for example, forested areas or the southern slopes of fells. Calf earmarking is carried out from midsummer onwards. Each reindeer must be marked with the owner's reindeer earmark (Reindeer Husbandry Act, 1990). In enclosure calving, pregnant hinds are separated into a section of their own within the enclosure from March-April until the end of May. In this practice, the calves are earmarked immediately after birth and hinds with a calf are let free thereafter (Turunen et al., 2016). Additional herding work in the summer includes hay-making for possible supplementary feeding during the following winter (Turunen & Vuojala-Magga, 2014).

In autumn, herders start collecting their herds and moving them to the round-up sites either on foot or with the aid of ATVs (all-terrain vehicles), motorbikes, snowmobiles, helicopters, or airplanes. The range of vehicle use can drastically change levels of cold exposure; though not always for the better as high-speed vehicles increase wind exposure and the risk of frostbite (Virokangas, Hassi, Anttonen, & Järvenpää, 1984). The work is facilitated by the rutting time, when male reindeer attract small herds of female reindeer around them. During round-ups the reindeer are counted, the animals to be left alive are separated from those to be slaughtered, and calves not marked in summer get their earmarks (Helle, 2015; Turunen et al., 2016). The reindeer to be left alive also receive medication to prevent parasitic infection. After the round-ups, reindeer are herded onto winter pastures and given supplementary feed, especially

TABLE 1 Size and herding characteristics of the reindeer herding districts included in this study

	Pyhä-Kallio	Poikajärvi	Palojärvi	Narkaus	Niemelä	Isosydänmaa	Oivanki	Reference
Total land area (km ²)	3652	2415	3629	2360	1104	2222	1281	Kumpula et al., 2019
Number of reindeer 2019-2020	5594	4423	4920	2029	1712	1448	2358	RHA, 2020
Reindeer/km ²	1.53	1.83	1.36	0,86	1.55	0.65	1.84	Kumpula et al., 2019, RHA, 2020
Number of reindeer owners	145	98	176	58	46	49	49	RHA, 2020
Infrastructure coverage (% of total land)	2.1	2.5	3.9	4.0	2.6	4.1	7.2	Kumpula et al., 2019

during difficult snow conditions (Turunen & Vuojala-Magga, 2014). During the late winter, reindeer feed on arboreal lichens in old-growth forests where available or on the fells, where snow conditions are more favorable for digging up terricolous lichens. Herders' regular annual work includes protection of reindeer from predators, searching for remains of reindeer lost to predators, and repair of fences among others (Helle, 2015).

2.2 | Participants

Participants in this study included 20 adult herders (20-64 years, 5 females and 15 males, Table 2) recruited from HDs within 180 km of Rovaniemi, Finland (66.5°N, 25.7°E), which is located on the Arctic Circle and served as the base of operations for much of the data collection. Overall, reindeer herding was the primary livelihood for half of the participating herders, and for the other half it was a subsidiary occupation in conjunction with meat-processing, tourism, land measurement, building, and research. However, for all of the females in this study, herding was a subsidiary occupation. Participating HDs included Palojärvi, Niemelä, Narkaus, Pyhä-Kallio, Oivanki, Isosydänmaa, and Poikajärvi (Figure 1). Mean annual temperature in Rovaniemi is 0.9°C (33.6°F) with an average January temperature of -11.3°C (11.7°F) and average July temperature of 15.2°C (59.4°F) (Pirinen et al., 2012).

TABLE 2 Descriptive statistics for age, anthropometrics, and resting metabolic rate

	Females (n = 5)	Males (n = 15)
Age	26.4 ± 6.9***	49.9 ± 9.9
Height (cm)	160.7 ± 3.4***	180.3 ± 7.2
Body mass (kg)	66.4 ± 12.5*	89.7 ± 17.1
BMI (kg/m ²)	25.6 ± 4.0	27.5 ± 4.4
Sum of skinfolds (mm)	87.3 ± 20.8	68.6 ± 29.5
Percent body fat (SoS)	34.6 ± 4.1	28.2 ± 7.6
Percent body fat (BIA)	35.5 ± 5.3**	26.4 ± 4.8
Fat mass (kg/m ²)	24.1 ± 7.4	24.3 ± 8.5
Fat-free mass (kg)	42.3 ± 5.1***	65.5 ± 9.8
RMR (kcal/day)	1798 ± 216	1753 ± 503
Per kilogram RMR (kcal/kg/day)	27 ± 2.6**	19 ± 4.2

Note: Values are represented as means with standard deviations. Significant differences between males and females indicated by: **P* < .05, ***P* < .01, ****P* < .001.

Abbreviations: BMI, body mass index; RMR, resting metabolic rates; SoS, sum of skinfolds.

All measurements for this study were taken in January of 2019, with most of the measurements taken at the Arctic Centre of the University of Lapland in Rovaniemi and others taken at herders' homes, cabins within the HD, or a hotel room near the HD of interest. All participants were active members of HDs and healthy at the time of measurement. Participating females were not pregnant or breastfeeding at the time of this study, and menstrual cycle was not documented. There was a sixth female participant who was breastfeeding, her data was not included in this analysis. This study was conducted with Institutional Review Board approval from the University at Albany (17-E-165) and with the approval of Ostrobothnian Health Care District from the University of Oulu (EETTMK: 4/2018). Participants were provided with an information sheet about the study, and informed written consent (written in Finnish) was obtained from all participants (University of Lapland, 2009).

2.3 | Anthropometry

Anthropometric measurements were taken the same morning of the RMR protocol; as such, participants were overnight fasted at the time of measurement. Height, weight, and skinfold thicknesses were all performed according to standard protocol (Lohman, Roche, & Martorell, 1988). Height was recorded to the nearest 1 mm using a portable stadiometer (Seca Corporation, Hanover, MD). Weight was recorded to the nearest 0.1 kg using an electronic scale (AccuWeight, New York, NY). Body composition was assessed two ways: bioelectrical impedance (RJL systems, Clinton, MI) and four-site skinfold thickness using Lange skinfold calipers (Beta Technology, Santa Cruz, CA). For bioelectrical impedance, participants were asked to refrain from alcohol the day before the measurement. Participants were in a supine position either on a cot or the floor, and small electrodes were placed on the dorsum of the wrist, middle finger, ankle, and middle toe all on the right side. Reactance and resistance were recorded and preset standard BIA-103 equations were used to determine fat-free mass (FFM), body fat percentage, and fat mass (FM). Skinfold thicknesses (bicep, tricep, subscapular, and suprailiac) were measured with no clothing to the 0.5 mm. All measurements were taken by one person (C. O.) and were taken three times at each site, though the average measurement for each site was used for analysis. Sum of skinfolds (SoS) equations from Durnin and Womersley (1974) were used to calculate body fat percentage and FFM.

2.4 | RMR measurements

For RMR measurements, participants were fasted overnight. Participants were familiarized, in Finnish, with the protocol before the start of the measurement. Each participant wore a BCS4 whole-body cooling suit (Med-Eng Ottawa, ON, Canada) during this measurement in anticipation of the brown adipose tissue activity protocol that was conducted immediately following the RMR protocol, results to be published separately. The BCS4 is a cotton sweat suit with tubing sewn into the fabric. No water was in the suit tubing at this time, and measurements took place in a thermoneutral environment. Participants rested in a supine position for 30 minutes before any measurement took place. Once this rest period concluded, indirect calorimetry (Cosmed K5, Cosmed, Chicago, IL) was employed to measure breath-by-breath oxygen consumption and carbon dioxide production in order to calculate RMR. A mask with bi-lateral unidirectional valves (allow inspiration through the valves, but not expiration) was placed over the participant's face, and the measurement period lasted 30 minutes with only the last 10 minutes of the measurement used to calculate volume of oxygen consumed, volume of carbon dioxide produced, and RMR (kcal/day) using the Cosmed Omnia software (Cosmed, Chicago, IL).

2.5 | RMR predictive equations

RMR measurements were compared to several different RMR estimates based on weight, height, age, sex, FFM, FM, and mean monthly temperature. Details of the RMR predictive equations used in this study can be found in Table 3. For the Froehle (2008) equations, the analysis was run twice: once using mean annual temperature and once using mean monthly temperature for January, the month included in this study. The results did not differ between these two methods, so only the mean monthly temperature analysis is presented. Measured RMRs and percent deviation from predictive equations are presented.

Metabolic rate measurements among circumpolar populations were also gathered from the literature and converted into kcal/day. In cases where metabolic rate was expressed per m², controlling for surface area, and surface area data was not made available, a mean surface area of 1.71 and 1.56m² were used for indigenous cold climate males and females respectively (Leonard et al., 2002).

2.6 | Statistical analysis

The data are normally distributed. They are presented as min-max ranges and as means \pm the SD. One-way

TABLE 3 Included variables and references for the resting metabolic rate predictive equations used in this study

Equation	Variables used	Reference
Froehle FFM	Age, sex, FFM, and mean temperature	Froehle, 2008
Froehle mass	Age, sex, body mass, and mean temperature	Froehle, 2008
Harris Benedict	Age, sex, height, and body mass	Harris & Benedict, 1919
Mifflin-St. Jeor	Sex, height, and body mass	Mifflin et al., 1990
Nelson FFM	Sex, FFM	Nelson et al., 1992
Nelson FFM + FM	Sex, FFM, FM	Nelson et al., 1992
Owen	Sex and body mass	Owen et al., 1986, 1987
Oxford	Age, sex, height, and body mass	Henry, 2005
Schofield	Age, sex, and body mass	Schofield et al., 1985

Abbreviations: FFM, fat-free mass; FM, fat mass.

analyses of variance (ANOVAs) were used to compare each age, height, weight, body mass index (BMI), SoS, percent body fat, FM, FFM, RMR, and RMR/kg between females and males. Paired samples *t* tests were used to compare measured RMR to RMR estimates for each of the predictive equations. Linear regressions were used to separately determine the effect of age, herding district, body mass, and FFM on RMR. The sample size for this study was too small to achieve adequate power to run multiple regressions analysis.

3 | RESULTS

3.1 | Participant demographics and anthropometrics

Descriptive statistics and a summary of the means can be found in Table 2. Males (36-64 years) were significantly older than females (20-37 years) ($P < .01$). Males were also significantly taller, heavier, and had more FFM compared to females ($P < .01$ in all instances). Female height ranged from 154.8 to 163.0 cm, weight ranged from 46.7 to 78.9 kg, and FFM ranged from 34.2 to 46.9 kg. Male height ranged from 169.5 to 194.6 cm, weight from 62.9 to 129.6 kg, and FFM from 48.2 to 86.0 kg. Only

bioelectrical impedance revealed a significant difference in body fat percentage with females, ranging from 26.8% to 40.5%, having significantly more body fat than males who ranged from 20.4% to 36.8% ($P < .01$). There was no significant difference in BMI, SoS, or SoS calculated body fat percentage ($P > .09$ in all instances). Female BMI ranged from 19.5 to 29.7 kg/m², SoS from 53.0 to 108.3 mm, and SoS calculated body fat percentage from 27.7% to 38.3%. Male BMI ranged from 20.0 to 34.2 kg/m², SoS ranged from 23.7 to 119.3 mm, and SoS calculated body fat percentage from 13.7% to 40.2%. Among females, 40% of participants were classified as normal weight (BMI = 18.5-24.9) and 60% as overweight (BMI = 25-29.9). Among males, 26.7% were classified as normal weight, 40% as overweight, and 33.3% as obese (BMI >30). There was no significant difference among HDs for body mass or FFM ($P > .1$ in both cases).

3.2 | Resting metabolic rate

Descriptive statistics and a summary of the means for RMR and RMR per kilogram are presented in Table 2. There was no significant difference in resting metabolic between females and males ($P = .32$), due to age ($P = .12$), or due to herding district ($P = .85$). Females ranged from 1427 to 1956 kcal/day, and males ranged from 1004 to 2614 kcal/day. However, the per kilogram RMR was significantly higher among females compared to males (Figure 2); the statistical difference remained when scaling for FFM ($P < .001$ in both cases). Females ranged from 25 to 31 kcal/kg/day, and males ranged from 13 to 30 kcal/kg/day (Figure 3).

3.3 | RMR predictive equation comparisons

Descriptive statistics and a summary of the means and percent differences for RMR predictive equations are summarized in Table 4. Across all participants there was no significant difference between measured RMR and any of the predictive equations ($P > .22$ in all cases). However, when females and males were analyzed separately, predictive equations consistently and significantly *underestimated* RMR among females only ($P < .01$ in all instances) (Figure 4). Females exhibited RMRs 4.3%-38.3% higher than predictive equations. There was no statistical difference between RMR measurements and estimates among males, though there was a high degree of interindividual variation ($P > .05$ in all instances). Measured RMR among males differed from predictive equations by -66.8% to +33.2%.

To account for climatic conditions that may impact RMR, the FAO (1957) recommended increasing RMR

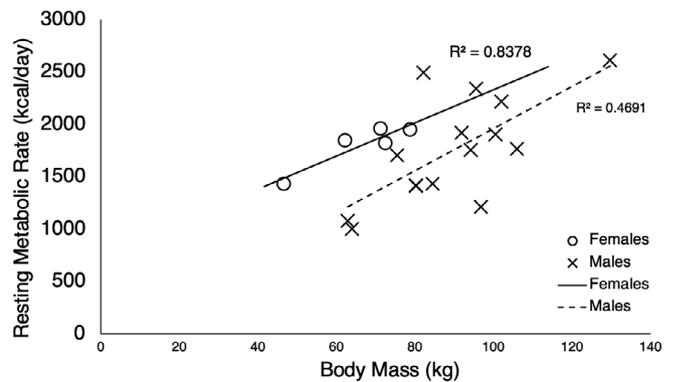


FIGURE 2 Resting metabolic rate relative to body mass among males and females. Females have a higher resting metabolic rate relative to body mass than males

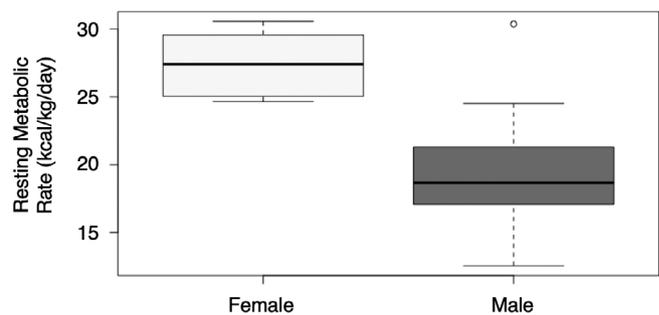


FIGURE 3 Resting metabolic rate per kilogram for female and male participants. Mass correct resting metabolic rates was ~30% higher in females compared to males

estimations by 3% for every 10°C below the reference temperature of 10°C. This recommendation has since been removed for a lack of evidence (FAO, 1973; FAO/WHO/UNU, 1985). However, even when correcting RMR estimations by 6% (mean January temperature of Rovaniemi is -11.3°C), females still had a significantly higher RMR than expected ($P < .01$ for all predictive equations), while men did not ($P > .1$ for all predictive equations). For ease of comparison to previous studies, a compilation of measured RMRs among cold climate populations and their associated deviations from predictive equations are presented in Table 5. Females from the present study follow a similar pattern of deviation as other cold climate populations, ~23% higher than predictive equations, whereas males do not.

4 | DISCUSSION

4.1 | Evidence for elevated RMR among females

In this study, resting metabolic rates were measured during the month of January 2019 among female and male

TABLE 4 Comparisons of measured RMR to RMR predictions for female and male herders as well as the overall sample for data collected during January 2019

	Females (n = 5)	Males (n = 15)	Overall (n = 20)
Measured RMR (kcal/day)	1798 ± 216	1753 ± 503	1764 ± 443
Froehle FFM			
Prediction	1479 ± 92*	1839 ± 148	1749 ± 209
Percent difference	19.0 ± 7.4	-8.3 ± 27.3	-1.5 ± 26.6
Froehle mass			
Prediction	1600 ± 141*	1968 ± 236	1876 ± 268
Percent difference	11.3 ± 5.3	-14.7 ± 22.9	-8.2 ± 22.9
Harris Benedict			
Prediction	1474 ± 102*	1865 ± 280	1767 ± 300
Percent difference	17.5 ± 5.5	-12.4 ± 26.5	-4.9 ± 26.4
Mifflin-St. Jeor			
Prediction	1376 ± 121**	1783 ± 217	1681 ± 265
Percent difference	23.1 ± 3.8	-8.1 ± 26.5	-0.3 ± 26.7
Nelson FFM			
Prediction	1246 ± 114	1764 ± 219	1634 ± 301
Percent difference	30.4 ± 4.0**	-6.8 ± 25.9	2.5 ± 27.7
Nelson FFM + FM			
Prediction	1189 ± 161**	1788 ± 279	1638 ± 366
Percent difference	33.9 ± 3.6	-7.5 ± 24.8	2.9 ± 28.2
Owen			
Prediction	1272 ± 90*	1794 ± 174	1664 ± 279
Percent difference	28.8 ± 5.0	-8.9 ± 25.9	0.5 ± 27.9
Oxford			
Prediction	1379 ± 156**	1838 ± 270	1723 ± 41
Percent difference	23.1 ± 3.6	-10.9 ± 25.8	-2.4 ± 26.9
Schofield			
Prediction	1436 ± 156*	1849 ± 270	1746 ± 304
Percent difference	19.9 ± 4.1	-11.4 ± 26.2	-3.5 ± 26.5

Abbreviations: FM, fat mass; RMR, resting metabolic rates.

* $P < .01$; ** $P < .001$.

reindeer herders in Lapland, Finland. Measured RMRs were compared to several RMR predictive equations which relied on different anthropometric and demographic variables. When controlling for body mass and FFM, females in this sample had significantly higher RMRs than males. To date, such a significantly higher RMR among females compared with males has not been previously documented. Furthermore, females had RMRs that ranged from 4.3% to 38% higher than expected based on predictive equations. Males, on the other hand, exhibited a high degree of variation with predictive equations both underestimating and overestimating RMR within this sample.

The poor performance by predictive equations and high RMRs exhibited among female participants in this study is similar to findings among other circumpolar populations. For example, among the Yakut (Sakha) of Siberia (aged 18-56), male RMR was roughly 1780 kcal/day while female RMR was roughly 1450 kcal/day. In this case both males and females had RMRs significantly higher than predictive equations: 7% to 18% higher in males and 7% to 23% higher in females (Snodgrass et al., 2005). Similarly, elevated RMRs and significant deviations from predictive equations have been found among the Inuit (Rode & Shephard, 1995), the Evenki and Keto (Galloway et al., 2000; Katzmarzyk et al., 1994;

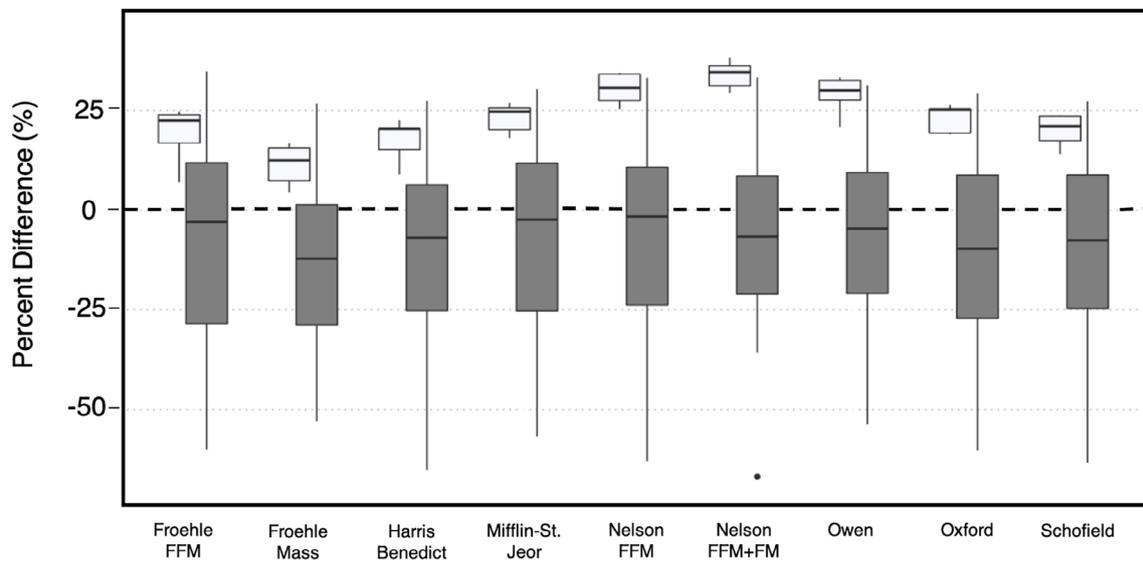


FIGURE 4 Percent difference between measured resting metabolic rates (RMR) and predictive equations for RMR. There was no significant difference between predicted and measured RMR among men (dark bar), but predictive equations consistently and significantly underestimated female RMR (white bar)

W. R. Leonard et al., 2002), and the Buryat (Sorensen et al., 1999). High RMRs and deviations from predictive equations were found only among females in the present study; however, other intriguing sex-based differences have been noted in previous RMR studies.

Among noncircumpolar populations, Owen et al. (1986) found that RMR predictive equations tended to *overestimate* RMR among lean and obese healthy, non-athletic women. Investigators also noted a high degree of variation in their sample independent of body mass and body composition. Among circumpolar peoples, Galloway et al. (2000) compared measured RMRs among indigenous Evenki reindeer herders to nonindigenous Russian immigrants in Central Siberia as well as to predictive equations. Here, investigators found that indigenous and nonindigenous males had elevated RMRs that were not significantly different from one another, though measurements were significantly higher than predictive equations. Indigenous females, on the other hand, had significantly higher RMRs compared to their nonindigenous counterparts. In this case, nonindigenous females appeared to have a depressed RMR relative to indigenous females, and RMR measurements did not appreciably deviate from predictive equations.

These results demonstrate that indigenous and nonindigenous males as well as indigenous females appear to have similar metabolic demands associated with inhabiting a cold environment. Neither the work of Owen et al. (1986) or Galloway et al. (2000) mirror the results of the present study with females exhibiting RMRs

significantly higher than males and males exhibiting a high degree of RMR variability. Furthermore, it is well documented that females have lower RMRs than males, though much of that difference is due to differences in fat free and body mass (Arciero, Goran, & Poehlman, 1993; Buchholz, Rafii, & Pencharz, 2001, for example). To the authors' knowledge, this is the first time RMRs have been observed to be higher among females than males in a human population.

4.2 | Potential causes of RMR differences between females and males

There are several potential causal mechanisms for the high RMR measurements among females relative to males, many are behavioral for which ethnographic data were not collected in this study. First, there could be a bias in participant adherence to pre-RMR protocol and anxiety during RMR measurements. Females may not have adhered as closely to the guidelines for RMR measurement such as being 12-hours fasted and abstaining from caffeine consumption. Females may also have been more anxious leading to higher RMR measurements. However, there was no evidence to suggest this was the case as all participants verbally acknowledged their adherence to the guidelines, did not exhibit anxious behavior, did not exhibit a significant decline in RMR throughout the measurement period, and ravenously consumed coffee and food when offered postmeasurement.

TABLE 5 A compilation of previous work and this present study comparing resting metabolic rate measurements among cold climate populations to predictive equation standards

Study reference	Study population, country	Sample	RMR (kcal/day)	Percent deviation
Heinbecker, 1928	Inuit, Canada	M = 1	1843	+28.8 ^a
		F = 2	1973	+35.5 ^a
Heinbecker, 1931	Inuit, Canada	M = 1	1766	+3.5 ^a
		F = 4	1398	+5.8 ^a
Rabinowitch, Smith, Bazin, & Mountford, 1936	Inuit, Canada	M = 7	1876	+25.7 ^a
		F = 3	1597	+26.7 ^a
Crile & Quiring, 1939	Inuit, Canada	M = 30	1900	+16.6 ^a
		F = 33	1733	+29.4 ^a
Crile & Quiring, 1939	Chippewa, USA	M = 5	2040	+23.2 ^a
		F = 7	1786	+25.0 ^a
Rodahl & Edwards Jr, 1952	Inuit, USA*	M = 52	1735**	+7.8 ^a
		F = 21		
Brown et al., 1954	Inuit, Canada	M = 7	2026	+25.1 ^a
		F = 6	1779	+30.4 ^a
Adams & Covino, 1958	Inuit, USA	M = 6	2052	+25.0 ^a
		F = 0	-	-
Hart et al., 1962	Inuit, Canada	M = 10	2002	+26.7 ^a
		F = 0	-	-
Rennie, Covino, Blair, & Rodahl, 1962	Inuit, USA	M = 6	2815	+52.5 ^a
		F = 0	-	-
Milan, Hannon, & Evonuk, 1963	Inuit, USA	M = 6	1895	+24.3 ^a
		F = 0	-	-
Milan et al., 1963	Athapascan, USA	M = 6	1800	+14.8 ^a
		F = 0	-	-
Milan & Evonuk, 1967	Inuit, USA	M = 6	1805	+12.8 ^a
		F = 0	-	-
Rode & Shephard, 1995	Inuit, Canada	M = 30	1764	+18.7, +11.3 ^{a,b}
		F = 22	1505	+8.9, +9.0 ^{a,b}
Sorensen, Leonard, Spencer, Spitsyn, & Shenin, 1999	Buryat, Russia	M = 50	1707	+9.2 ^a
		F = 59	1351	+3.6 ^a
Galloway et al., 2000	Evenki, Russia	M = 19	1585	+14.0, +3.6 ^{a,b}
		F = 39	1274	+5.6, +2.4 ^{a,b}
Galloway et al., 2000	Russian, Russia	M = 8	1896	+10.4, +10.9 ^{a,b}
		F = 16	1359	-3.6, -5.7 ^{a,b}
Snodgrass et al., 2005	Yakut, Russia	M = 50	1781	+11.5, +6.6, +18.0 ^{a,b,c}
		F = 75	1451	+7.1, +6.5, +23.2 ^{a,b,c}
Present study	Reindeer Herders, Finland	M = 15	1753	-9.9 ^d
		F = 5	1798	+23.0 ^d

Notes: Superscripts refer to the predictive equations used to determine percent deviation.

Abbreviation: RMR, resting metabolic rates.

^aPredictions based on surface area (DuBois, 1924; Consolazio, Johnson, & Pecora, 1963; compiled and compared by Leonard et al., 2002).

^bPredictions based on body mass (Schofield et al., 1985 adopted by FAO, 1985).

^cPredictions based on fat-free mass (Poehlman & Toth, 1995).

^dSee Table 4 for complete list of predictive equations used.

*Mean across four Inuit populations in Alaska included in the study.

**Data for males and females was not presented separately in the original work.

Second, there was a large discrepancy in ages between females and males within this sample. Males tended to skew older and females younger. Differential patterns in RMR with age among circumpolar populations have been previously documented. For example, older individuals who adhered to more traditional lifestyles exhibited higher RMRs than younger individuals (Rode & Shephard, 1995), and Evenki females exhibited a greater decline in RMR with age which investigators associated with increased body fatness and decreased physical activity (Galloway et al., 2000). However, substantial evidence now exists suggesting that this decline is almost entirely due to the loss of FFM associated with aging (Flynn, Nolph, Baker, Martin, & Krause, 1989; Keys, Taylor, & Grande, 1973; Manini, 2010; Piers, Soares, McCormack, & O'Dea, 1998; Tzankoff & Norris, 1977; Zurlo, Larson, Bogardus, & Ravussin, 1990), and there was no significant difference in RMR due to age. Similarly, among the Yakut, there were no significant differences in RMR associated with age once FFM was controlled for (Snodgrass et al., 2005). Furthermore, RMR remained high among females in the present study even when differences in FFM were controlled for. This suggests that differences in age are not the cause of the RMR differences between the sexes.

Third, it has been proposed that genetic differences could account for the high RMRs observed in a number of circumpolar populations (Galloway et al., 2000; Katzmarzyk et al., 1994; W. R. Leonard et al., 2002; Rode & Shephard, 1995; Snodgrass et al., 2005). Previously mentioned differences between indigenous and nonindigenous inhabitants of Central Siberia demonstrated a depressed RMR among nonindigenous females but not males, which could be due to sex-based differences in occupation and cold exposure rather than genetic underpinnings. However, a genetic basis for physiological cold adaptations cannot be ruled out in the present study.

Fourth, occupation associated differences have been previously implicated as a source of RMR variation. For example, Galloway et al. (2000) found that Evenki herders from one region, Surinda, had significantly higher RMRs relative to herders from another region, Poligus. Herders from Surinda followed a more traditional and nomadic style of herding that consisted of higher levels of physical activity and greater exposure to cold conditions relative to the herders from Poligus. Such differences could explain the RMR variation between these two regions. However, HD location did not explain the observed RMR variation in the present study.

Furthermore, one might expect that if there were differences in RMR due to occupation, that it would impact males and females equally unless there was a form of

sexual division of labor. Though this study does not currently have the ethnographic data to explore this possibility, it is an important avenue for future research. When discussing the results with one of the participants, she commented that in her view, male herders tend to use snowmobiles more often and women relied more upon "muscle power." Though anecdotal in nature, her comment suggests the potential for sexual division of labor; though, use of snowmobiles also carries a risk for greater wind exposure (Virokangas et al., 1984). If there were a sexual division of labor such that women were using less technological power and more "muscle power," then one might expect differences in FFM and for the significant difference in RMR to disappear once FFM was controlled for; however, that was not the case in this sample.

Fifth, one potential physiological mechanism for the observed sex-based difference in metabolic rates directly linked to cold climates is the production of thyroid hormone. It is well established that TH increases metabolic rate, and therefore heat production, in response to cold exposure and increased dietary intake (Andersen, Pedersen, Bruun, & Laurberg, 2002; Berry, Clark, Grivell, & Wallace, 1985; Berry et al., 1989; Danforth Jr & Burger, 1989; Laurberg, Andersen, & Karmisholt, 2005; W. R. Leonard et al., 2014; W. T. Leonard et al., 2005; W. R. Leonard et al., 2002; Leonard et al., 1999; Levine, Duffy, Moore, & Matej, 1995; Silva, 1995; Tkachev, Ramenskaya, & Bojko, 1991; Ulijazek, 1996). Work among indigenous and nonindigenous Russians in the subarctic region of Arkhangelsk found increases in thyroxine levels, the predominate form of TH secreted by the thyroid, among both groups in winter, but levels were higher among the indigenous Nenet population relative to nonindigenous individuals (Tkachev et al., 1991). Similarly, indigenous Evenki reindeer herders and nonindigenous Russians living in Siberia had elevated thyroxine levels in the winter. Interestingly, when the sexes were compared separately, Evenki women had significantly higher thyroxine levels and RMRs compared to their female nonindigenous counterparts, whereas there was no significant difference between indigenous and nonindigenous males (Galloway et al., 2000). The combined high thyroxine levels and high RMR among Evenki women as well as the high RMR among Finnish reindeer herding women relative to men in the present study point to a potential nonthermogenic role of TH driving this sex-based difference.

One aspect concerning the nonthermogenic role of TH is the interaction between hypothalamic-pituitary-thyroid axis and the hypothalamic-pituitary-reproductive axis, especially how this interaction functions and changes throughout the menstrual cycle among females. The impacts of menstrual cycle on RMR and TH



production are still understudied and poorly understood. However, there is increasing evidence that TH receptors on the ovaries may play an important role in reproductive physiology. It has been suggested that the thyroid gland may undergo anatomical and functional changes during different phases of the menstrual cycle, though results are few and often contradictory (Doufas & Mastorakos, 2000). For example, De Remigis et al. (1990) examined thyroid size throughout the menstrual cycle, and found it to peak around mid-cycle. Thyroglobulin levels (thyroid hormone precursor) also peaked at mid-cycle, though a change in active TH levels has not yet been demonstrated (Rasmussen, Hornnes, Hegedüs, & Feldt-Rasmussen, 1989). However, Hegedüs, Karstrup, and Rasmussen (1986) found thyroid gland volume to peak in mid-luteal phase, but found no corresponding changes in thyroid function.

Sanchez-Franco, Garcia, Cacicedo, Martin-Zurro, and REY (1973), administered thyrotropin releasing hormone, which leads to TH production via thyroid stimulating hormone (TSH), to evaluate TSH response in men and women. They found that women had a significantly greater TSH response than men, but there was no impact of menstrual cycle phase on this response. It has been suggested that the higher TSH response was mediated by estrogen, but results demonstrating this have been conflicting (Gross, Appleman Jr, & Nicoloff, 1971; Lemarchand-Beraud, Rappoport, Magrini, Berthier, & Reymond, 1974; Ramey, Burrow, Polackwich, & Donabedian, 1975). This suggests that there is an interconnectedness of the hypothalamic-pituitary-thyroid axis with the hypothalamic-pituitary-reproductive axis, and perhaps this interaction works differently between males and females. A better understanding of how this relationship impacts metabolic rate, as metabolic rate is sensitive to TH levels, between females and males as well as throughout the menstrual cycle and pregnancy among females is critically needed. Furthermore, how these interactions may be altered by environmental influences on thyroid hormone production (ie, cold climate) could provide clarity into the sex-based differences in RMR observed in the present study.

4.3 | Cold climates, thyroid hormone, and pregnancy: A hypothesis

Metabolic hormonal axes and reproductive hormonal axes working in concert is never more obvious than during pregnancy. From a strictly metabolic standpoint, thyroid hormone is important for increased metabolism in response to cold exposure, but also plays a key role in

intermediary metabolism of macronutrients (protein, carbohydrates, and fat) for tissue repair and de novo tissue generation (Berry et al., 1985, 1989; Silva, 1995). From a reproductive stand point, de novo tissue anabolism drastically increases during pregnancy and is supported by a 30% to 100% increase in TH (Fantz, Dagogo-Jack, Ladenson, & Gronowski, 1999). If a pregnant woman is unable to produce sufficient amounts of TH, known as maternal thyroid deficiency, there is an increased risk of altered fetal brain developmental as well as increased risk of fetal and neonatal loss (Andersen, Olsen, & Laurberg, 2015; Klein et al., 1991). Furthermore, if maternal hypothyroidism is detected and treated early, there is a significant risk reduction (Yassa, Marqusee, Fawcett, & Alexander, 2010). It is likely that cold climate inhabiting women have adaptively higher TH levels for coping with extreme cold climates, which has been previously demonstrated (Galloway et al., 2000; W. R. Leonard et al., 2002; Tkachev et al., 1991; Ulijazek, 1996). In order to maintain a successful pregnancy, cold climate women must increase TH levels ~30% to 100% higher than an already elevated baseline. It is possible that successful pregnancies in cold climates require an absolutely higher TH level than successful pregnancies in temperate or hot climates.

Advanced technologies, particularly with clothing and home heating, have reduced the thermogenic demands of living and working in Arctic regions, thereby potentially reducing the environmental pressures that increase TH levels and RMRs. These relaxed thermogenic pressures could explain the highly variable RMRs among men; more detailed ethnographic work would help elucidate this potential transition in cold climate cultural coping mechanisms. However, women experience a dual role for TH: maintain a higher thermogenic output, but also maintain a successful pregnancy. Even if thermogenic pressures were relaxed, an absolutely higher TH level may still be needed to maintain a successful pregnancy in circumpolar populations. This could explain the persistently high RMR levels in women in the present study—maintain a higher baseline in order to attain the higher TH level needed should she become pregnant. The dual metabolic demands of a cold climate and reproduction suggest women may be more resistant to environmental changes that could reduce TH levels relative to men. There are currently no studies among humans examining the impact the interaction between cold climate and pregnancy has on TH levels. Future work needs to be conducted investigating thyroid hormone levels among cold climate inhabiting pregnant women, nonpregnant women throughout the menstrual cycle, and men with extensive accompanying ethnographic work.

4.4 | Limitations and avenues for future work

Though the results of this study are highly intriguing, there are a number of limitations. First, the data in this study was collected during the month of January. It is likely that a high degree of seasonal variation exists in this population. Seasonal variation in thyroxine levels, correlated with RMR, is well documented among indigenous and nonindigenous Siberian populations (W. R. Leonard et al., 2002; Tkachev et al., 1991). Measuring RMR at different points throughout the year would clarify if seasonality is a potential source of variation. Second, the overall sample size is small. It is possible that the high RMR among females is due to sampling error, and that with a larger number of participants a high degree of RMR variability would be observed among females similar to what was seen among males in this population. Third, menstrual cycle was not documented or controlled for in this study and could be a confounding factor. Fourth, heart rates were not collected simultaneously with RMR; doing so would rule out the potential for sex-based differences in anxiety levels during RMR measurement. Fifth, northern Finland is home to the indigenous Sámi, but for sociopolitical reasons we were unable to inquire if participants identified as Sámi, leaving the potential for uniquely indigenous cold climate adaptations confounding the results of this study. However, Finland does not restrict reindeer herding exclusively to individuals identifying as Sámi; as such Sámi and non-Sámi have intermarried and participated in this culturally important occupation for generations (Soppela & Turunen, 2017).

5 | CONCLUSION

The results of this study both support and contradict previous work done among cold climate populations. High resting metabolic rates were observed, but only among female participants, even when controlling for differences in body mass. The high RMRs among women in this study are likely due to both behavior and physiology. We hypothesize that the driving force behind differential metabolic and thyroid activity are potentially related to the energetic demands of pregnancy and cold climate adaptation. In order to better understand this observed variation in RMR, further study is needed, examining not only metabolic rate but also thyroid hormone levels and differences in division and style of labor within this population.

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AUTHOR CONTRIBUTIONS

Cara Ocobock, Päivi Soppela, Minna T. Turunen, and Karl-Heinz Herzig designed this study. Cara Ocobock, Päivi Soppela, Minna T. Turunen, and Ville Stenbäck collected data. Cara Ocobock, Päivi Soppela, Minna T. Turunen, Ville Stenbäck, and Karl-Heinz Herzig all wrote and edited this manuscript.

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