Received: 25 April 2023 | Revised: 16 August 2023 | Accepted: 28 August 2023

DOI: 10.1002/ajpa.24846

AMERICAN JOURNAL OF BIOLOGICAL ANTHROPOLOGY WILEY

RESEARCH ARTICLE

# Lifestyle and patterns of physical activity in Hadza foragers

M. Katherine Sayre[1] | Mariamu Anyawire[2] | Bunga Paolo[2] | Audax Z. P. Mabulla[3] | Herman Pontzer[4,5] | Brian M. Wood[6,7] | David A. Raichlen[1,8]

[1]Human and Evolutionary Biology Section, Department of Biological Sciences, University of Southern California, Los Angeles, California, USA

[2]Mang'ola, Karatu, Tanzania

[3]Department of Archaeology and Heritage Studies, University of Dar es Salaam, Dar es Salaam, Tanzania

[4]Department of Anthropology, Duke University, Durham, North Carolina, USA

[5]Duke Global Health Institute, Duke University, Durham, North Carolina, USA

[6]Department of Anthropology, University of California Los Angeles, Los Angeles, California, USA

[7]Department of Human Behavior, Ecology, and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[8]Department of Anthropology, University of Southern California, Los Angeles, California, USA

**Correspondence**
M. Katherine Sayre, Human and Evolutionary Biology Section, Department of Biological Sciences, University of Southern California, Los Angeles, CA, USA.
Email: mksayre@ucsb.edu

**Funding information**
Max-Planck-Institut für Evolutionäre Anthropologie; National Institute on Aging, Grant/Award Numbers: R01AG72445, R56AG067200; National Science Foundation, Grant/Award Numbers: NSF-BCS 1440671, NSF-BCS 1440867, NSF-BCS 2051519

## Abstract

**Objectives:** Physically active lifestyles are associated with several health benefits. Physical activity (PA) levels are low in post-industrial populations, but generally high throughout life in subsistence populations. The Hadza are a subsistence-oriented foraging population in Tanzania known for being physically active, but it is unknown how recent increases in market integration may have altered their PA patterns. In this study, we examine PA patterns for Hadza women and men who engage in different amounts of traditional foraging.

**Materials and Methods:** One hundred and seventy seven Hadza participants (51% female, 19–87 years) wore an Axivity accelerometer (dominant wrist) for ~6 days during dry season months. We evaluated the effects of age, sex, and lifestyle measures on four PA measures that capture different aspects of the PA profile.

**Results:** Participants engaged in high levels of both moderate-intensity PA and inactivity. Although PA levels were negatively associated with age, older participants were still highly active. We found no differences in PA between participants living in more traditional "bush" camps and those living in more settled "village" camps. Mobility was positively associated with step counts for female participants, and schooling was positively associated with inactive time for male participants.

**Conclusions:** The similarity in PA patterns between Hadza participants in different camp types suggests that high PA levels characterize subsistence lifestyles generally. The sex-based difference in the effects of mobility and schooling on PA could be a reflection of the Hadza's gender-based division of labor, or indicate that changes to subsistence-oriented lifestyles impact women and men in different ways.

KEYWORDS
accelerometry, Hadza hunter-gatherers, MVPA, physical activity, step counts

## 1 | INTRODUCTION

Engaging in a physically active lifestyle is associated with a wide range of health benefits. Physical activity (PA) is positively associated with physical and cognitive function throughout the lifespan, and with benefits to mental health, sleep, and overall quality of life (Blodgett et al., 2015; Bull et al., 2020; Erickson et al., 2019; Marquez et al., 2020; Piercy et al., 2018). Furthermore, in addition to associations with lower risk of all-cause mortality, engaging in a physically active lifestyle is linked with decreased risk of cardiovascular disease, type 2 diabetes, several types of cancer, and dementia (Ekelund et al., 2015; Piercy et al., 2018; Ramakrishnan et al., 2021). The health benefits of PA become increasingly important with age, as the risk of developing one or more of these chronic diseases or conditions increases (Bull et al., 2020; Piercy et al., 2018).

In post-industrial populations, levels of PA are low and decrease with age (Bull et al., 2020; Lee & Park, 2021; Piercy et al., 2018; Ussery et al., 2021; Wolff-Hughes et al., 2015). People living in subsistence-oriented populations, on the other hand, often display high levels of PA throughout life and into older adulthood (Caldwell, 2016; Pontzer et al., 2018). Here, we examine physical activity and sedentary behavior in the Hadza, a subsistence-oriented population of hunter-gatherers who live in northern Tanzania and are known for engaging in high levels of PA throughout life (Hawkes et al., 1989; Marlowe, 2010; Pontzer et al., 2015; Raichlen et al., 2017; Raichlen et al., 2020; Sayre et al., 2020). As with most subsistence-oriented populations, though, increased market integration (MI) has altered the lifestyles of many Hadza women and men, and it is unknown how those changes in lifestyle have impacted their patterns of PA. In this study, we aim to characterize the PA patterns of Hadza women and men who engage in traditional foraging, as well as those who are more market integrated.

### 1.1 | Patterns of PA in post-industrial and subsistence populations

The increased use and availability of activity-tracking devices, which provide an objective measure of PA, facilitate both the study and comparison of PA patterns in post-industrial and subsistence-level populations around the globe (Ramirez Varela et al., 2021). Data from large-scale epidemiological studies highlight several consistent trends in PA patterns among people living in post-industrial populations: Levels of activity are generally low and decline with age, and levels of inactivity are high and increase with age (DiPietro, 2001; Doherty et al., 2017; Du et al., 2019; Hallal et al., 2012; Lee & Park, 2021; Piercy et al., 2018; Troiano et al., 2008; Trost et al., 2002; Tucker et al., 2011; Ussery et al., 2021; Varma et al., 2017; Yen & Li, 2019). Men and people with higher educational attainment are generally more active than women and those with less education (Azevedo et al., 2007; Lee & Park, 2021; Piercy et al., 2018; Plotnikoff et al., 2004; Shaw & Spokane, 2008; Troiano et al., 2008; Trost et al., 2002; Yen & Li, 2019).

The lifestyles of people in subsistence-oriented societies have long been characterized as more physically demanding than those of people in post-industrial societies (e.g., Eaton et al., 1988). Studies that use accelerometers and heart-rate monitors to measure PA in subsistence-level populations have confirmed that characterization: People who engage in traditional foraging, hunting and gathering, pastoralism, and small-scale agriculture display high levels of PA throughout life (see Caldwell, 2016 for review). Men are frequently more physically active than women (Christensen et al., 2012; Gurven et al., 2013; Kraft et al., 2021; Madimenos et al., 2011; Sayre et al., 2018) though not always (Raichlen et al., 2017; Sarma et al., 2020; Sayre et al., 2020; Yamauchi et al., 2001). Significant age-related differences have been detected in some populations (Christensen et al., 2012; Gurven et al., 2013; Kashiwazaki et al., 2009), but not in others (Gurven et al., 2013; Madimenos et al., 2011; Raichlen et al., 2017). While it is possible that there exist populations whose activity levels do not decline with age, a lack of age-related differences in PA may also stem from aspects of study design, including smaller sample sizes and limited age ranges of participants.

For decades, increased market integration (MI) has altered the lifestyles of people in subsistence-oriented populations. Market integration involves commodifying resources like labor, land, and goods and services (Lu, 2007). In the last few decades, MI has become a growing focus of research in biological anthropology. While several studies have examined the heterogeneous health effects of increased MI (e.g., Lea et al., 2020; Urlacher et al., 2016, 2021), fewer studies have carefully documented corresponding changes in behavior and physical activity. Yamauchi et al. (2001) documented differences in work-related PA levels of rural- versus urban-dwelling Huli in Papua New Guinea. But Urlacher et al. (2021) found no differences in the physical activity levels or total energy expenditure of Shuar children living in peri-urban versus rural contexts, despite displaying differences in other cardiometabolic measures. Gurven et al. (2013) measured activity levels in the Tsimané in Bolivia and found no differences in PA levels between those who live near to or further from a large city where market activities are concentrated. Given the ubiquity of MI in subsistence-oriented populations, it is critical that we examine both how the lifestyles of people in these populations are changing, and how those changes impact health and well-being.

In this study, we characterize patterns of physical activity (PA) for Hadza women and men aged 19–87 years old. We then evaluate how three measures of foraging and lifestyle—type of camp of residence, annual mobility, and schooling experience—impact patterns of PA for Hadza participants (see Section 2: Methods for further description of lifestyle variables). The use of these measures of lifestyle allows us to better understand how transitions in foraging practices of Hadza women and men may impact PA as a key health-related aspect of their lifestyle. Most anthropological research with the Hadza community, including that of our team, has focused primarily on those women and men who live in more remote bush camps, and continue to engage in traditional foraging practices on a (more or less) full-time basis. These more traditional "bush" Hadza engage in high levels of PA, and display low prevalence of biomarkers for cardiovascular disease (Pontzer et al., 2015; Raichlen et al., 2017, 2020; Sayre et al., 2020). Other recent work has compared Hadza adults and children living in bush and non-bush camps and highlights how changes in subsistence engagement over the past several decades have impacted health measures and other dimensions of lifestyle in complex ways. For example, Crittenden et al. (2017) found that the oral health of Hadza women living in bush camps was better than that of women living in villages, but the opposite was true for Hadza men. Pollom et al., (2020) found that a mixed subsistence diet had positive effects on growth for younger Hadza boys and girls. The current study is the first to examine how PA differs among groups of Hadza with variable access to and engagement with markets, and will help us better understand the implications of MI for PA-related health outcomes.

## 2 | METHODS

### 2.1 | Study population: Hadza foragers of Tanzania

The Hadza are a subsistence-oriented population comprised of approximately 1200 women and men who live near Lake Eyasi in northern Tanzania (Marlowe, 2010). The Hadza traditionally live in mobile camps of ~30 people (range of 1–100 people), and individuals are highly mobile, moving between different camp locations in response to changes in the availability of key resources (wild foods, water), to visit kin and friends, and to resolve social disputes. In Hadza society, a gendered division of labor prevails in which women typically target plant foods (tubers, berries, leafy greens) and men typically target animals and harvest wild honey. Women typically forage in groups (with and without children), and men typically forage solitarily. This gender-based division of labor arises early in life, around age 6 (Wood, Harris, et al., 2021). The foraging activities of both women and men are physically intensive; although daily step counts are higher in Hadza men compared to Hadza women (Wood, Harris, et al., 2021), all adults spend large amounts of time in moderate-to-vigorous physical activity (MVPA) every day (Raichlen et al., 2017; Sayre et al., 2020).

Over the past several decades, large-scale changes to the environment and the transformation of the Tanzanian economy have posed challenges to the Hadza community's ability to continue engaging in subsistence-level foraging on a full-time basis (Gibbons, 2018; Marlowe, 2002). For example, increased migration into the region and land conversion owing to agriculture and pastoralism have lowered the availability of prey animals and other wild foods (Wood, Millar, et al., 2021). A growing public interest in the lives of traditional hunter-gatherers has also resulted in an increase in ethnotourism since the mid-1990s, especially in the Mang'ola area (Gibbons, 2018; Marlowe, 2002). As a result of these and other changes, many Hadza women and men choose to live in more permanent or settled camps and villages, which have better access to medical care, schooling, roads, and the market economy. In these more settled camps, Hadza women and men engage in different kinds of subsistence activities, including small-scale agriculture, selling and trading craft goods, and seasonal work employed on farms to either protect or harvest crops (Gibbons, 2018; Marlowe, 2002).

We recruited 177 Hadza participants ($n_{female} = 91$; $n_{male} = 86$) from ages 19 to 87 (age mean ± SD = 45.32 ± 17.90 years) from 11 different camps to participate in this study. In addition to a willingness to participate, our inclusion criteria for recruitment were that the participant self-identify as a member of the Hadza community, and that they be able to speak Hadzane (their native language). Upon arrival in each camp, we met with Hadza community members to discuss the project and recruit participants. We did not proceed with data collection until we had verbal consent from both the community and individual participants to conduct research there. Data collection took place between June and December 2021. Typically, the dry season in this region spans June to November, and the short rains begin in December. When we finished data collection in early December 2021, the rains had not yet begun. Data collection therefore only occurred during dry months. Lead author MKS spoke with Hadza research participants in Kiswahili while research assistants MA and BP, who are members of the Hadza community, translated and further explained instructions in Hadzane.

Research permits and approval were acquired from all appropriate agencies, including the Institutional Review Board of the University of Southern California (UP-20-00465) and the Tanzania Commission for Science and Technology (COSTECH). We took several precautions to minimize the risk of COVID-19 transmission among the researchers, research assistants, and both Hadza and non-Hadza community members throughout the field season. Details of our COVID-19 precautions can be found in the Supplementary Information S1.

### 2.2 | Measures of lifestyle

We evaluated aspects of foraging engagement and lifestyle using three measures that could impact patterns of PA: type of camp of residence, annual mobility, and schooling experience. A subset of 152 participants ($n_{female} = 79$; $n_{male} = 73$) completed a mobility questionnaire (see Supplementary Information S1) with questions about current and previous camp residency, as well as the number of different places the participant visited during the previous year. Most participants ($n_{female} = 83$; $n_{male} = 75$) completed a schooling questionnaire (see Supplementary Information S1), which allowed us to measure their schooling experience.

#### 2.2.1 | Resident camp type

In this study, we worked with Hadza living in more remote "bush" camps, where individuals relied mostly on foraging for subsistence, as well as those living in more permanent and accessible "village" camps, where residents had a more mixed subsistence lifestyle. We use "camp type" (bush or village) as a proxy measure for a participant's degree of foraging engagement. We used the data collected from the mobility questionnaire to determine which camp a participant considered their home or most persistent residential location. We categorized each of the Hadza camps where we worked (or where a participant considered home, for those individuals who self-identified as visitors) as either a "bush" or "village" camp, based on discussions with MA and BP, who have both traveled widely throughout the region and have local expertise, as well-connected members of the Hadza community. From our discussions, Hadza bush camps were identified as those in which the adults engage in traditional foraging practices more frequently and regularly than those living in village camps.

#### 2.2.2 | Annual mobility

One of the key elements of the Hadza's traditional lifestyle is their high degree of mobility, which likely impacts PA (Marlowe, 2010). In addition to moving camp locations or residences, Hadza women and men also regularly visit other camps and locations for a variety of reasons—

for example, to set up a temporary camp to access ephemeral resources, or sometimes just to visit family members or friends who live in more distant places. In this study, we use "annual mobility" as a proxy measure for each participant's degree of mobility (e.g., Davis et al., 2021). Specifically, participant responses to the mobility questionnaire were used to count the number of different places where a participant reported staying for at least one night over the previous year.

#### 2.2.3 | Schooling

Government initiatives to send all Tanzanian children to school over the past several decades have resulted in many Hadza children being sent to school, with varying degrees of continued engagement with formal schooling. Education has consistently been linked to PA patterns in post-industrial populations (Plotnikoff et al., 2004; Shaw & Spokane, 2008; Trost et al., 2002; Yen & Li, 2019), and is often used as a proxy measure for increased market integration (MI) in subsistence-oriented populations (Gurven et al., 2013; Veile et al., 2014). Self-reported years of schooling, collected in our schooling questionnaire, is our measure of engagement with formal education.

### 2.3 | Measures of physical activity

Participants were asked to wear a triaxial accelerometer (Axivity AX3, Newcastle, UK) on the dominant wrist continuously for between two and ten days. Differences in wear time across participants arose as a result of field logistics and the challenges of accessing and working in different camp locations. Hand dominance was determined by asking about which hand was used for important tasks (see Supplementary Information S1). Accelerometers were set to initialize collecting data at 100 Hz for 10 days, beginning at midnight of the first day the participant wore the accelerometer. Accelerometers were collected from participants at the end of the wear time period, and the data were immediately downloaded using OMGUI software (Open Movement, Newcastle University, UK).

Raw accelerometry data were downloaded through the open-source OMGUI software and processed using the R package *GGIR* (v2.4) (Migueles et al., 2019; Sabia et al., 2014; Team, 2021; van Hees et al., 2013, 2014, 2018). We followed the accelerometry data processing and analysis methods outlined by Doherty et al. (2017). Briefly, using *GGIR*, non-wear time is identified as periods of time in which the movement of all three axes has a standard deviation of less than 13 m*g* for 60 consecutive minutes. The data are divided into 5 s epochs, and acceleration data from the three axes are used to calculate an average acceleration vector magnitude for each epoch. One gravitational unit is subtracted from the vector magnitude to account for Earth's gravity, and the data are output as the Euclidean Norm Minus One (ENMO), which is a measure of an individual's average acceleration in m*g*.

We followed the accelerometer wear-time-based inclusion criteria that Doherty and colleagues used to analyze physical activity patterns in the UK Biobank dataset (Doherty et al., 2017): Participant accelerometry data is included if the data includes (1) at least three valid days (one day = at least 16 of 24 h) of wear-time, and (2) valid data for each of the 24 hours in one day. We excluded 14 participants who did not meet this wear-time inclusion criteria ($n_{female} = 7$; $n_{male} = 7$). We further excluded two participants ($n_{female} = 1$; $n_{male} = 1$) whose average daily acceleration values exceeded four standard deviations above the mean. A total of 161 participants ($n_{female} = 83$; $n_{male} = 78$) met our inclusion criteria for accelerometry data analysis. Finally, we excluded participants who were missing mobility and/or schooling data, and a total of 136 ($n_{female} = 71$; $n_{male} = 65$) participants were analyzed to evaluate our research questions.

Time spent in different levels of physical activity (PA) intensity were calculated using ENMO-based cut-offs published by Hildebrand and colleagues (Hildebrand et al., 2014, 2017): light-intensity (between 45 and 100 m*g*), moderate-intensity (between 100 and 420 m*g*), and vigorous-intensity (at or above 420 m*g*). We used these cut-offs to calculate several PA measurements in *GGIR*:

1. *Average daily minutes in moderate-to-vigorous physical activity (MVPA)*: The health benefits of engaging in MVPA (activity at or above three METs; Norton et al., 2010) are well-established (Ekelund et al., 2015; Moore et al., 2012; Rey Lopez et al., 2020; Warburton et al., 2006). Health officials recommend engaging in at least 150 min/week of MVPA (Bull et al., 2020; Piercy et al., 2018). Average daily minutes spent in moderate-to-vigorous physical activity (MVPA) was calculated as time spent above the moderate-intensity activity threshold (100 m*g*).
2. *Percent of total time in MVPA in moderate-intensity activities (% $MVPA_{mod}$)*: Evaluating whether time in MVPA is accumulated in primarily moderate- or vigorous-intensity activities allows us to better characterize the nature of the high levels of PA that Hadza women and men display. The percent of MVPA time spent in moderate- as opposed to vigorous-intensity activities was calculated as the amount of time in moderate-intensity activities (between 100 and 420 m*g*) divided by the total time spent in MVPA (above 100 m*g*).
3. *Average daily step count*: Step counts are becoming an increasingly popular way to evaluate a person's overall PA engagement (King et al., 2019; Kraus et al., 2019; Piercy et al., 2018). Higher daily step counts are associated with reduced risk of all-cause mortality, several chronic diseases (Hall et al., 2020; Hamer et al., 2022; Paluch et al., 2022; Raichlen & Lieberman, 2022; Saint-Maurice et al., 2020), and dementia (Del Pozo Cruz et al., 2022). Furthermore, step counts are particularly important for understanding the PA patterns of subsistence-oriented populations, whose lifestyles are characterized by a high amount of walking (e.g., Leonard & Robertson, 1997; Marlowe, 2005; Pontzer et al., 2015; Raichlen & Lieberman, 2022). We used an algorithm developed by Verisense to calculate average daily step counts in *GGIR*. The algorithm is based on work conducted by Gu et al. (2017) to detect steps from tri-axial accelerometry data.
4. *Average daily time spent inactive*: Time spent inactive is associated with a range of health effects, including greater risk of all-cause mortality and cardiometabolic diseases (Biswas et al., 2015; Brocklebank et al., 2015; Cavallo et al., 2022; de Rezende et al., 2014; Patterson

et al., 2018). Furthermore, decreases in PA and increases in inactivity are frequently cited as important lifestyle changes associated with increased market integration (e.g., Assah et al., 2011; Eaton et al., 1988; Katzmarzyk & Mason, 2009). Average daily waking time spent inactive was calculated as time spent below the light-activity threshold (45 mg).

## 2.4 | Statistical analysis

We used linear regression analysis to characterize the physical activity patterns of Hadza research participants, and to examine associations between measures of lifestyle and physical activity. Modeled on the statistical approach of Gurven et al. (2013), we first evaluated the effects of age, sex, camp type, annual mobility, and schooling on each PA measure, without interactions (Model 1). Then, we used a simultaneous inclusion procedure to add all two-way interactions between age and sex, and age or sex and lifestyle measures, if they resulted in lower AIC values relative to Model 1 (Model 2). We controlled for accelerometer wear-time in all analyses. All regression models were inspected graphically and numerically for normality of residuals, and all met the criteria for use of generalized linear models (independence of observations, normality of residuals, linearity, and constant variance). We used a Benjamini-Hochberg FDR (Benjamini & Hochberg, 1995) to correct for multiple hypothesis testing. Results were considered significant if the FDR-adjusted $p$-value was less than 0.05.

# 3 | RESULTS

## 3.1 | Descriptive statistics

Descriptive summaries are presented in Table 1. Of the 161 participants who met our inclusion criteria for accelerometry analysis (see Section 2: Methods), 51.6% were female, and average age was 45.5 (SD 18.3) years. Average accelerometer wear-time was 6.2 (SD 2.1) days. Almost half ($n = 67$; 41.6%) of the participants lived in a bush camp. Among the participants who completed the mobility questionnaire ($n_{female} = 71$; $n_{male} = 65$), average annual mobility was 2.5 (SD 2.1) places per year, and

**TABLE 1** Descriptive characteristics

| | | Female participants $n = 83$ | Male participants $n = 78$ | Total $n = 161$ |
|---|---|---|---|---|
| *Physical activity measures* | | | | |
| Age (years) | Mean (SD) | 47.16 (18.96) | 43.80 (17.40) | 45.54 (18.25) |
| | Range | 19–87 | 19–86 | 19–87 |
| Accelerometer wear-time (days) | Mean (SD) | 6.36 (2.09) | 6.08 (2.02) | 6.22 (2.06) |
| | Range | 3–11 | 3–11 | 3–11 |
| MVPA (minutes) | Mean (SD) | 173.70 (76.95) | 173.21 (78.50) | 173.66 (77.46) |
| | Range | 19.13–375.40 | 27.50–369.55 | 19.13–375.40 |
| % $MVPA_{mod}$ | Mean (SD) | 94.76 (3.95) | 94.56 (3.66) | 94.66 (3.80) |
| | Range | 81.88–99.85 | 83.60–99.40 | 81.88–99.85 |
| Step count | Mean (SD) | 14,186.33 (4,959.90) | 15,963.63 (5,676.60) | 15,047.38 (5,376.75) |
| | Range | 2,543.05–24,685.75 | 2,957.32–30,672.38 | 2,543.05–30,672.38 |
| Inactive time (hours) | Mean (SD) | 11.26 (2.53) | 12.32 (2.42) | 11.78 (2.53) |
| | Range | 5.24–17.05 | 6.09–16.68 | 5.24–17.05 |
| *Lifestyle measures* | | | | |
| Camp type | Bush camp resident No. (%) | 36 (43.37%) | 31 (39.74%) | 67 (41.61%) |
| | Village camp resident No. (%) | 47 (56.62%) | 47 (60.26%) | 94 (58.39%) |
| Annual mobility (no. places) | *n* | 71 | 65 | 136 |
| | Mean (SD) | 1.81 (1.68) | 3.21 (2.22) | 2.48 (2.07) |
| | Range | 0–7 | 0–9 | 0–9 |
| Schooling experience (years) | *n* | 83 | 75 | 158 |
| | Mean (SD) | 1.73 (3.04) | 3.04 (3.59) | 2.35 (3.37) |
| | Range | 0–11 | 0–11 | 0–11 |
| | Yes schooling No. (%) | 29 (34.94%) | 40 (53.33%) | 69 (43.67%) |
| | No schooling No. (%) | 54 (65.06%) | 35 (46.67%) | 89 (56.33%) |

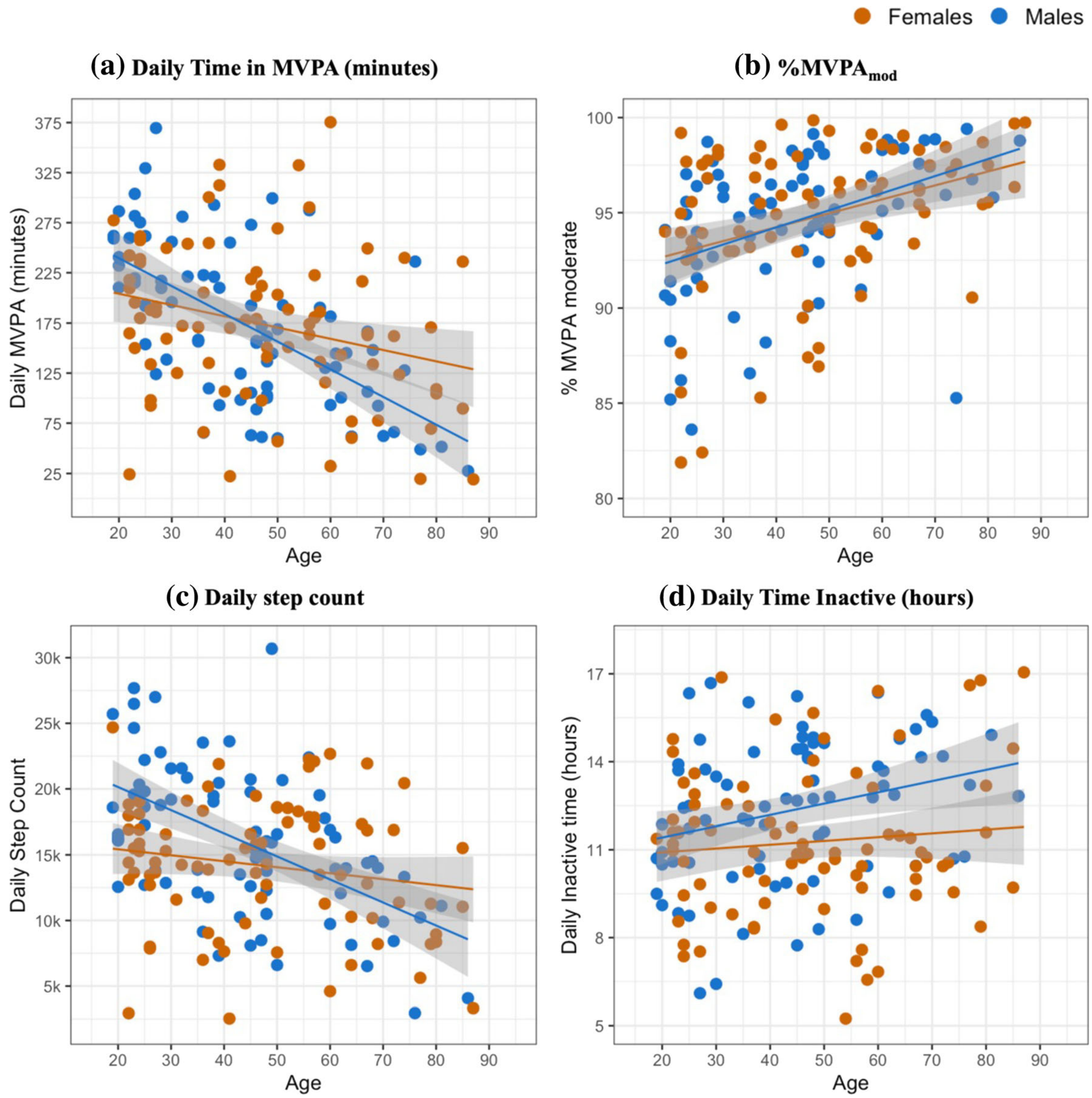


**FIGURE 1** Physical activity measures by age and sex for Hadza participants. Each filled orange circle represents one Hadza female participant (ages 19–87 years), and one filled blue circle represents one Hadza male participant (ages 19–86 years). Orange and blue lines represent a generalized linear model for female and male participants, respectively. Gray shaded area represents the 95% confidence interval for the regression line. Physical activity measures here are derived from wrist-worn accelerometers, and represent average daily (a) time (minutes) spent in moderate-to-vigorous physical activity (MVPA); (b) percent of MVPA time spent in moderate-intensity activities; (c) step count; (d) time (hours) spent inactive.

was higher for male than for female participants ($mobility_{female} = 1.8 \pm 1.7$ places; $mobility_{male} = 3.2 \pm 2.2$ places; $p < 0.001$). Among the participants who completed the schooling questionnaire ($n_{female} = 83$; $n_{male} = 75$), almost half ($n = 69$; 43.7%) had some schooling experience, ranging from 1 to 11 years. Male participants had more years of schooling, on average, compared to female participants ($schooling_{female} = 1.7 \pm 3.0$ years; $schooling_{male} = 3.0 \pm 3.6$ years; $p = 0.015$).

## 3.2 | Time spent in moderate-to-vigorous physical activity (MVPA)

Figure 1a displays average daily time spent in MVPA by age for Hadza female and male participants. Average time spent in MVPA was high for all participants: Hadza female participants spent 173.7 ± 77.0 min/day in MVPA, and Hadza males spent 173.6 ± 78.5 min/day in MVPA (Table 1). This is well above the 150 min/*week* of MVPA that health officials in the United States recommend (Piercy et al., 2018). Age was significantly negatively associated with average daily time in MVPA (Table 2), but even participants aged 60 years and older ($n = 40$) spent an average of more than two hours per day in MVPA (mean ± SD = 125.6 ± 74.7 min). Time in MVPA did not significantly differ between female and male participants (Table 2), but the effect of age was different for female and male participants (Table 2): Male participants displayed more pronounced age-related differences in MVPA than did female participants (Figures 1a and 2a).

Measures of lifestyle were not significantly associated with time in MVPA. Time spent in MVPA did not differ for participants in bush versus village camps (Table 2), and was not associated with either annual mobility (Table 2) or schooling (Table 2). Although our second model includes interactions between sex and annual mobility, and sex and schooling, these interactions were not significant after adjusting for multiple hypothesis testing (Table 2). Accelerometer wear time was not associated with time spent in MVPA in Model 1 ($\beta_{\text{wear time}}$ [95% confidence interval (CI)] = 6.31 [0.29, 12.33], $p_{adj} = 0.07$) or Model 2 ($\beta_{\text{wear time}}$ [95% CI] = 7.03 [1.22, 12.85], $p_{adj} = 0.05$).

**TABLE 2** Generalized linear regression model of average daily time spent in moderate-to-vigorous physical activity (MVPA) for 161 Hadza female and male participants.

| | Model 1 (AIC = 1539.3) | | | | Model 2 (AIC = 1531.6) | | | |
|---|---|---|---|---|---|---|---|---|
| Variable | Estimate | ±SE | 95% CI [lower, upper] | *p*-Value† | Estimate | ±SE | 95% CI [lower, upper] | *p*-Value† |
| Age | −1.730 | 0.331 | [−2.379, −1.080] | **8.95e−06*** ** | −0.895 | 0.422 | [−1.723, −0.067] | 0.082° |
| Sex (male) | −6.476 | 12.496 | [−30.968, 18.017] | 0.656 | 121.750 | 38.793 | [45.717, 197.783] | **0.014*** |
| Camp type (village) | −17.906 | 12.092 | [−41.606, 5.794] | 0.183 | −17.967 | 11.708 | [−40.914, 4.981] | 0.183 |
| Annual mobility | 3.391 | 3.123 | [−2.730, 9.511] | 0.330 | 9.844 | 4.611 | [0.807, 18.880] | 0.082° |
| School (years) | −3.915 | 1.864 | [−7.568, −0.262] | 0.082° | 1.052 | 2.775 | [−4.386, 6.490] | 0.705 |
| Age × sex (male) | | | | | −1.817 | 0.634 | [−3.060, −0.574] | **0.021*** |
| Sex (male) × annual mobility | | | | | −11.282 | 6.139 | [−23.314, 0.750] | 0.111 |
| Sex (male) × School (years) | | | | | −7.267 | 3.669 | [−14.458, −0.076] | 0.093° |

*Note*: Model 1 results are from a generalized linear regression model with all variables present and no interactions. Model 2 results are from a generalized linear regression model with all variables present, as well as any two-way interactions between age, sex, and lifestyle variables that reduce the AIC of Model 1. Interactions for Model 2 were chosen using a simultaneous inclusion procedure. All results shown are adjusted for accelerometer wear-time. Bold *p*-values are those that are significant at the $p < 0.05$ level.

†*p* Values shown are FDR-adjusted for multiple hypothesis testing; °$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

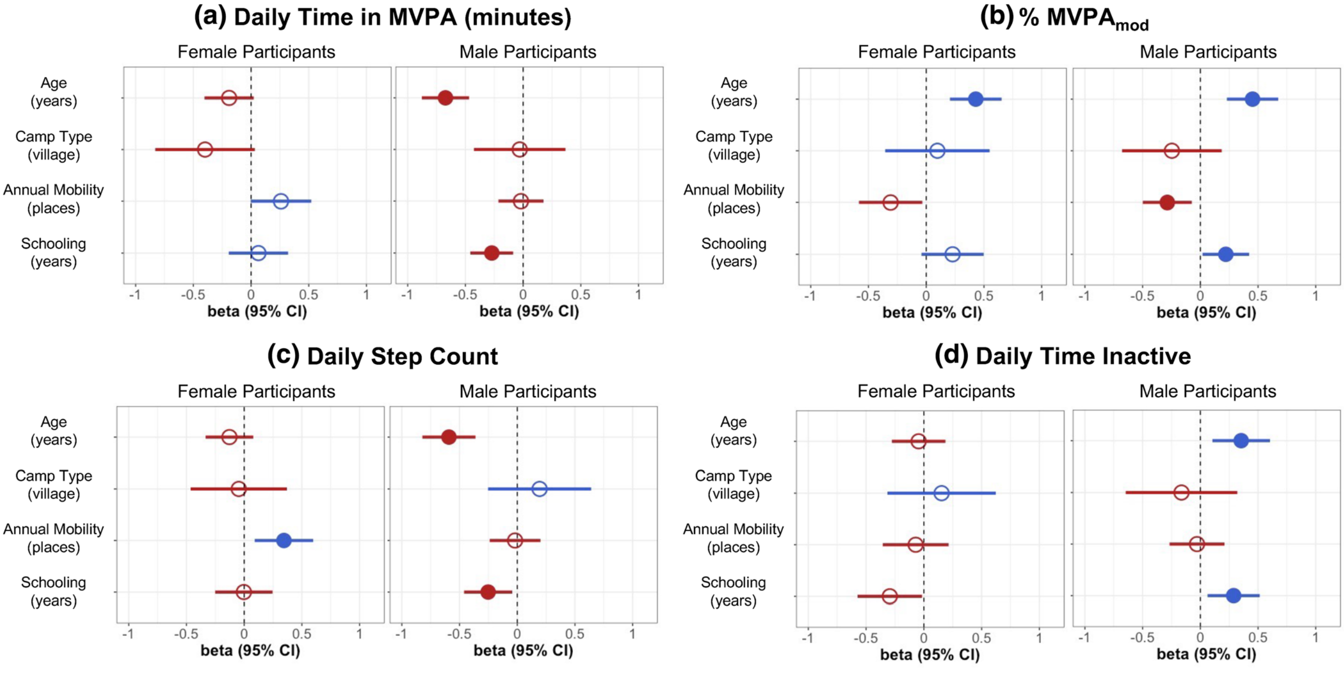


**FIGURE 2** Effects of age, sex, and foraging and lifestyle variables on physical activity measures. Beta coefficient plots represent results from generalized linear models, stratified by sex. Results of models with female participants are on the left of each panel, and results of models with male participants are on the right of each panel. Blue circles represent a positive beta coefficient, and red circles represent a negative beta coefficient. Unfilled circles represent a non-significant effect, and filled circles represent a significant effect, after FDR adjustment. Panels represent beta coefficient plots for average daily (a) time (minutes) spent in moderate-to-vigorous physical activity (MVPA); (b) percent of MVPA time spent in moderate-intensity activities; (c) step count; (d) time (hours) spent inactive.

### 3.3 | Percent of MVPA spent in moderate-intensity activities (%$MVPA_{mod}$)

Figure 1b displays the percent of average daily time in MVPA spent in moderate-intensity activities by age for Hadza female and male participants. Hadza female and male participants accumulated the vast majority of their time in MVPA in moderate- (as opposed to vigorous-) intensity activities: Moderate-intensity activities made up 94.8 ± 4.0% of MVPA time for female participants, and 94.6 ± 3.7% of MVPA time for male participants (Table 1; Figure 3). Age was significantly positively associated with %$MVPA_{mod}$ (Table 3), and %$MVPA_{mod}$ did not differ for female and male participants (Table 3).

All three measures of lifestyle were associated with %$MVPA_{mod}$ for participants in this study. Although participants in bush versus village camps did not display differences in %$MVPA_{mod}$ (Table 3), the effect of age differed for participants in different camp types (Table 3): The effect of age on %$MVPA_{mod}$ was more pronounced for participants in bush camps compared to those in village camps. Annual mobility was negatively associated with %$MVPA_{mod}$ (Table 3), and schooling experience was positively associated with %$MVPA_{mod}$ (Table 3). Accelerometer wear time was not associated with %$MVPA_{mod}$ in Model 1 ($\beta_{wear\ time}$ [95% CI] $= -0.27$ [$-0.56$, 0.03], $p_{adj} = 0.10$) or Model 2 ($\beta_{wear\ time}$ [95% CI] $= -0.32$ [$-0.61$, $-0.02$], $p_{adj} = 0.06$).

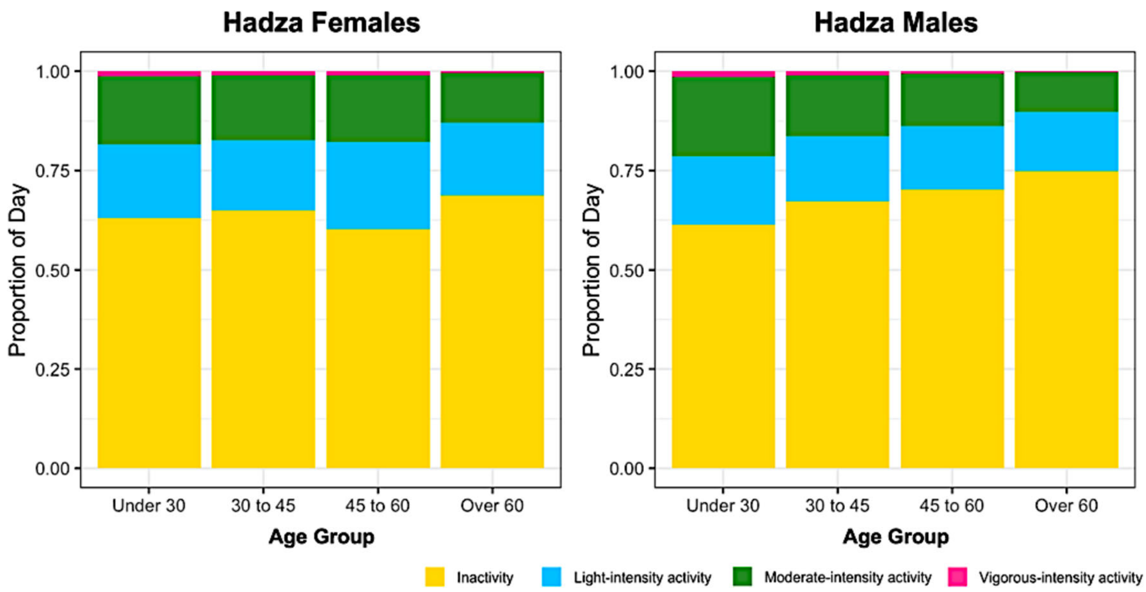


**FIGURE 3** Proportion of waking hours spent in different levels of activity intensities for Hadza female (left panel) and male (right panel) participants. Yellow shaded area represents proportion of waking hours spent inactive; blue shaded area represents proportion of waking hours spent in light-intensity activities; green shaded area represents proportion of waking hours spent in moderate-intensity activities; and pink shaded area represents proportion of waking hours spent in vigorous-intensity activities.

**TABLE 3** Generalized linear regression model of percent of average daily MVPA spent in moderate-intensity activities (%$MVPA_{mod}$) for 136 Hadza female and male participants.

| | Model 1 (AIC = 721.62) | | | | Model 2 (AIC = 717.79) | | | |
|---|---|---|---|---|---|---|---|---|
| Variable | Estimate | ±SE | 95% CI [lower, upper] | *p*-Value† | Estimate | ±SE | 95% CI [lower, upper] | *p*-Value† |
| Age | 0.090 | 0.016 | [0.057, 0.122] | **1.39e−06*** ** | 0.133 | 0.024 | [0.085, 0.181] | **1.39e−06*** ** |
| Sex (male) | 0.533 | 0.618 | [−0.679, 1.745] | 0.429 | 0.621 | 0.609 | [−0.572, 1.814] | 0.378 |
| Camp type (village) | −0.220 | 0.598 | [−1.393, 0.952] | 0.713 | 3.327 | 1.610 | [0.172, 6.482] | 0.056° |
| Annual mobility | −0.530 | 0.154 | [−0.833, −0.227] | **2.95e−03** ** | −0.466 | 0.154 | [−0.769, −0.164] | **8.26e−03** ** |
| School (years) | 0.252 | 0.092 | [0.071, 0.433] | **0.016*** | 0.216 | 0.092 | [0.035, 0.396] | **0.032*** |
| Age × camp type (village) | | | | | −0.077 | 0.032 | [−0.140, −0.013] | **0.032*** |

*Note*: Model 1 results are from a generalized linear regression model with all variables present and no interactions. Model 2 results are from a generalized linear regression model with all variables present, as well as any two-way interactions between age, sex, and lifestyle variables that reduce the AIC of Model 1. Interactions for Model 2 were chosen using a simultaneous inclusion procedure. All results shown are adjusted for accelerometer wear-time. Bold *p*-values are those that are significant at the *p* < 0.05 level.

†*p* Values shown are FDR-adjusted for multiple hypothesis testing; °*p* < 0.1; **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

**TABLE 4** Generalized linear regression model of average daily step count for 136 Hadza female and male participants.

| Variable | Model 1 (AIC = 2699) | | | | Model 2 (AIC = 2692.2) | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | ±SE | 95% CI [lower, upper] | p-Value† | Estimate | ±SE | 95% CI [lower, upper] | p-Value† |
| Age | −97.926 | 23.531 | [−144.046, −51.806] | **6.88e−04*****| −52.616 | 29.463 | [−110.364, 5.131] | 0.115 |
| Sex (male) | 1032.467 | 887.879 | [−707.743, 2772.677] | 0.296 | 8866.941 | 2662.024 | [3649.470, 14084.412] | **6.80e−03**** |
| Camp type (village) | 352.875 | 859.171 | [−1331.069, 2036.820] | 0.682 | 364.831 | 837.475 | [−1276.590, 2006.252] | 0.682 |
| Annual Mobility | 353.324 | 221.874 | [−81.542, 788.190] | 0.152 | 902.459 | 329.875 | [255.915, 1549.002] | **0.028*** |
| School (years) | −307.526 | 132.432 | [−567.087, −47.965] | **0.044*** | −242.808 | 130.226 | [−498.047, 12.431] | 0.111 |
| Age × sex (male) | | | | | −112.663 | 44.722 | [−200.317, −25.010] | **0.036*** |
| Sex (male) × annual mobility | | | | | −1072.213 | 434.374 | [−1923.570, −220.856] | **0.036*** |

*Note*: Model 1 results are from a generalized linear regression model with all variables present and no interactions. Model 2 results are from a generalized linear regression model with all variables present, as well as any two-way interactions between age, sex, and lifestyle variables that reduce the AIC of Model 1. Interactions for Model 2 were chosen using a simultaneous inclusion procedure. All results shown are adjusted for accelerometer wear-time. Bold *p*-values are those that are significant at the $p < 0.05$ level.

†*p* Values shown are FDR-adjusted for multiple hypothesis testing; °$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

## 3.4 | Daily step count

Figure 1c displays average daily step count by age for Hadza participants. Average daily step count was high for all: Hadza female participants took an average of 14,186 ± 4960 steps per day, and Hadza male participants took an average of 15,964 ± 5677 steps per day (Table 1). Step count was significantly negatively associated with age (Table 4). Step counts for female participants were not significantly different from those of male participants (Table 4), but the effect of age differed for female and male participants (Table 4). As with time in MVPA, male participants in this study displayed more pronounced age-related differences in step count compared to female participants (Figures 1c and 2c).

Daily step count did not differ for participants in bush versus village camps (Table 4), but was negatively associated with participants' schooling experience (Table 4). After adjusting for interactions (Model 2), we found that the relationship between mobility and step counts differed by sex (Table 4): Annual mobility was positively associated with step counts for female participants, but not associated with step counts for male participants (Figure 2c). Accelerometer wear time was not associated with average daily step counts in Model 1 ($ß_{\text{wear time}}$ [95% CI] = 197 [−231, 625], $p_{\text{adj}} = 0.42$) or Model 2 ($ß_{\text{wear time}}$ [95% CI] = 210 [−204, 625], $p_{\text{adj}} = 0.40$).

## 3.5 | Inactive time

Figure 1d displays average daily waking time (hours) spent inactive by age for Hadza participants. Average daily time spent inactive was high: 11.3 ± 2.5 h/day for females, and 12.3 ± 2.4 h/day for males (Table 1). Neither age nor sex was significantly associated with time spent inactive (Table 5). Although our second model included an interaction between age and sex, this interaction was not significant (Table 5).

Somewhat surprisingly, none of the three-lifestyle measures were significantly associated with time spent inactive in model 1 (Table 5). In our second model (which includes interaction terms), however, we found that the relationship between schooling and inactivity differed by sex (Table 5): Schooling was not significantly associated with time spent inactive for female participants, but positively associated with time spent inactive for male participants (Figure 2d). Accelerometer wear time was significantly negatively associated with time spent inactive in Model 1 ($ß_{\text{wear time}}$ [95% CI] = −19.51 [−32.88, −6.13], $p_{\text{adj}} = 0.02$) and Model 2 ($ß_{\text{wear time}}$ [95% CI] = −21.63 [−34.56, −8.71], $p_{\text{adj}} < 0.01$).

# 4 | DISCUSSION

In this study, Hadza female and male participants engaged in high levels of both physical activity *and* inactivity during dry season months. Younger participants generally engaged in higher amounts of physical activity (PA) than older participants, but older participants were still highly active compared to adults in post-industrial populations. We found no

**TABLE 5** Generalized linear regression model of average daily time (minutes) inactive for 136 Hadza female and male participants.

| | Model 1 (AIC = 1756.4) | | | | Model 2 (AIC = 1747.9) | | | |
|---|---|---|---|---|---|---|---|---|
| Variable | Estimate | ±SE | 95% CI [lower, upper] | p-Value† | Estimate | ±SE | 95% CI [lower, upper] | p-Value† |
| Age | 1.334 | 0.736 | [−0.108, 2.776] | 0.173 | −0.154 | 0.937 | [−1.991, 1.682] | 0.970 |
| Sex (male) | 55.645 | 27.761 | [1.235, 110.056] | 0.150 | −131.596 | 76.433 | [−281.402, 18.210] | 0.175 |
| Camp type (village) | 1.132 | 26.864 | [−51.520, 53.783] | 0.970 | 0.985 | 25.969 | [−49.913, 51.882] | 0.970 |
| Annual mobility | −0.829 | 6.937 | [−14.425, 12.768] | 0.970 | −2.901 | 6.825 | [−16.277, 10.476] | 0.970 |
| School (years) | 2.933 | 4.141 | [−5.182, 11.049] | 0.823 | −12.468 | 6.166 | [−24.554, −0.382] | 0.150 |
| Age × sex (male) | | | | | 2.752 | 1.391 | [0.026, 5.478] | 0.150 |
| Sex (male) × school (years) | | | | | 26.010 | 8.063 | [10.206, 41.813] | **0.019*** |

*Note*: Model 1 results are from a generalized linear regression model with all variables present and no interactions. Model 2 results are from a generalized linear regression model with all variables present, as well as any two-way interactions between age, sex, and lifestyle variables that reduce the AIC of Model 1. Interactions for Model 2 were chosen using a simultaneous inclusion procedure. All results shown are adjusted for accelerometer wear-time. Bold *p*-values are those that are significant at the $p < 0.05$ level.

†*p* Values shown are FDR-adjusted for multiple hypothesis testing; °$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

evidence for sex-based differences in PA engagement, nor did we find differences in PA engagement between participants living in bush versus village camps. Mobility and schooling impacted PA patterns, sometimes in different ways for female and male participants. We believe the results of this study can help us understand how changes in subsistence engagement impact an important aspect of lifestyle—physical activity patterns—for Hadza women and men.

### 4.1 | High levels of mostly moderate-intensity physical activity

Physical activity levels during dry season months are high among Hadza participants in this study compared to their counterparts in post-industrial societies. Health officials in the United States and other developed countries recommend engaging in at least 150 minutes per week of moderate-to-vigorous physical activity (MVPA; Bull et al., 2020; Piercy et al., 2018). Recommendations for daily step counts are less consistent, but range from 6000 to 10,000 per day (Del Pozo Cruz et al., 2022; Hamer et al., 2022; Paluch et al., 2022; Saint-Maurice et al., 2020). In this study, participants engaged in an average of more than 150 minutes *per day* of MVPA, and daily step counts averaged 15,000 (Table 1). Although older Hadza participants displayed lower levels of PA than younger participants, they were still highly active. Participants aged 70 and above ($n = 18$) engaged in an average of 109.0 ± 73.7 min/day of MVPA and took an average of 10,055 ± 4611 steps/day. Not only do these levels of PA exceed health-based PA recommendations, they also exceed levels of PA displayed by older adults in post-industrial populations like the United States, where older adults engage in less than 10 min/day of MVPA (Evenson et al., 2011; Troiano et al., 2008).

For participants in this study, physical activity was primarily of moderate-intensity. On average, more than 90% of time in MVPA was spent in moderate-intensity (as opposed to vigorous-intensity) activities (%$MVPA_{mod}$; Table 1). Although younger participants displayed lower %$MVPA_{mod}$ compared to older participants, the majority of their time in MVPA was still spent in moderate-intensity activities. In this study, %$MVPA_{mod}$ ranged from 81.8% to 99.8% (Table 1), which is notable for two reasons. First, even the most highly active participants still accumulated the vast majority of their time in MVPA in moderate-intensity activities. These results complement those of Gurven et al. (2013), who report that PA for Tsimané foragers in Bolivia can be characterized as primarily light- to moderate-intensity.

Second, none of the participants in this study spent 100% of their time in MVPA in moderate-intensity activities; even older adults engaged in a few minutes of vigorous-intensity PA per day. Regular engagement in even small amounts of vigorous-intensity PA may offer several cardioprotective benefits (e.g., Rankin et al., 2012; Stamatakis et al., 2021). In fact, a recent study found that short (one- to two-minute) intermittent bouts of vigorous-intensity physical activity were associated with substantial decreases in both all-cause and cardiovascular mortality (Stamatakis et al., 2022). Hadza women and men show no evidence of risk factors for cardiovascular disease (CVD; Raichlen et al., 2017). It is possible that regular engagement in small amounts of vigorous-intensity activity, in addition to the high levels of moderate-intensity activity, could contribute to the cardiovascular health of Hadza women and men, especially at older ages.

### 4.2 | High levels of physical inactivity

Participants in this study also displayed high levels of *in*activity—female and male participants spent more than 11 h/day inactive (Table 1). Spending large amounts of time sedentary is associated with several health risks (e.g., Biswas et al., 2015; Cavallo et al., 2022; Patterson et al., 2018). The high amounts of physical inactivity displayed by participants in this study, though, do not necessarily indicate negative health risks. First, time spent inactive by Hadza may be quite different from time spent inactive in post-industrial populations. Many of the health risks associated with sedentary time in post-industrial populations are specific to time spent sitting and watching TV (Dunstan et al., 2011; Patterson et al., 2018; Raichlen et al., 2022). Raichlen et al. (2020) report high amounts of non-ambulatory time in Hadza adults (more than 9 h/day), but found that Hadza women and men spent much of that time in active rest postures (e.g., squatting instead of chair sitting; Raichlen et al., 2020). Therefore, the sedentary behavior in this study might not be associated with the same risks of sedentary time seen in post-industrial populations if inactive time is spent in more active rest postures. Second, high levels of moderate-intensity PA appear to attenuate the health risks associated with too much sedentary time for many chronic conditions, and could eliminate them at the highest levels of PA (i.e., 60–75 min/day of MVPA; Biswas et al., 2015; Ekelund et al., 2016). The high levels of PA displayed by participants in this study could offset the risks of high levels of inactivity.

## 4.3 | No sex-based differences in measures of PA

In this study, PA measures did not differ between female and male participants. In our models without interactions, sex was not significantly associated with time spent in MVPA, $\%MVPA_{mod}$, daily step counts, or time spent inactive. The similarity in PA measures between female and male participants in this study contrasts with the sex-based patterns observed in post-industrial populations, where women consistently display lower PA levels and higher inactive time compared to men (Hallal et al., 2012; Lee & Park, 2021; Piercy et al., 2018; Varma et al., 2017; Yen & Li, 2019). The relationship between female and male PA levels in subsistence-based populations is more variable. In many subsistence populations—including Ecuadorian Shuar foragers, Bolivian Tsimané forager-horticulturalists, several Kenyan agriculturalists, and Kenyan Pokot agro-pastoralists—men display higher levels of PA than women (Christensen et al., 2012; Gurven et al., 2013; Madimenos et al., 2011; Sayre et al., 2018). In Huli–speaking agriculturalists in Papua New Guinea, though, women and men engage in similar amounts of PA (Yamauchi et al., 2001). In BaYaka foragers in the Congo basin, women display *higher* amounts of PA compared to men (Sarma et al., 2020).

Previous work examining sex differences in PA among Hadza foragers has yielded mixed results. Kraft et al. (2021) found that the energy costs of subsistence activities was higher for men than for women in both Hadza foragers and Tsimané forager-horticulturalists. Our team has found little-to-no sex differences in accelerometer- or heart-rate monitor (HRM)-based MVPA for Hadza foragers (Raichlen et al., 2017; Sayre et al., 2020), but a pronounced sex difference in GPS-based daily step counts (Wood, Harris, et al., 2021): as early as 6 years old, Hadza males in bush camps travel further per day than Hadza females in bush camps, a difference only attenuated at older ages. A sex–based difference in daily step counts but similarity in overall MVPA would suggest that more of Hadza men's time in MVPA is spent walking, while more of women's time in MVPA is spent in other activities (e.g., digging for tubers, processing food). Indeed, Kraft and colleagues report that Hadza men spend the majority of their subsistence-based energy walking, while Hadza women spend a large portion of their subsistence-based energy digging and processing food (Kraft et al., 2021).

In this study, we did not find sex-based differences in overall MVPA or daily step counts (Tables 2 and 4). While our previous work has focused on Hadza women and men in foraging camps, this study includes participants from a range of Hadza communities who engage in different subsistence activities. However, we also did not find evidence of camp-based differences in the effect of sex on PA measures. Our study also included data from only dry season months. The GPS–based step count sample (Wood, Harris, et al., 2021) reflects data collected over a longer period of time and could therefore capture both seasonality and variations in Hadza ranging behavior over time, potentially accounting for differences in outcomes between the two studies. Future work that combines different methodologies (GPS, accelerometry, and heart rate) and/or examines specific subsistence activities participants engage in while wearing the devices will help us better understand how PA patterns compare for Hadza women and men.

While we did not find sex-based differences in overall PA for participants in this study, we found that the associations between age and both MVPA and daily step count were more pronounced for male compared to female participants. Although this differential association between age and female and male PA differs from some of our previous work (Sayre et al., 2020), it is consistent with prior research showing that men's travel after age 35 (km/day walked) decreases more so than women's (Pontzer et al., 2015; Wood, Harris, et al., 2021). This results in smaller sex differences in daily travel being observed at older ages, a pattern also evident in the current study.

## 4.4 | No camp-based differences in measures of PA

Subsistence-oriented populations around the world have experienced changes to their traditional lifestyles as a result of increased engagement in the market economy, or market integration (MI). The health effects of increasing MI are often attributed to changes in diet and activity patterns. When examining how MI impacted cardiovascular health among the Turkana of Kenya, Lea et al. (2020) found that diet mediated health differences between rural- and urban-dwelling Turkana. But Lea and colleagues found no health-related differences between rural Turkana who continued to engage in traditional pastoralism, and those who did not. Similarly, Gurven et al. (2013) did not find evidence for differences in Tsimané PA patterns across geographic regions with differential access to the market economy, likely because the Tsimané across those regions still relied heavily on horticulture and foraging for subsistence.

In this study, we found little-to-no evidence of camp-based differences in patterns of PA displayed by participants during dry season months. We categorized camps as either bush or village according to local knowledge regarding the regularity and frequency of foraging engagement (see Section 2: Methods). Hadza adults' traditional foraging way of life is frequently characterized as physically demanding because of the subsistence activities they engage in, but foraging is certainly not the only physically demanding mode of subsistence. People living in a variety of subsistence-oriented populations display high levels of PA throughout life (Gurven et al., 2013; and see Caldwell, 2016 for review). Many Hadza women and men who do not engage in full-time foraging have adopted other subsistence practices that are also physically demanding, including small-scale agriculture. During data collection, we also informally observed that several Hadza women and men in non-foraging communities spend their days engaging in day labor (e.g., making bricks, operating corn-grinding machines) or collecting firewood or honey from community bee hives to sell or trade to non-Hadza community members.

Furthermore, Hadza women and men may engage in activities not related to subsistence that are still physically active. Kraft et al. (2021) found that, compared to our great ape relatives, humans spend more energy but less time on subsistence activities. Compared to other great apes, then, human subsistence strategies allow for more time spent in leisure activities, like social interactions. Indeed, Hadza women and men in both foraging and non-foraging communities appeared to spend a good deal of time engaged in non-subsistence activities, like visiting with friends and family. In the larger and more spread-out non-foraging communities, especially, we often informally observed participants walking to and from different households, the village center, and the Hadza-specific community meeting space. Our informal observations underscore the importance, in future work, of documenting the subsistence and non-subsistence activities that participants engage in to better understand how the PA patterns of Hadza women and men compare across different types of communities.

It is important to note that although Hadza bush and village camps may differ in their subsistence activities or in access to the market economy, none of them represent an *urban* context. Our results suggest that the generally high levels of mostly moderate-intensity activity displayed by study participants reflect both a rural lifestyle context and multiple economic pursuits, all of which are physically demanding.

## 4.5 | Associations with mobility and schooling

Both annual mobility and experience schooling impacted PA patterns in this study. In our models without interactions, annual mobility and schooling were only significantly associated with $\%MVPA_{mod}$: Participants with lower annual mobility and those with more schooling experience displayed higher $\%MVPA_{mod}$. In our models with interactions, we found that these lifestyle effects were significantly associated with both daily step counts and time spent inactive, and those effects differed for female and male participants. The differential impact of mobility and schooling on measures of PA for female and male participants could be a reflection of their gender-based division of labor, and/or indicate that changes in subsistence activities impact Hadza women and men in different ways.

In this study, annual mobility was positively associated with step counts for female participants, but negatively associated with step counts for male participants. The sex-based difference in the effect of mobility on step counts in this study seems primarily driven by how much more pronounced and positive the effect of mobility is for female step counts. When we stratify analyses by sex, mobility continues to be positively associated with step counts for female participants ($\beta$ [95% confidence interval (CI)] $= 892$ steps [235, 1549]; Table S3) but is not associated with step counts for male participants ($\beta$ [95% CI] $= -49$ steps [$-618$, 521]; Table S3). It is unclear to us why mobility during the previous year would impact daily step counts differently for women and men. We used annual mobility—the total number of places visited during the previous year—to represent general mobility in this study. However, we did not take into account the number of times a participant visited a place, the length of their stay, or distance traveled. Future work that examines the nature of Hadza women's and men's mobility patterns in more detail (e.g., total distance traveled or total time away from home) may help us understand why general mobility was positively associated with step counts for female participants in this study, but not for male participants.

We also found sex-based differences in the effect of schooling on time spent inactive. School was associated with significantly more inactive time for male participants ($\beta$ [95% CI] $= 13.0$ min [2.8, 23.2]; Table S4), and was not associated with inactive time in women ($\beta$ [95% CI] $= -13.3$ min [$-25.9$, $-0.7$]; Table S4). In post-industrial populations, education often reflects socio-economic status (SES), and is positively associated with leisure-time PA (Azevedo et al., 2007; Lee & Park, 2021; Shaw & Spokane, 2008). In work with subsistence-oriented populations, access to schooling is frequently used as a proximate measure for market integration (MI), and its effect on PA patterns is less clear. Among Tsimané forager-farmers in Bolivia, for example, neither schooling nor Spanish fluency (another measure of MI) were associated with levels of PA, though Spanish fluency was associated with women's BMI (Gurven et al., 2013).

The differential effect of schooling on inactivity for Hadza female and male participants could reflect differences in how MI has impacted Hadza women and men. A little less than half of the participants in this study had schooling experience, and male participants had, on average, more years of schooling compared to female participants. Schooling experience may provide different work-related opportunities for Hadza women and men, or differential access to the market economy. Future work that compares the kinds of work that Hadza adults with and without schooling have access to and participate in might help us better understand why the relationship between schooling and inactivity differed for female and male participants in this study.

## 4.6 | Limitations

In this study, we used accelerometry to characterize the PA patterns of Hadza women and men across adulthood. To measure PA, participants wore an accelerometer on their wrist for several days (wear-time mean ± SD $= 6.22 \pm 2.06$ days; Table 1). In post-industrial populations, at least 3 days of accelerometer wear-time is sufficient to capture habitual PA (Matthews et al., 2012; Trost et al., 2005), but the same may not be true for subsistence-oriented populations, who do not necessarily adhere to the same week-based calendar. Furthermore, our data collection took place between June and December, so this study only reflects PA in the dry season. Examining PA across seasons would allow us to better represent habitual PA patterns among the Hadza, as seasonality impacts subsistence activities and PA in other groups (e.g., Gurven et al., 2013; Panter-Brick, 1996).

We used wrist-worn accelerometry to estimate daily steps. Although hip-based accelerometry generally provides a more accurate measure of step counts (e.g., Nuss et al., 2020), we used an algorithm developed by Verisense to estimate daily step counts from wrist-worn tri-axial accelerometry, specifically (Gu et al., 2017). We would like to note that this step count algorithm, as with other accelerometry-based algorithms, was validated with community–dwelling adults in post-industrial populations. People in subsistence-oriented communities, like Hadza foragers, often engage in activities requiring repeated upper limb movements (e.g., chopping firewood, pounding baobab seeds or corn). As stated above, future work that combines different technologies and includes observations of the subsistence activities participants engage in while wearing accelerometers will help us better characterize PA patterns in non-industrialized populations.

We used type of camp of residence (bush or village) as a crude measure for foraging engagement in this study, following methods used in several prior studies with the Hadza (Apicella et al., 2014; Crittenden et al., 2017; Pollom et al., 2020). But we did not directly measure diet or subsistence activities in the camps where we worked. Because Hadza adults often move back and forth between bush and village camps, current residence may not strongly reflect persistent differences in resident type or engagement with physically demanding tasks. A simple binary classification between bush and village camps may be appropriate for some types of research, but may be too coarse a categorization to identify the main determinants of habitual physical activity.

In this study, we used annual mobility and schooling as proximate measures for aspects of foraging and lifestyle that could impact PA patterns for Hadza women and men. And while we found that both mobility and schooling were associated with several measures of PA, other unmeasured confounding variables could be responsible for the associations we observed. For example, we found a sex difference in the effect of schooling on time spent inactive. We did not examine how participants spent their time while wearing the accelerometer, so we do not know what kinds of activities participants engaged in while inactive, and whether those activities differed depending on schooling experience. Overall, future work that examines what kinds of activities Hadza women and men engage in while wearing an accelerometer could help us better understand why we observed a sex-based difference in how aspects of lifestyle impacted measures of PA in this study.

## 5 | CONCLUSIONS

The results of this study complement several previous studies that highlight the physically active nature of the Hadza people's way of life, which includes large amounts of time spent active and inactive (Hawkes et al., 1989; Pontzer et al., 2015; Raichlen et al., 2017, 2020; Sayre et al., 2020). Time in MVPA and daily step counts were high in this study—even among older adults, whose levels of PA still far exceed baseline levels recommended by health officials in post-industrial populations. Similar to findings in other subsistence populations (e.g., Gurven et al., 2013), PA in this study can be characterized as primarily light-to-moderate, although participants of all ages engaged in some amount of vigorous-intensity PA. We found no evidence for strong camp-based differences in measures of PA. The similarity in patterns of PA between bush and village camps in this study may also highlight the physically active nature of subsistence lifestyles more generally. None of the camps in this study represent an *urban* context, where we might expect to see more pronounced differences in both lifestyle and health (e.g., Lea et al., 2020).

Overall, female and male participants in this study display similar levels of PA measures, but differences in how age, annual mobility, and schooling impact daily MVPA, step counts, and inactive time. These findings could be manifestations of Hadza adults' gender-based division of labor and spatial use (Marlowe, 2010; Wood, Harris, et al., 2021), and could also indicate potential differences in how market integration (MI) impacts Hadza women and men. Moving forward, it will be important to examine how the subsistence activities and lifestyle of Hadza women and men change alongside increasing MI, and how those changes ultimately impact the health and well-being of the Hadza community.

## AUTHOR CONTRIBUTIONS

**M. Katherine Sayre:** Conceptualization (equal); formal analysis (lead); funding acquisition (equal); investigation (lead); methodology (equal); resources (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Mariamu Anyawire:** Investigation (supporting); methodology (supporting); writing – review and editing (equal). **Bunga Paolo:** Investigation (supporting); methodology (supporting); writing – review and editing (equal). **Audax Z. P. Mabulla:** Resources (equal); writing – review and editing (equal). **Herman Pontzer:** Conceptualization (supporting); writing – review and editing (equal). **Brian M. Wood:** Conceptualization (supporting); funding acquisition (equal); resources (equal); writing – review and editing (equal). **David A. Raichlen:** Conceptualization (equal); funding acquisition (equal); methodology (equal); resources (equal); writing – review and editing (equal).

## ACKNOWLEDGMENTS

The authors would like to thank the Hadza research participants and community for their generosity and hospitality. Special thanks to Chris and Nani Schmelling for their hospitality and guidance. Thank you to Ibrahim Mabulla for providing in-country support, and to Dr. Gandhi Yetish, who provided invaluable mentorship throughout data collection. The authors also wish to thank the following generous funding sources that made this project possible: the National Science Foundation (Award NSF-BCS 2051519 [DAR, MKS], NSF-BCS 1440867 [DAR], NSF-BCS 1440671 [BMW]), the National Institute on Aging (R56AG067200

[GEA, DAR], R01AG72445 [DAR, GEA]), and the Max Planck Institute for Evolutionary Anthropology (BMW).

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Due to privacy and ethical restrictions, data is available upon reasonable request and discussion with corresponding author.

## ORCID

*M. Katherine Sayre* https://orcid.org/0000-0003-2554-4058
*Audax Z. P. Mabulla* https://orcid.org/0000-0001-9591-5497
*Herman Pontzer* https://orcid.org/0000-0003-2397-6543
*Brian M. Wood* https://orcid.org/0000-0002-8187-9429
*David A. Raichlen* https://orcid.org/0000-0002-4940-7886

## REFERENCES

Apicella, C. L., Azevedo, E. M., Christakis, N. A., & Fowler, J. H. (2014). Evolutionary origins of the endowment effect: Evidence from hunter-gatherers. *American Economic Review*, *104*(6), 1793–1805. https://doi.org/10.1257/aer.104.6.1793

Assah, F. K., Ekelund, U., Brage, S., Mbanya, J. C., & Wareham, N. J. (2011). Urbanization, physical activity, and metabolic health in sub-Saharan Africa. *Diabetes Care*, *34*(2), 491–496. https://doi.org/10.2337/dc10-0990

Azevedo, M. R., Araujo, C. L., Reichert, F. F., Siqueira, F. V., da Silva, M. C., & Hallal, P. C. (2007). Gender differences in leisure-time physical activity. *International Journal of Public Health*, *52*(1), 8–15. https://doi.org/10.1007/s00038-006-5062-1

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B: Methodological*, *57*, 289–300.

Biswas, A., Oh, P. I., Faulkner, G. E., Bajaj, R. R., Silver, M. A., Mitchell, M. S., & Alter, D. A. (2015). Sedentary time and its association with risk for disease incidence, mortality, and hospitalization in adults: a systematic review and meta-analysis. *Annals of Internal Medicine*, *162*(2), 123–132. https://doi.org/10.7326/M14-1651

Blodgett, J., Theou, O., Kirkland, S., Andreou, P., & Rockwood, K. (2015). The association between sedentary behaviour, moderate-vigorous physical activity and frailty in NHANES cohorts. *Maturitas*, *80*(2), 187–191. https://doi.org/10.1016/j.maturitas.2014.11.010

Brocklebank, L. A., Falconer, C. L., Page, A. S., Perry, R., & Cooper, A. R. (2015). Accelerometer-measured sedentary time and cardiometabolic biomarkers: A systematic review. *Preventive Medicine*, *76*, 92–102. https://doi.org/10.1016/j.ypmed.2015.04.013

Bull, F. C., Al-Ansari, S. S., Biddle, S., Borodulin, K., Buman, M. P., Cardon, G., Carty, C., Chaput, J. P., Chastin, S., Chou, R., Dempsey, P. C., DiPietro, L., Ekelund, U., Firth, J., Friedenreich, C. M., Garcia, L., Gichu, M., Jago, R., Katzmarzyk, P. T., … Willumsen, J. F. (2020). World Health Organization 2020 guidelines on physical activity and sedentary behaviour. *British Journal of Sports Medicine*, *54*(24), 1451–1462. https://doi.org/10.1136/bjsports-2020-102955

Caldwell, A. E. (2016). *Physical activity and energy expenditure in humans* (pp. 27–37). Springer. https://doi.org/10.1007/978-3-319-30409-0_4

Cavallo, F. R., Golden, C., Pearson-Stuttard, J., Falconer, C., & Toumazou, C. (2022). The association between sedentary behaviour, physical activity and type 2 diabetes markers: A systematic review of mixed analytic approaches. *PLoS One*, *17*(5), e0268289. https://doi.org/10.1371/journal.pone.0268289

Christensen, D. L., Faurholt-Jepsen, D., Boit, M. K., Mwaniki, D. L., Kilonzo, B., Tetens, I., Kiplamai, F. K., Cheruiyot, S. C., Friis, H., Borch-Johnsen, K., Wareham, N. J., & Brage, S. (2012). Cardiorespiratory fitness and physical activity in Luo, Kamba, and Maasai of rural Kenya. *American Journal of Human Biology*, *24*(6), 723–729. https://doi.org/10.1002/ajhb.22303

Crittenden, A. N., Sorrentino, J., Moonie, S. A., Peterson, M., Mabulla, A., & Ungar, P. S. (2017). Oral health in transition: The Hadza foragers of Tanzania. *PLoS One*, *12*(3), e0172197. https://doi.org/10.1371/journal.pone.0172197

Davis, H. E., Stack, J., & Cashdan, E. (2021). Cultural change reduces gender differences in mobility and spatial ability among seminomadic pastoralist-forager children in Northern Namibia. *Human Nature*, *32*(1), 178–206. https://doi.org/10.1007/s12110-021-09388-7

de Rezende, L. F., Rodrigues Lopes, M., Rey-Lopez, J. P., Matsudo, V. K., & Luiz Odo, C. (2014). Sedentary behavior and health outcomes: An overview of systematic reviews. *PLoS One*, *9*(8), e105620. https://doi.org/10.1371/journal.pone.0105620

Del Pozo Cruz, B., Ahmadi, M., Naismith, S. L., & Stamatakis, E. (2022). Association of daily step count and intensity with incident dementia in 78430 adults living in the UK. *JAMA Neurology*, *79*(1), 1059–1063. https://doi.org/10.1001/jamaneurol.2022.2672

DiPietro, L. (2001). Physical activity in aging: Changes in patterns and their relationship to health and function. *Journal of Gerontology: Series A*, *56A*, 13–22.

Doherty, A., Jackson, D., Hammerla, N., Plotz, T., Olivier, P., Granat, M. H., White, T., van Hees, V. T., Trenell, M. I., Owen, C. G., Preece, S. J., Gillions, R., Sheard, S., Peakman, T., Brage, S., & Wareham, N. J. (2017). Large scale population assessment of physical activity using wrist worn accelerometers: The UK Biobank study. *PLoS One*, *12*(2), e0169649. https://doi.org/10.1371/journal.pone.0169649

Du, Y., Liu, B., Sun, Y., Snetselaar, L. G., Wallace, R. B., & Bao, W. (2019). Trends in adherence to the physical activity guidelines for Americans for aerobic activity and time spent on sedentary behavior among US adults, 2007 to 2016. *JAMA Network Open*, *2*(7), e197597. https://doi.org/10.1001/jamanetworkopen.2019.7597

Dunstan, D. W., Thorp, A. A., & Healy, G. N. (2011). Prolonged sitting: Is it a distinct coronary heart disease risk factor? *Current Opinion in Cardiology*, *26*(5), 412–419. https://doi.org/10.1097/HCO.0b013e3283496605

Eaton, S. B., Konner, M., & Shostak, M. (1988). Stone agers in the fast lane: Chronic degenerative diseases in evolutionary perspective. *American Journal of Medicine*, *84*, 739–749.

Ekelund, U., Steene-Johannessen, J., Brown, W. J., Fagerland, M. W., Owen, N., Powell, K. E., Bauman, A., & Lee, I. M. (2016). Does physical activity attenuate, or even eliminate, the detrimental association of sitting time with mortality? A harmonised meta-analysis of data from more than 1 million men and women. *The Lancet*, *388*(10051), 1302–1310. https://doi.org/10.1016/s0140-6736(16)30370-1

Ekelund, U., Ward, H. A., Norat, T., Luan, J., May, A. M., Weiderpass, E., Sharp, S. J., Overvad, K., Ostergaard, J. N., Tjonneland, A., Johnsen, N. F., Mesrine, S., Fournier, A., Fagherazzi, G., Trichopoulou, A., Lagiou, P., Trichopoulos, D., Li, K., Kaaks, R., … Riboli, E. (2015). Physical activity and all-cause mortality across levels of overall and abdominal adiposity in European men and women: The European Prospective Investigation into Cancer and Nutrition Study (EPIC). *The American Journal of Clinical Nutrition*, *101*(3), 613–621. https://doi.org/10.3945/ajcn.114.100065

Erickson, K. I., Hillman, C., Stillman, C. M., Ballard, R. M., Bloodgood, B., Conroy, D. E., Macko, R., Marquez, D. X., Petruzzello, S. J., & Powell, K. E. For Physical Activity Guidelines Advisory, C. (2019). Physical activity, cognition, and brain outcomes: A review of the 2018 physical activity guidelines. *Medicine and Science in Sports and Exercise*, *51*(6), 1242–1251. https://doi.org/10.1249/MSS.0000000000001936

Evenson, K. R., Buchner, D. M., & Morland, K. B. (2011). Objective measurement of physical activity and sedentary behavior among US adults aged 60 years or older. *Preventing Chronic Disease*, *9*, E26. https://doi.org/10.5888/pcd9.110109

Gibbons, A. (2018). Hadza on the Brink: Farmers, tourists, and cattle threaten some of the world's last hunter-gatherers, long a magnet for researchers. *Science*, *360*, 700–704.

Gu, F., Khoshelham, K., Shang, J., Yu, F., & Wei, Z. (2017). Robust and accurate smartphone-based step counting for indoor localization. *IEEE Sensors Journal*, *17*(11), 3453–3460. https://doi.org/10.1109/jsen.2017.2685999

Gurven, M., Jaeggi, A. V., Kaplan, H., & Cummings, D. (2013). Physical activity and modernization among Bolivian Amerindians. *PLoS One*, *8*(1), e55679. https://doi.org/10.1371/journal.pone.0055679

Hall, K. S., Hyde, E. T., Bassett, D. R., Carlson, S. A., Carnethon, M. R., Ekelund, U., Evenson, K. R., Galuska, D. A., Kraus, W. E., Lee, I. M., Matthews, C. E., Omura, J. D., Paluch, A. E., Thomas, W. I. & Fulton, J. E. (2020). Systematic review of the prospective association of daily step counts with risk of mortality, cardiovascular disease, and dysglycemia. *International Journal of Behavioral Nutrition and Physical Activity*, *17*(1), 78. https://doi.org/10.1186/s12966-020-00978-9

Hallal, P. C., Andersen, L. B., Bull, F. C., Guthold, R., Haskell, W., & Ekelund, U. (2012). Global physical activity levels: Surveillance progress, pitfalls, and prospects. *The Lancet*, *380*(9838), 247–257. https://doi.org/10.1016/s0140-6736(12)60646-1

Hamer, M., Blodgett, J. M., & Stamatakis, E. (2022). Dose-response association between step count and cardiovascular disease risk markers in middle-aged adults. *Scandinavian Journal of Medicine & Science in Sports*, *32*(7), 1161–1165. https://doi.org/10.1111/sms.14173

Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (1989). Hardworking Hadza grandmothers. In V. Standen & R. A. Foley (Eds.), *Comparative socio-ecology of humans and other mammals* (pp. 341–366). London, Basil Blackwell.

Hildebrand, M., Hansen, B. H., van Hees, V. T., & Ekelund, U. (2017). Evaluation of raw acceleration sedentary thresholds in children and adults. *Scandinavian Journal of Medicine & Science in Sports*, *27*(12), 1814–1823. https://doi.org/10.1111/sms.12795

Hildebrand, M., van Hees, V. T., Hansen, B. H., & Ekelund, U. (2014). Age group comparability of raw accelerometer output from wrist- and hip-worn monitors. *Medicine and Science in Sports and Exercise*, *46*(9), 1816–1824. https://doi.org/10.1249/MSS.0000000000000289

Kashiwazaki, H., Uenishi, K., Kobayashi, T., Rivera, J. O., Coward, W. A., & Wright, A. (2009). Year-round high physical activity levels in agropastoralists of Bolivian Andes: Results from repeated measurements of DLW method in peak and slack seasons of agricultural activities. *American Journal of Human Biology*, *21*(3), 337–345. https://doi.org/10.1002/ajhb.20864

Katzmarzyk, P. T., & Mason, C. (2009). The physical activity transition. *Journal of Physical Activity and Health*, *6*, 269–280.

King, A. C., Whitt-Glover, M. C., Marquez, D. X., Buman, M. P., Napolitano, M. A., Jakicic, J., Fulton, J. E., & Tennant, B. L. Physical Activity Guidelines Advisory, C. (2019). Physical activity promotion: Highlights from the 2018 physical activity guidelines advisory committee systematic review. *Medicine and Science in Sports and Exercise*, *51*(6), 1340–1353. https://doi.org/10.1249/MSS.0000000000001945

Kraft, T. S., Venkataraman, V. V., Wallace, I. J., Crittenden, A. N., Holowka, N. B., Stieglitz, J., Harris, J., Raichlen, D. A., Wood, B., Gurven, M., & Pontzer, H. (2021). The energetics of uniquely human subsistence strategies. *Science*, *374*(6575), eabf0130.

Kraus, W. E., Janz, K. F., Powell, K. E., Campbell, W. W., Jakicic, J. M., Troiano, R. P., Sprow, K., Torres, A., & Piercy, K. L. Physical Activity Guidelines Advisory, C. (2019). Daily step counts for measuring physical activity exposure and its relation to health. *Medicine and Science in Sports and Exercise*, *51*(6), 1206–1212. https://doi.org/10.1249/MSS.0000000000001932

Lea, A. J., Martins, D., Kamau, J., Gurven, M., & Ayroles, J. F. (2020). Urbanization and market integration have strong, nonlinear effects on cardiometabolic health in the Turkana. *Science Advances*, *6*(43), eabb1430.

Lee, Y., & Park, S. (2021). Understanding of physical activity in social ecological perspective: Application of multilevel model. *Frontiers in Psychology*, *12*, 622929. https://doi.org/10.3389/fpsyg.2021.622929

Leonard, W. R., & Robertson, M. L. (1997). Comparative primate energetics and hominid evolution. *American Journal of Physical Anthropology*, *102*, 265–281.

Lu, F. (2007). Integration into the market among indigenous peoples. *Current Anthropology*, *48*(4), 593–602.

Madimenos, F. C., Snodgrass, J. J., Blackwell, A. D., Liebert, M. A., & Sugiyama, L. S. (2011). Physical activity in an indigenous Ecuadorian forager-horticulturalist population as measured using accelerometry. *American Journal of Human Biology*, *23*(4), 488–497. https://doi.org/10.1002/ajhb.21163

Marlowe, F. (2010). *The Hadza: Hunter-gatherers of Tanzania*. University of California Press.

Marlowe, F. W. (2002). Why the Hadza are still hunter-gatherers. In S. Kent (Ed.), *Ethnicity, hunter-gatherers and the "other": Assimilation in Africa* (pp. 247–275). Smithsonian Institution Press.

Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *14*(2), 54–67. https://doi.org/10.1002/evan.20046

Marquez, D. X., Aguinaga, S., Vasquez, P. M., Conroy, D. E., Erickson, K. I., Hillman, C., Stillman, C. M., Ballard, R. M., Sheppard, B. B., Petruzzello, S. J., King, A. C., & Powell, K. E. (2020). A systematic review of physical activity and quality of life and well-being. *Translational Behavioral Medicine*, *10*(5), 1098–1109. https://doi.org/10.1093/tbm/ibz198

Matthews, C. E., Hagstromer, M., Pober, D. M., & Bowles, H. R. (2012). Best practices for using physical activity monitors in population-based research. *Medicine and Science in Sports and Exercise*, *44*(1 Suppl 1), S68–S76. https://doi.org/10.1249/MSS.0b013e3182399e5b

Migueles, J. H., Rowlands, A. V., Huber, F., Sabia, S., & van Hees, V. T. (2019). GGIR: A research community–driven open source r package for generating physical activity and sleep outcomes from multi-day raw accelerometer data. *Journal for the Measurement of Physical Behaviour*, *2*(3), 188–196. https://doi.org/10.1123/jmpb.2018-0063

Moore, S. C., Patel, A. V., Matthews, C. E., Berrington de Gonzalez, A., Park, Y., Katki, H. A., Linet, M. S., Weiderpass, E., Visvanathan, K., Helzlsouer, K. J., Thun, M., Gapstur, S. M., Hartge, P., & Lee, I. M. (2012). Leisure time physical activity of moderate to vigorous intensity and mortality: A large pooled cohort analysis. *PLoS Medicine*, *9*(11), e1001335. https://doi.org/10.1371/journal.pmed.1001335

Norton, K., Norton, L., & Sadgrove, D. (2010). Position statement on physical activity and exercise intensity terminology. *Journal of Science and Medicine in Sport*, *13*(5), 496–502. https://doi.org/10.1016/j.jsams.2009.09.008

Nuss, K. J., Hulett, N. A., Erickson, A., Burton, E., Carr, K., Mooney, L., Anderson, J., Comstock, A., Schlemer, E. J., Archambault, L. J., & Li, K. (2020). Comparison of energy expenditure and step count measured by ActiGraph accelerometers among dominant and nondominant wrist and hip sites. *Journal for the Measurement of Physical Behaviour*, *3*(4), 315–322. https://doi.org/10.1123/jmpb.2019-0064

Paluch, A. E., Bajpai, S., Bassett, D. R., Carnethon, M. R., Ekelund, U., Evenson, K. R., Galuska, D. A., Jefferis, B. J., Kraus, W. E., Lee, I., Matthews, C. E., Omura, J. D., Patel, A. V., Pieper, C. F., Rees-Punia, E., Dallmeier, D., Klenk, J., Whincup, P. H., Dooley, E. E. … Fulton, J. E. (2022). Daily steps and all-cause mortality: A meta-analysis of 15 international cohorts. *The Lancet Public Health*, *7*(3), e219–e228. https://doi.org/10.1016/s2468-2667(21)00302-9

Panter-Brick, C. (1996). Seasonal and sex variation in physical activity levels among agro-pastoralists in Nepal. *American Journal of Physical Anthropology*, *100*, 7–21.

Patterson, R., McNamara, E., Tainio, M., de Sa, T. H., Smith, A. D., Sharp, S. J., Edwards, P., Woodcock, J., Brage, S., & Wijndaele, K. (2018). Sedentary behaviour and risk of all-cause, cardiovascular and cancer mortality, and incident type 2 diabetes: A systematic review and dose response meta-analysis. *European Journal of Epidemiology*, *33*(9), 811–829. https://doi.org/10.1007/s10654-018-0380-1

Piercy, K. L., Troiano, R. P., Ballard, R. M., Carlson, S. A., Fulton, J. E., Galuska, D. A., George, S. M., & Olson, R. D. (2018). Physical activity guidelines for Americans. *JAMA*, *320*, 2020–2028.

Plotnikoff, R. C., Mayhew, A., Birkett, N., Loucaides, C. A., & Fodor, G. (2004). Age, gender, and urban-rural differences in the correlates of physical activity. *Preventive Medicine*, *39*(6), 1115–1125. https://doi.org/10.1016/j.ypmed.2004.04.024

Pollom, T. R., Cross, C. L., Herlosky, K. N., Ford, E., & Crittenden, A. N. (2020). Effects of a mixed-subsistence diet on the growth of Hadza children. *American Journal of Human Biology*, *33*(1), e23455. https://doi.org/10.1002/ajhb.23455

Pontzer, H., Raichlen, D. A., Wood, B. M., Emery Thompson, M., Racette, S. B., Mabulla, A. Z., & Marlowe, F. W. (2015). Energy expenditure and activity among Hadza hunter-gatherers. *American Journal of Human Biology*, *27*(5), 628–637. https://doi.org/10.1002/ajhb.22711

Pontzer, H., Wood, B. M., & Raichlen, D. A. (2018). Hunter-gatherers as models in public health. *Obesity Reviews*, *19*(Suppl 1), 24–35. https://doi.org/10.1111/obr.12785

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing https://www.R-project.org/

Raichlen, D. A., Klimentidis, Y. C., Sayre, M. K., Bharadwaj, P. K., Lai, M. H. C., Wilcox, R. R., & Alexander, G. E. (2022). Leisure-time sedentary behaviors are differentially associated with all-cause dementia regardless of engagement in physical activity. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(35), e2206931119. https://doi.org/10.1073/pnas.2206931119

Raichlen, D. A., & Lieberman, D. E. (2022). The evolution of human step counts and its association with the risk of chronic disease. *Current Biology*, *32*(21), R1206–R1214. https://doi.org/10.1016/j.cub.2022.09.030

Raichlen, D. A., Pontzer, H., Harris, J. A., Mabulla, A. Z., Marlowe, F. W., Josh Snodgrass, J. J., Eick, G., Berbesque, J. C., Sancilio, A., & Wood, B. M. (2017). Physical activity patterns and biomarkers of cardiovascular disease risk in hunter-gatherers. *American Journal of Human Biology*, *29*(2), e22919. https://doi.org/10.1002/ajhb.22919

Raichlen, D. A., Pontzer, H., Zderic, T. W., Harris, J. A., Mabulla, A. Z. P., Hamilton, M. T., & Wood, B. M. (2020). Sitting, squatting, and the evolutionary biology of human inactivity. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(13), 7115–7121. https://doi.org/10.1073/pnas.1911868117

Ramakrishnan, R., Doherty, A., Smith-Byrne, K., Rahimi, K., Bennett, D., Woodward, M., Walmsley, R., & Dwyer, T. (2021). Accelerometer measured physical activity and the incidence of cardiovascular disease: Evidence from the UK Biobank cohort study. *PLoS Medicine*, *18*(1), e1003487. https://doi.org/10.1371/journal.pmed.1003487

Ramirez Varela, A., Cruz, G. I. N., Hallal, P., Blumenberg, C., da Silva, S. G., Salvo, D., Martins, R., da Silva, B. G. C., Resendiz, E., Del Portillo, M. C., Monteiro, L. Z., Khoo, S., Chong, K. H., Cozzensa da Silva, M., Mannocci, A., Ding, D., & Pratt, M. (2021). Global, regional, and national trends and patterns in physical activity research since 1950: A systematic review. *International Journal of Behavioral Nutrition and Physical Activity*, *18*(1), 5. https://doi.org/10.1186/s12966-020-01071-x

Rankin, A. J., Rankin, A. C., MacIntyre, P., & Hillis, W. S. (2012). Walk or run? Is high-intensity exercise more effective than moderate-intensity exercise at reducing cardiovascular risk? *Scottish Medical Journal*, *57*(2), 99–102. https://doi.org/10.1258/smj.2011.011284

Rey Lopez, J. P., Sabag, A., Martinez Juan, M., Rezende, L. F. M., & Pastor-Valero, M. (2020). Do vigorous-intensity and moderate-intensity physical activities reduce mortality to the same extent? A systematic review and meta-analysis. *BMJ Open Sport & Exercise Medicine*, *6*(1), e000775. https://doi.org/10.1136/bmjsem-2020-000775

Sabia, S., van Hees, V. T., Shipley, M. J., Trenell, M. I., Hagger-Johnson, G., Elbaz, A., Kivimaki, M., & Singh-Manoux, A. (2014). Association between questionnaire- and accelerometer-assessed physical activity: The role of sociodemographic factors. *American Journal of Epidemiology*, *179*(6), 781–790. https://doi.org/10.1093/aje/kwt330

Saint-Maurice, P. F., Troiano, R. P., Bassett, D. R., Jr., Graubard, B. I., Carlson, S. A., Shiroma, E. J., Fulton, J. E., & Matthews, C. E. (2020). Association of daily step count and step intensity with mortality among US adults. *JAMA*, *323*(12), 1151–1160. https://doi.org/10.1001/jama.2020.1382

Sarma, M. S., Boyette, A. H., Lew-Levy, S., Miegakanda, V., Kilius, E., Samson, D. R., & Gettler, L. T. (2020). Sex differences in daily activity intensity and energy expenditure and their relationship to cortisol among BaYaka foragers from the Congo Basin. *American Journal of Physical Anthropology*, *172*(3), 423–437. https://doi.org/10.1002/ajpa.24075

Sayre, M. K., Pike, I. L., & Raichlen, D. A. (2018). High levels of objectively measured physical activity across adolescence and adulthood among the Pokot pastoralists of Kenya. *American Journal of Human Biology*, *31*(1), e23205. https://doi.org/10.1002/ajhb.23205

Sayre, M. K., Pontzer, H., Alexander, G. E., Wood, B. M., Pike, I. L., Mabulla, A. Z. P., & Raichlen, D. A. (2020). Ageing and physical function in East African foragers and pastoralists. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *375*(1811), 20190608. https://doi.org/10.1098/rstb.2019.0608

Shaw, B. A., & Spokane, L. S. (2008). Examining the association between education level and physical activity changes during early old age. *Journal of Aging and Health*, *20*, 767–787.

Stamatakis, E., Ahmadi, M. N., Gill, J. M. R., Thogersen-Ntoumani, C., Gibala, M. J., Doherty, A., & Hamer, M. (2022). Association of wearable device-measured vigorous intermittent lifestyle physical activity with mortality. *Nature Medicine*, *28*(1), 2521–2529. https://doi.org/10.1038/s41591-022-02100-x

Stamatakis, E., Huang, B. H., Maher, C., Thogersen-Ntoumani, C., Stathi, A., Dempsey, P. C., Johnson, N., Holtermann, A., Chau, J. Y., Sherrington, C., Daley, A. J., Hamer, M., Murphy, M. H., Tudor-Locke, C., & Gibala, M. J. (2021). Untapping the health enhancing potential of vigorous intermittent lifestyle physical activity (VILPA): Rationale, scoping review, and a 4-pillar research framework. *Sports Medicine*, *51*(1), 1–10. https://doi.org/10.1007/s40279-020-01368-8

Troiano, R., Berrigan, D., Dodd, K. W., Masse, L. C., Tilert, T., & McDowell, M. (2008). Physical activity in the United States measured by accelerometer. *Medicine and Science in Sports and Exercise*, *40*(1), 181–188.

Trost, S. G., McIver, K. L., & Pate, R. R. (2005). Conducting accelerometer-based activity assessments in field-based research. *Medicine and Science in Sports and Exercise*, *37*(11 Suppl), S531–S543. https://doi.org/10.1249/01.mss.0000185657.86065.98

Trost, S. G., Pate, R. R., Sallis, J. F., Freedson, P. S., Taylor, W. C., Dowda, M., & Sirard, J. (2002). Age and gender differences in objectively measured physical activity in youth. *Medicine and Science in Sports and Exercise*, *34*(2), 350–355.

Tucker, J. M., Welk, G. J., & Beyler, N. K. (2011). Physical activity in U.S.: Adults compliance with the physical activity guidelines for Americans. *American Journal of Preventive Medicine*, *40*(4), 454–461. https://doi.org/10.1016/j.amepre.2010.12.016

Urlacher, S. S., Liebert, M. A., Josh Snodgrass, J., Blackwell, A. D., Cepon-Robins, T. J., Gildner, T. E., Madimenos, F. C., Amir, D., Bribiescas, R. G., & Sugiyama, L. S. (2016). Heterogeneous effects of market integration on sub-adult body size and nutritional status among the Shuar of Amazonian Ecuador. *Annals of Human Biology*, *43*(4), 316–329. https://doi.org/10.1080/03014460.2016.1192219

Urlacher, S. S., Snodgrass, J. J., Dugas, L. R., Madimenos, F. C., Sugiyama, L. S., Liebert, M. A., Joyce, C. J., Teran, E., & Pontzer, H.

(2021). Childhood daily energy expenditure does not decrease with market integration and is not related to adiposity in Amazonia. *The Journal of Nutrition*, *151*(3), 695–704. https://doi.org/10.1093/jn/nxaa361

Ussery, E. N., Whitfield, G. P., Fulton, J. E., Galuska, D. A., Matthews, C. E., Katzmarzyk, P. T., & Carlson, S. A. (2021). Trends in self-reported sitting time by physical activity levels among US Adults, NHANES 2007/2008-2017/2018. *Journal of Physical Activity & Health*, *18*(S1), S74–S83. https://doi.org/10.1123/jpah.2021-0221

van Hees, V. T., Fang, Z., Langford, J., Assah, F., Mohammad, A., da Silva, I. C., Trenell, M. I., White, T., Wareham, N. J., & Brage, S. (2014). Autocalibration of accelerometer data for free-living physical activity assessment using local gravity and temperature: An evaluation on four continents. *Journal of Applied Physiology (Bethesda, MD: 1985)*, *117*(7), 738–744. https://doi.org/10.1152/japplphysiol.00421.2014

van Hees, V. T., Gorzelniak, L., Dean Leon, E. C., Eder, M., Pias, M., Taherian, S., Ekelund, U., Renstrom, F., Franks, P. W., Horsch, A., & Brage, S. (2013). Separating movement and gravity components in an acceleration signal and implications for the assessment of human daily physical activity. *PLoS One*, *8*(4), e61691. https://doi.org/10.1371/journal.pone.0061691

van Hees, V. T., Sabia, S., Jones, S. E., Wood, A. R., Anderson, K. N., Kivimaki, M., Frayling, T. M., Pack, A. I., Bucan, M., Trenell, M. I., Mazzotti, D. R., Gehrman, P. R., Singh-Manoux, B. A., & Weedon, M. N. (2018). Estimating sleep parameters using an accelerometer without sleep diary. *Scientific Reports*, *8*(1), 12975. https://doi.org/10.1038/s41598-018-31266-z

Varma, V. R., Dey, D., Leroux, A., Di, J., Urbanek, J., Xiao, L., & Zipunnikov, V. (2017). Re-evaluating the effect of age on physical activity over the lifespan. *Preventive Medicine*, *101*, 102–108. https://doi.org/10.1016/j.ypmed.2017.05.030

Veile, A., Martin, M., McAllister, L., & Gurven, M. (2014). Modernization is associated with intensive breastfeeding patterns in the Bolivian Amazon. *Social Science & Medicine*, *100*, 148–158. https://doi.org/10.1016/j.socscimed.2013.10.034

Warburton, D. E., Nicol, C. W., & Bredin, S. S. (2006). Health benefits of physical activity: The evidence. *Canadian Medical Association Journal*, *174*(6), 801–809. https://doi.org/10.1503/cmaj.051351

Wolff-Hughes, D. L., Fitzhugh, E. C., Bassett, D. R., & Churilla, J. R. (2015). Waist-worn actigraphy: Population-referenced percentiles for total activity counts in U.S Adults. *Journal of Physical Activity and Health*, *12*(4), 447–453. https://doi.org/10.1123/jpah.2013-0464

Wood, B. M., Harris, J. A., Raichlen, D. A., Pontzer, H., Sayre, K., Sancilio, A., Berbesque, C., Crittenden, A. N., Mabulla, A., McElreath, R., Cashdan, E., & Jones, J. H. (2021). Gendered movement ecology and landscape use in Hadza hunter-gatherers. *Nature Human Behaviour*, *5*(4), 436–446. https://doi.org/10.1038/s41562-020-01002-7

Wood, B. M., Millar, R. S., Wright, N., Baumgartner, J., Holmquist, H., & Kiffner, C. (2021). Hunter-gatherers in context: Mammal community composition in a northern Tanzania landscape used by Hadza foragers and Datoga pastoralists. *PLoS One*, *16*(5), e0251076. https://doi.org/10.1371/journal.pone.0251076

Yamauchi, T., Umezaki, M., & Ohtsuka, R. (2001). Physical activity and subsistence pattern of the Huli, a Papua New Guinea highland population. *American Journal of Physical Anthropology*, *114*, 258–268.

Yen, H. Y., & Li, C. (2019). Determinants of physical activity: A path model based on an ecological model of active living. *PLoS One*, *14*(7), e0220314. https://doi.org/10.1371/journal.pone.0220314

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Sayre, M. K., Anyawire, M., Paolo, B., Mabulla, A. Z. P., Pontzer, H., Wood, B. M., & Raichlen, D. A. (2023). Lifestyle and patterns of physical activity in Hadza foragers. *American Journal of Biological Anthropology*, 1–17. https://doi.org/10.1002/ajpa.24846