Sitting, squatting, and the evolutionary biology of human inactivity

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Edited by C. Owen Lovejoy, Kent State University, Kent, OH, and approved January 27, 2020 (received for review July 12, 2019)

Recent work suggests human physiology is not well adapted to prolonged periods of inactivity, with time spent sitting increasing cardiovascular disease and mortality risk. Health risks from sitting are generally linked with reduced levels of muscle contractions in chair-sitting postures and associated reductions in muscle metabolism. These inactivity-associated health risks are somewhat paradoxical, since evolutionary pressures tend to favor energy-minimizing strategies, including rest. Here, we examined inactivity in a hunter-gatherer population (the Hadza of Tanzania) to understand how sedentary behaviors occur in a nonindustrial economic context more typical of humans' evolutionary history. We tested the hypothesis that nonambulatory rest in hunter-gatherers involves increased muscle activity that is different from chair-sitting sedentary postures used in industrialized populations. Using a combination of objectively measured inactivity from thigh-worn accelerometers, observational data, and electromygraphic data, we show that hunter-gatherers have high levels of total nonambulatory time (mean ± SD = 9.90 ± 2.36 h/d), similar to those found in industrialized populations. However, nonambulatory time in Hadza adults often occurs in postures like squatting, and we show that these "active rest" postures require higher levels of lower limb muscle activity than chair sitting. Based on our results, we introduce the Inactivity Mismatch Hypothesis and propose that human physiology is likely adapted to more consistently active muscles derived from both physical activity and from nonambulatory postures with higher levels of muscle contraction. Interventions built on this model may help reduce the negative health impacts of inactivity in industrialized populations.

sedentary | hunter-gatherer | posture | physical activity | cardiovascular disease

The evolution of the genus *Homo* was marked by a shift toward high levels of physical activity in a hunting and gathering lifestyle that included long-distance walking and possibly running at moderate to high intensities (1–4). Thus, many suggest our physiological reliance on moderate-to-vigorous physical activity (MVPA) to prevent chronic diseases is a product of this evolutionary history (5–8). However, a separate set of physiological changes occur during inactivity and may also lead to chronic diseases in sedentary populations, even in individuals who are highly active (9–13). The effects of the competing demands of activity and inactivity on the body represent an evolutionary paradox. Resting and inactivity reduce metabolic energy costs, often considered a key target of natural selection (14), so why is inactivity harmful for the human body? Here, we test the hypothesis that the ways in which urban populations rest, rather than the amount of time spent resting, represents an inactivity mismatch with an evolutionarily relevant hunting and gathering lifestyle, and propose that this mismatch may contribute to the negative health impacts of sedentary behavior today.

During periods of inactivity, individuals living in industrialized societies generally sit in chairs or recline, greatly reducing muscle activity and energy costs needed to support the body (15, 16). Hypotheses seeking to explain the negative health impacts of sitting often focus on these prolonged periods of muscular inactivity. For example, Hamilton and coworkers (10, 17) have argued that, with little muscle activity requiring fuel, sitting leads to reduced production of enzymes that hydrolyze lipids for energy (e.g., lipoprotein lipase). Thus, total time spent in inactivity is associated with the accumulation of higher levels of circulating triglycerides and cholesterol, increasing cardiovascular disease (CVD) risk (9, 10). Importantly, the health risks of sitting may not be fully eliminated by increased MVPA, suggesting the potential for a distinct physiology of inactivity, rather than a lack of exercise-induced benefits, that links sedentary behaviors to chronic disease (10, 18–21). As with the physiology of exercise, an evolutionary perspective on rest and sitting may help us understand exactly how and why long periods of inactivity negatively impact human health.

One way to model evolutionary links between inactivity and health is to examine styles of rest observed in contemporary hunter-gatherers (4, 8, 22). While we should not think of modern hunter-gatherer populations as perfect models of human ancestors, they do provide an example of activity and inactivity patterns that are undoubtedly more typical of our species' evolutionary history than are those seen in contemporary industrial populations (4, 8, 22). Owing to the "labor-saving" technologies present in industrialized economies, researchers often assume that time spent sedentary is more limited in hunting and gathering populations than in

Significance

Inactivity is a growing public health risk in industrialized societies, leading some to suggest that our bodies did not evolve to be sedentary. Here, we show that, in a group of hunter-gatherers, time spent sedentary is similar to that found in industrialized populations. However, sedentary time in hunter-gatherers is often spent in postures like squatting that lead to higher levels of muscle activity than chair sitting. Thus, we suggest human physiology likely evolved in a context that included substantial inactivity, but increased muscle activity during sedentary time, suggesting an inactivity mismatch with the more common chair-sitting postures found in contemporary urban populations.

Author contributions: D.A.R., H.P., A.Z.P.M., M.T.H., and B.M.W. designed research; D.A.R., H.P., J.A.H., and B.M.W. performed research; D.A.R., H.P., T.W.Z., J.A.H., M.T.H., and B.M.W. contributed new reagents/analytic tools; D.A.R., H.P., T.W.Z., M.T.H., and B.M.W. analyzed data; and D.A.R., H.P., T.W.Z., J.A.H., A.Z.P.M., M.T.H., and B.M.W. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1911868117/-/DCSupplemental.

First published March 9, 2020.

industrialized societies, and that human physiology is simply not well adapted to long periods of inactivity (23). However, some ethnographic data suggests human foragers engage in large amounts of rest and inactivity (24–26), and foraging populations remain relatively free from CVD (5, 6, 22, 27). While inactivity may be more common than assumed in these populations, people living in small-scale foraging societies may practice styles of inactivity distinct from those seen in urban populations. For example, individuals do not typically sit in chairs when inactive, but instead, squat, kneel or otherwise sit with interruptions that require low-intensity muscle activity, potentially reducing the negative physiological impact of inactivity (28–30). Thus, it is possible that time spent inactive is not as important as the intensity (i.e., muscular effort) of inactivity.

Here, we present results from an objective study of inactivity in a population living a hunting and gathering lifestyle and propose the Inactivity Mismatch Hypothesis for the negative effects of sitting on human health. This hypothesis posits that our physiology evolved within the context of a high duration of sustained muscle activity throughout all parts of the waking day, both through physical activity and through resting postures that maintain low levels of muscle activity. Prolonged periods of muscular inactivity during chair sitting, a common element of daily life in industrialized populations, are best viewed as a key mismatch with our evolutionary past.

To test assumptions of this hypothesis, we collected objective measures of inactivity from a group of hunter-gatherers, the Hadza, who live in northern Tanzania. The participants in this study live in a traditional settlement far from any villages, subsist off of wild foods for nearly their entire diet, and have low levels of CVD risk based on common biomarkers (Table 1 and *SI Appendix*, Table S1, and see also ref. 22). Using accelerometers affixed to their thigh (activPal devices, PAL Technologies Ltd), we measured time spent in resting postures during waking hours. Waking hours were determined using sleep onset and wake time defined by accelerometers following methods developed by Chastin et al. (31). In addition, we documented the styles of resting postures used throughout the day using instantaneous scan sampling in camp and, with electromyography (EMG), we measured muscle activity used in common resting postures. Because we hypothesize increased muscle activity in rest postures, we defined postures other than standing and walking (i.e., resting postures) as nonambulatory rather than inactive behaviors.

Results

Summary data for activity measures are provided in Table 2. Hadza adults spend an average of 9.82 (SD = 2.38) h in nonambulatory postures per day during waking hours (Fig. 1 and see *SI Appendix*, Tables S2 and S3 for similar analyses using sleep and wake onset defined by previous studies of Hadza sleep patterns). This amount of total nonambulatory time is broadly similar to objectively measured time spent sitting in industrialized populations [Netherlands: ∼9.3 h (13); United States: ∼9.0 h (32); Australia: ∼8.8 h (33)]. In addition, average duration of sedentary bouts (mean ± SD = 15.22 ± 8.77 min) and number of transitions per day between nonambulatory and active postures (mean ± SD = 49.98 ± 15.57 transitions) were very similar in Hadza adults compared with individuals living in industrialized societies. For example, in a large study of objectively measured sedentary behavior in European adults (n = 2,024), sedentary bouts averaged 11.1 (SD = 3.5) min and there were an average of 37.6 (SD = 8.5) transitions between sitting and standing per day (13). In addition to engaging in large amounts of sedentary time, Hadza individuals are highly active, with levels of MVPA that far exceed health guidelines of ∼22 min/d developed by the US Department of Health and Human Services (Table 2). Measures of nonambulatory postures do not differ by sex or age (age range = 18–61 y), while MVPA shows some slight but significant age- and sex-related differences (Table 3).

Table 1. Biomarkers of cardiovascular disease risk

	Female (n = 15)		Male (n = 23)		Total (n = 38)	
Variable	Mean	SD	Mean	SD	Mean	SD
Total cholesterol, mg/dL	116.93	20.67	107.70	16.70	111.34	18.66
HDL, mg/dL	41.67	7.08	32.78	11.81	36.29	11.01
LDL, mg/dL	56.87	21.45	60.34	16.48	58.97	18.40
Triglycerides, mg/dL	92.00	27.97	72.87	30.07	80.42	30.39
Glucose*, mg/dL	83.24	14.83	82.87	21.68	83.00	19.36

*Sample sizes differ for glucose measurements (n = 17 female, n = 31 male, n = 48 total).

Table 2. Summary data for Hadza adults

	Female (n = 12)		Male (n = 16)	
Variable	Mean	SD	Mean	SD
Age	36.50	15.36	38.94	13.13
Nonambulatory time, h/d	10.12	2.25	9.61	2.45
Standing time, h/d	2.23	0.81	1.85	1.05
Average sedentary bout, min	14.51	5.45	15.72	10.49
Transitions, no. per day	50.16	12.17	49.85	17.62
MVPA, min/d	75.21	74.51	101.86	78.13
MVPA bouts, min/d	48.04	72.67	76.15	74.89
Sleep onset	21:27:51	61.29	21:05:55	57.38
Sleep end	6:23:51	66.68	6:20:32	67.2

Although nonambulatory time is high, this behavior occurs in a wide variety of postures that differ from postures used during inactivity in industrialized populations (Fig. 2). Proportions of time spent in postures differed significantly ($X^2[6]$ = 1,132.1, $P < 2.2e\text{-}16$; see *SI Appendix*, Table S4 for pairwise comparisons). Ground-sitting postures dominate Hadza inactive time with sitting in postures that resemble Western-style chair sitting having the lowest occurrence. In addition to ground-sitting postures, Hadza individuals also spend a large percentage of their nonambulatory time in squatting (∼18%) and kneeling postures (∼12.5%) that differ from ground sitting by individuals maintaining an elevated buttocks.

Some of these postures used by Hadza participants during nonambulatory time elicit significantly higher muscle activity compared with chair sitting (Fig. 3). For soleus, the assisted squat posture (squatting with heels in ground contact and with the buttocks resting on a small rock) elicited significantly higher muscle activity compared with chair sitting (Table 4). For soleus, vastus lateralis, and tibialis anterior, the full squatting posture (squatting with heels in ground contact and buttocks elevated from the ground) elicited higher levels of muscle activity compared with chair sitting (Table 4). The two other ground-sitting postures did not alter muscle activity magnitudes compared with chair sitting (Table 4).

Discussion

Our results show that Hadza hunter-gatherers spend long periods of time in nonambulatory postures. In fact, despite high levels of MVPA, Hadza participants are nonambulatory for about as long or longer than individuals living in industrialized societies. Thus, our results suggest that, based on conventional standards, individuals living a hunting and gathering lifestyle are no less inactive than urban-dwelling adults from more industrialized societies. However, while long total time spent sitting is often linked with increased CVD risk, our results presented here, combined with our previous work (22), show that Hadza adults are generally free of biomarkers of high CVD risk.

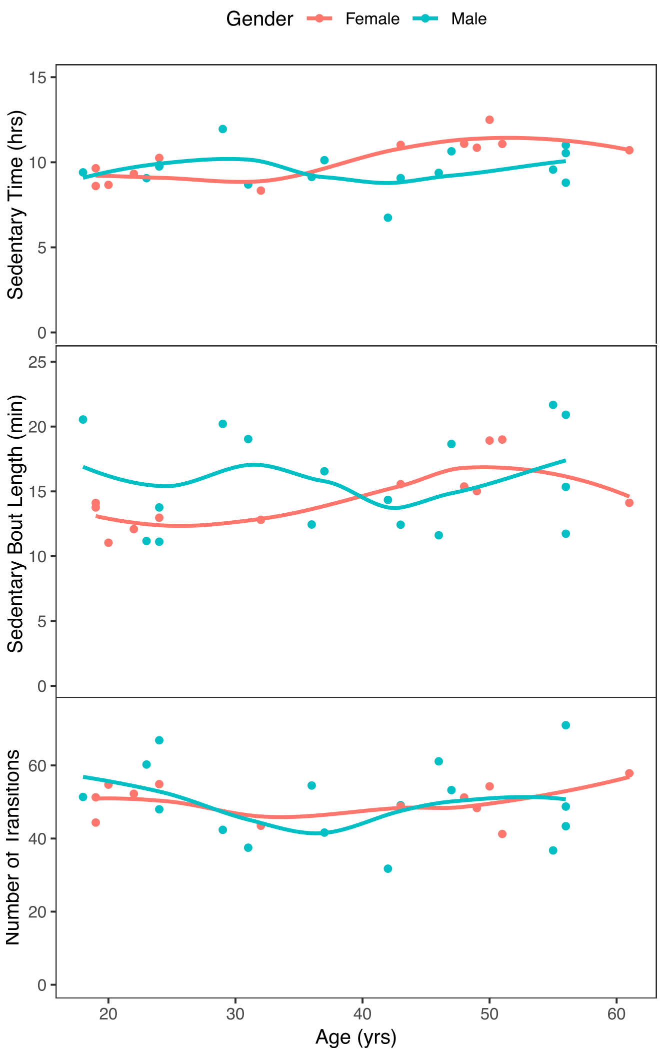

Fig. 1. Nonambulatory behavior in Hadza adults. (*Top*) Total time spent nonambulatory. (*Middle*) Average sedentary bout lengths. (*Bottom*) Number of transitions from nonambulatory to ambulatory behaviors. Lines are for visualization purposes and were fit using Loess methods.

This finding is important because there is evidence that some of the negative impacts of objectively measured time spent sitting on CVD and metabolic disease risk may remain after adjusting for time spent in MVPA (18, 21). While some epidemiological studies have shown that high levels of MVPA can counter the mortality risk associated with large amounts of time spent sitting (34, 35), these results were focused on mortality rather than morbidity and were based on self-reported sitting, which may not be well correlated with objectively measured inactive time. In contrast, a recent large metaanalysis of accelerometer-derived activity and inactivity found that high levels of sedentary time (>9.5 h/d) were significantly associated with mortality risk after adjusting for time spent in MVPA (36). Additionally, when health-related outcomes are analyzed in the context of time spent sitting measured objectively, adjustment for MVPA does not always fully counter the effects of inactivity on metabolic syndrome (13, 21) and CVD risk (18). Although these studies suggest that sedentary time may carry health risks in ways that are not fully ameliorated by MVPA, it is important to note that these are cross-sectional, observational studies, and measurement error associated with these behaviors, combined with residual confounds, make it premature to draw strong conclusions.

More direct tests of the interaction between physical activity and sitting comes from randomized crossover trials that examine the effects of interrupting sitting with various intensities of other activities and are better able to experimentally separate physiological effects of inactivity from activity. It is important to note that these studies generally induce short interruptions to otherwise long periods of sitting, which differs from the more sustained nonambulatory postures used by the Hadza. Nonetheless, meta-analyses of these experimental studies suggest interrupting sitting with MVPA and with lighter intensity activities seems to improve biomarkers associated with CVD and metabolic disease (37–39). Studies of interrupted sitting with periods of standing have generated more mixed results (37–39). Although results of these studies underscore the importance of MVPA for cardiometabolic health, some interventions hint at the idea that interrupting sitting with lower activity intensities can produce differential effects on physiological markers associated with cardiometabolic disease risk. For example, one study found that, in individuals with type 2 diabetes, breaking up sitting with standing and light activity had a greater effect on insulin sensitivity than engaging in MVPA (40). In addition, an intriguing randomized crossover trial in a sample that included normal, overweight, and diabetic individuals suggests that replacing sitting time with light activities may be associated with reduced blood biomarkers of CVD risk, whereas replacing sitting time with MVPA improved endothelial function but did not alter blood markers that were impacted by long sedentary periods (41). While it is still too early to draw firm conclusions, and characteristics of the participants in these interventions do not allow generalization to the overall population, these experimental studies suggest activities that induce light muscle contractions may affect different aspects of physiological health than MVPA. Taken together, both observational studies and randomized controlled trials support the hypothesis that, while MVPA is clearly a key factor in improving cardiovascular health, replacing inactivity with activities that induce light muscle contractions may have benefits for CVD risk.

Thus, we hypothesize that postures used when nonambulatory may provide additional protection against the negative health effects of sedentary behaviors. Indeed, some nonambulatory postures used by Hadza individuals at rest elicit higher levels of

Table 3. Linear mixed effects models

Outcome	Estimate	Value	SE	*t* value	*P* value
Nonambulatory time, h/d	(Intercept)	8.93	0.70	12.80	2.41e-13
	Age	0.03	0.02	2.11	0.05
	Sex (male)	−0.62	0.44	−1.42	0.17
Standing time, h/d	(Intercept)	2.74	0.35	7.82	2.47e-08
	Age	−0.01	0.01	−1.77	0.09
	Sex (male)	−0.33	0.23	−1.45	0.16
Sedentary bout duration, min	(Intercept)	12.01	2.20	5.47	8.18e-06
	Age	0.08	0.05	1.66	0.11
	Sex (male)	0.69	1.29	0.54	0.60
Transitions, no. per day	(Intercept)	50.99	5.74	8.88	6.98e-10
	Age	−0.04	0.13	−0.33	0.75
	Sex (male)	0.49	3.53	0.14	0.89
MVPA bouts, min/d	(Intercept)	86.72	23.75	3.65	1.03e-03
	Age	−1.12	0.54	−2.08	0.05
	Sex (male)	32.99	14.89	2.22	0.04
MVPA total, min/d	(Intercept)	116.38	25.60	4.55	8.37e-05
	Age	−1.22	0.56	−2.16	0.04
	Sex (male)	32.78	15.56	2.11	0.05

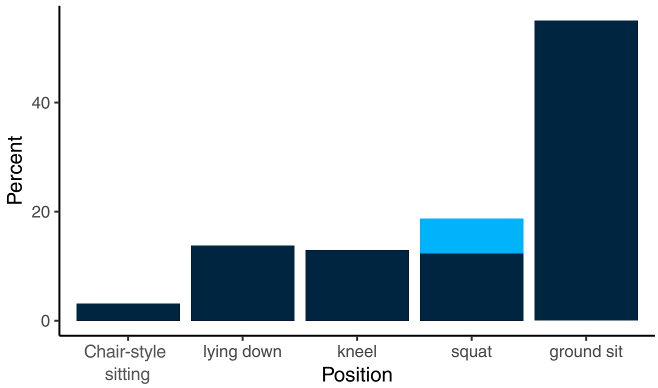

Fig. 2. Percent of observations in different nonambulatory postures. For squatting postures, light blue is assisted squat and dark blue is unassisted squat. Pairwise comparisons of these postures can be found in *SI Appendix*.

muscle activity than chair-sitting postures typical of industrialized societies. EMG data presented here suggest that lower limb muscle activity is altered by sitting posture, with muscle activity in squatting and assisted squatting postures rising to ∼20–40% of walking values for some muscles. In studies focused on the use of muscle activity as a marker of sedentary behaviors and physical activity, values in this range are generally similar to or greater than one would see in standing postures and may be classified as light activity (15, 42). Our observational data show that Hadza adults spend ∼18% (∼2 h/d) of nonambulatory time in squatting postures, with ∼2/3 of that time in unassisted squatting postures. While we have not measured muscle activity in kneeling postures, there is evidence that these postures also lead to high levels of lower limb muscle activity, although not as high as squatting (43), and Hadza adults spend ∼12.5% of nonambulatory time kneeling. Therefore, our results are consistent with a hypothesized increase in muscle activity during some sedentary postures and allows us to define these postures as "active" rest.

These findings provide the context for our Inactivity Mismatch Hypothesis. We suggest human physiology is adapted to more consistent muscle activity throughout the day associated with a combination of both physical activity (e.g., MVPA) and nonambulatory time spent in active rest postures. Recent work suggests that it is prolonged muscular inactivity that drives the negative health effects of sitting (10). Sitting in postures that do not require much muscle activity (i.e., chair sitting) leads to reduced local muscle metabolism, with detrimental effects on lipid and glucose metabolism, blood flow and endothelial health, and regulation of inflammation (9, 10, 44, 45). While the mechanisms for these inactivity-induced health effects remain unclear, most hypotheses revolve around the reduced energy needs of slow oxidative postural muscles during sitting via distinct processes that may not be impacted by brief amounts of MVPA. For example, Hamilton and coworkers (10, 17, 46) have argued that muscle inactivity reduces lipoprotein lipase (LPL) activity locally in otherwise

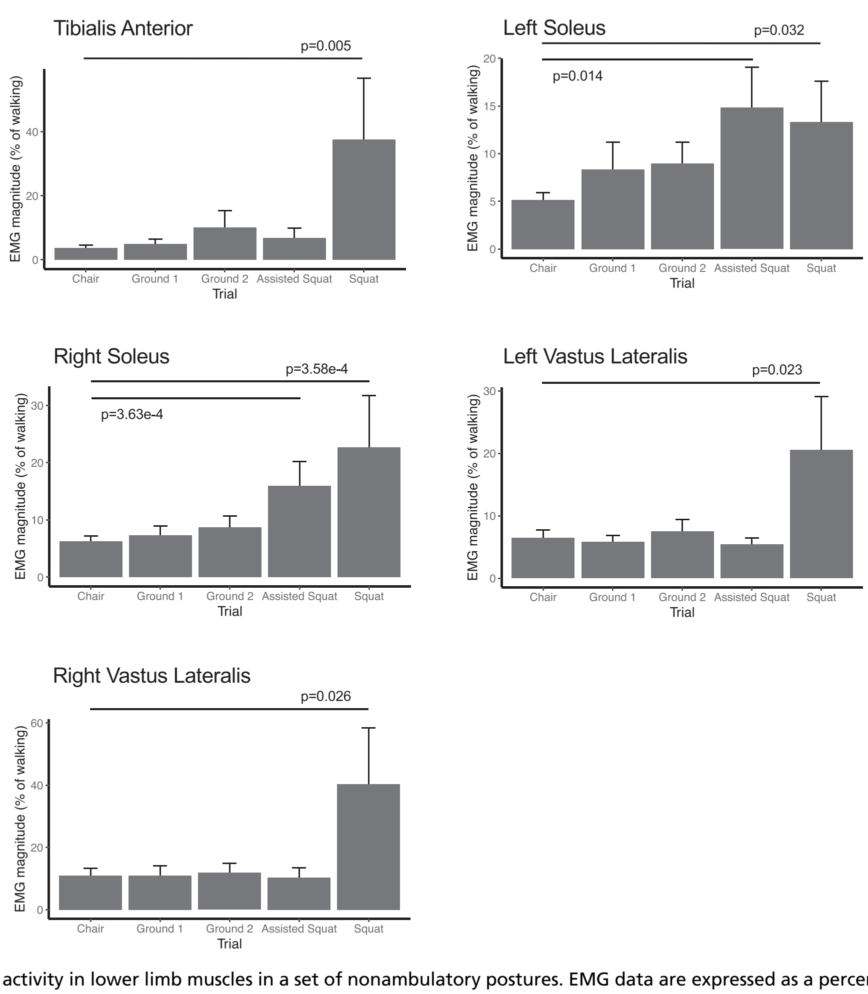

Fig. 3. Normalized muscle activity in lower limb muscles in a set of nonambulatory postures. EMG data are expressed as a percent of walking magnitudes. *P* values are FDR adjusted from post hoc pairwise comparisons with chair sitting.

Table 4. Linear mixed effects models from EMG analyses

Muscle	Parameter	Estimate	SE	*t* value	*P* value
Tibialis anterior (%walking)	(Intercept)	3.742	6.717	0.557	0.580
	Ground 1	1.192	8.944	0.133	0.895
	Ground 2	6.193	9.185	0.674	0.504
	Assisted Squat	4.218	9.470	0.445	0.659
	Squat	33.239	9.812	3.388	0.002
Left soleus (%walking)	(Intercept)	4.943	2.783	1.777	0.084
	Ground 1	3.403	3.320	1.025	0.311
	Ground 2	4.659	3.418	1.363	0.180
	Assisted Squat	10.883	3.554	3.062	0.004
	Squat	8.395	3.320	2.529	0.015
Right soleus (%walking)	(Intercept)	5.754	2.411	2.387	0.025
	Ground 1	1.578	2.607	0.605	0.549
	Ground 2	2.914	2.698	1.080	0.287
	Assisted Squat	10.831	2.716	3.988	3.22E-04
	Squat	15.086	3.619	4.168	1.87E-04
Left vastus lateralis (%walking)	(Intercept)	5.927	3.768	1.573	0.123
	Ground 1	−0.155	5.026	−0.031	0.976
	Ground 2	2.174	5.166	0.421	0.676
	Assisted Squat	0.822	5.353	0.153	0.879
	Squat	14.616	5.026	2.908	0.006
Right vastus lateralis (%walking)	(Intercept)	10.508	8.026	1.309	0.198
	Ground 1	0.485	10.407	0.047	0.963
	Ground 2	3.407	10.704	0.318	0.752
	Assisted Squat	2.656	11.104	0.239	0.812
	Squat	29.800	10.407	2.863	0.007

Statistics for parameters are provided relative to values for chair sitting. EMG values included in models were average muscle activity in a given posture normalized to average muscle activity during walking.

highly active muscles due to a decreased local energy demand. This effect alters lipid metabolism and increases circulating blood biomarkers associated with CVD. In a similar vein, lack of local muscle contractions can reduce insulin-mediated glucose uptake and may be associated with insulin resistance (12, 47). Thus, active rest postures used throughout the day lead to higher levels of muscle activity and, potentially, a reduction in the associated health effects of prolonged inactive lower limb muscle contractions (10, 33).

While our results suggest that styles and patterns of nonambulatory behaviors differ across lifestyles in ways that may be associated with health, our study has some limitations that lay the groundwork for future research into the evolutionary biology of inactivity. First, Hadza data were collected on a relatively small sample over a restricted period of time. Increased sample sizes and longer-term data collection are needed to demonstrate that our results are representative of hunter-gatherers. Data from other groups living in small-scale societies would enhance our ability to model plausible lifestyles of ancestral populations. In addition, we only examined muscle activity in the lower limb, however, seated postures may have effects on muscle activity in the trunk and upper body. Future work should examine a wider range of muscle groups and focus on how back postures in these positions may alter muscle activity. Examinations of other key postures, including kneeling, will help us better understand how a broader set of potential active rest postures impacts muscle activity in these populations. Finally, experimental work is needed to confirm that levels of muscle activity measured in active resting postures elicit specific health benefits such as enhanced LPL activity. Muscle activity in squatting postures, while higher than chair sitting, is still lower than we see during walking. Fully testing our model will require experimental examinations of the effects of different nonambulatory postures on biomarkers associated with CVD risk across populations. In addition, previous behavioral interventions that interrupt sitting with some form of activity generally do so for short periods of time. Our model entails use of nonambulatory postures that can be sustained over long periods of time, and future work should explore how longer durations of light contractile activity differs in physiological effects compared with shorter interruptions to sitting.

Despite these limitations, our results provide clear evidence of long periods of nonambulatory time in a population engaged in a hunting and gathering lifestyle. While behaviors are notoriously challenging to reconstruct for past populations, fossil evidence is consistent with our hypothesis that Paleolithic populations regularly engaged in more active resting postures, like those observed with the Hadza. For example, facets on the distal tibia associated with squatting and kneeling are present in early *Homo erectus* (48), Neandertals (49), and early anatomically modern humans (50, 51). Thus, human physiology was likely not presented with long periods of muscular inactivity until relatively recently in our evolutionary history. It seems probable that our bodies are simply not well-built for spending much of our day with muscular inactivity. When compared with data from humans in industrialized societies, Hadza styles of nonambulatory behavior allow us to better understand why they lack CVD morbidity that is associated with similar time spent inactive in urban-living adults (22). While time spent nonambulatory is high, a portion of this time includes low levels of muscle activity that may trigger health-related benefits throughout the day. Replacing chair sitting and associated muscular inactivity with more sustained active rest postures may represent a behavioral paradigm that should be explored in future experimental work. While squatting is not a likely alternative, spending more time in postures that elicit low-level muscle activity could lead to more beneficial health outcomes.

Methods

Sample. The Hadza are a traditional hunter-gatherer population inhabiting the Lake Eyasi region of northern Tanzania (52, 53). This region is a seasonal savannah-woodland habitat. Data collection for this study took place during the dry season of 2015 (June/July). Although there are a mix of subsistence strategies currently used by Hadza individuals across the region, individuals included in this study continue to live in traditional ways and foraged daily for wild resources. During our study, people acquired honey, small game, large game, berries, baobab, and tubers. By weight, only 3% of their diet (recorded in daily food returns) was not wild foods.

Participants were recruited from the camp of Sengeli (n = 28; n_{male} = 16, n_{female} = 12; age range = 18–61 y) to wear activPal accelerometers (Pal Technologies Ltd.) affixed to their thigh. These devices were wrapped in latex to make them water-resistant and were taped to the anterior thigh. Participants were asked to wear them for 8 d. Tape was reapplied when needed, but no devices were removed during the course of data collection. Approval for this research was provided by all governing organizations (Institutional Review Boards at Yale University, Hunter College, and the University of Arizona; The Tanzania Commission for Science and Technology and the National Institute for Medical Research in Tanzania). All subjects provided their informed consent prior to participating in this project.

Accelerometry. Accelerometry data were processed into 15-s epochs using activPal software. ActivPal software provides time spent in sedentary postures, standing, stepping, and number of transitions from sitting to standing within each 15-s epoch. We define sedentary behavior as time spent in nonambulatory postures, which exclude standing and walking. These data were imported into R statistical computing environment (R version 3.5.1) for further processing. Using output from activPal software, we calculated total time spent inactive during waking periods, with waking time determined using two methods. First, following methods detailed by Chastin et al. (31), we determined waking and sleeping onset directly from accelerometer data. Sleep onset was considered the end of the last standing event after 2100 that was followed by at least 3 h of nonupright posture. Waking onset was the first standing event that followed 2 h of continuous inactive posture between 0000 and 0900. Second, we used average sleep and wake onsets taken from Yetish et al.'s (54) and Samson et al.'s (55) previous studies of Hadza sleep patterns using wrist-worn accelerometry. All activity and nonambulatory variables of interest were then calculated for each day of waking hours, with all days included in statistical analyses below. On 1 d, we note that five individuals used a car for transportation to a community meeting, and these days for these individuals were removed from the analysis. Finally, time spent in MVPA was calculated as time spent above a 100 steps per min threshold following Barreira et al. (32). We determined both total MVPA and MVPA in bouts that lasted for at least 10 consecutive minutes.

Posture Observation. Instantaneous scan sampling was used to record postural data for all individuals in camp who wore activPal accelerometers throughout the day. For 12 h, beginning at 0700, scan samples were taken every hour and postures of all individuals in camp were recorded. Postures were documented using a modified typology developed by Hewes (29) and were categorized as lying down, ground sitting, squatting, kneeling, and chair sitting. Lying down included postures where individuals had the majority of the body in ground contact, lying on either the back or front. Ground-sitting postures were any nonambulatory posture that included the buttocks in contact with the ground. Squatting included two postures: heels down with buttocks elevated off the ground and knees flexed so that the thigh and shank are in contact, and heels down with buttocks rested on a small rock and knees flexed so that the thigh and shank are in contact (an assisted squat). Kneeling included postures where the anterior shank was in contact with the ground, knees are flexed, and buttocks rests on the posterior shank. Chair sitting is any posture that resembles Western-style chair sitting that can include sitting on a rock, log, or mound with knees flexed to ∼90°. For this study, we include analysis of individuals that also wore activPal devices. Scan samples were conducted for all 8 d of accelerometer wear leading to 96 scans and a total of 2,396 postures observed.

EMG. Muscle activity was measured using portable EMG with wireless surface electrodes (Delsys). Electrodes were affixed to the skin overlying the following muscles: vastus lateralis (left and right), soleus (left and right), tibialis anterior (right). Data were collected at 1,000 Hz and were bandpass filtered (20–450 Hz). EMG trial order was randomized for each participant. Each trial lasted for 2 min, and subjects were asked to maintain inactive postures throughout the entire trial. EMG data were collected in the following trials: squatting (heels down), assisted squatting (squatting with buttocks supported by a small rock), ground sitting in two postures commonly found in this population (with legs flexed to the side and with legs crossed in front), and chair sitting with the back supported by a backrest. We also collected EMG data during 2-min walking trials where subjects walked at a self-determined usual walking pace. We used a 30-s window of EMG data for this analysis that began 1 min into each trial. Thus, we captured EMG of muscles after they had accommodated to each posture and prior to the anticipation of the trial end. For each 30-s window, we rectified the signal and normalized each muscle's EMG magnitude by dividing by the average rectified magnitude for a given muscle calculated during the walking trial (normalized values were multiplied by 100 to convert to percent of walking magnitudes). We chose to normalize EMG data using walking trials because, while we attempted to elicit maximum voluntary contractions for each muscle, this process proved difficult for most participants to execute. Use of walking data ensured more consistent normalization across participants.

Blood Biomarkers. We used portable professional blood test devices (CardioChek PA, Polymer Technology Systems, Inc., and Contour OneTouch, Ascensia Diabetes Care) to measure blood lipids and fasting glucose during the 2015 and October 2019 field seasons (OneTouch devices were used for glucose measurements only during the 2019 field season; see *SI Appendix*, Table S1). Calibration of the devices occurred prior to each measurement session. For glucose and blood lipids in 2015, and blood lipids in 2019, we collected fingerstick capillary whole blood samples and analyzed them using the CardioChek point of care meter following package instructions. Based on recent studies, the CardioChek system provides results that are within 10% of serum reference values for all blood lipids (56). We measured total cholesterol, high-density lipoprotein (HDL) levels, triglyceride levels, and calculated low-density lipoprotein (LDL) levels from total cholesterol, HDL, and triglyceride values by following ref. 57. Note that the CardioChek does not calculate values of total cholesterol below 100 mg/dL, triglycerides below 50 mg/dL, or HDL below 20 mg/dL. In cases where these values fell below the threshold for measurement, the next lowest value was imputed (e.g., total cholesterol of <100 was imputed as 99; HDL <20 was imputed as 19) for calculation of group means. LDL was calculated using the Friedewald equation (LDL = Total Cholesterol – HDL Triglycerides/5), which has been shown to be accurate in populations, like the Hadza, with low triglycerides (57). Group means should therefore be considered upper bounds for estimated blood biomarkers of CVD risk. In the 2019 field season, fasting glucose measurements were collected using the OneTouch device following manufacturer guidelines. Complete blood biomarker data for these individuals are found in *SI Appendix*, Table S1, and overlap between the blood biomarker and actigraphy samples is noted in the table.

Statistics. To account for repeated measurements of accelerometry data on consecutive days, linear mixed effects models (LMM) were used to compare time spent in nonambulatory postures across individuals, with participant and accelerometer wear-day included as random effects and sex and age included in models as fixed effects. We used a χ^2 test to analyze proportion of time spent in different postures and adjusted P values using false discovery rate (FDR) to account for multiple pairwise comparisons. EMG data were analyzed using LMMs to account for repeated measurements on the same individuals, and we adjusted P values using FDR to account for multiple pairwise comparisons between resting postures. For EMG data, participant was included in the model as a random effect (random intercept), and sex and age were included as fixed effects. All statistics were performed in R statistical computing (version 3.5.1) using the lme4, mulcomp, and RVAideMemoire packages. All datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

ACKNOWLEDGMENTS. We thank Hadza participants for their involvement in this study and Carla Wood, Fides Kirei, Shani Msafiri, Ibrahim Mabulla, Layne Vashro, David Armstrong, Charis Jonathan, Ruth Matiyas, Holiness, and Herieth Cleophace for their invaluable assistance in the field. Funding was provided by National Science Foundation Grants NSF-BCS-0850815 (to H.P), NSF-BCS 1440867 (to D.A.R), NSF-BCS 1440841 (to H.P), NSF-BCS 1440671 (to B.M.W.), The L.S.B. Leakey Foundation (B.M.W.), The University of Arizona Bio5 Institute (D.A.R.), and American Diabetes Association Grant 1-15-TS-14 (to M.T.H.).

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