RESEARCH ARTICLE

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Hadza sleep biology: Evidence for flexible sleep-wake patterns in hunter-gatherers

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Abstract

Objectives: Cross-cultural sleep research is critical to deciphering whether modern sleep expression is the product of recent selective pressures, or an example of evolutionary mismatch to ancestral sleep ecology. We worked with the Hadza, an equatorial, hunter-gatherer community in Tanzania, to better understand ancestral sleep patterns and to test hypotheses related to sleep segmentation.

Methods: We used actigraphy to analyze sleep-wake patterns in thirty-three volunteers for a total of 393 days. Linear mixed effects modeling was performed to assess ecological predictors of sleep duration and quality. Additionally, functional linear modeling (FLM) was used to characterize 24-hr time averaged circadian patterns.

Results: Compared with post-industrialized western populations, the Hadza were characterized by shorter (6.25 hr), poorer quality sleep (sleep efficiency = 68.9%), yet had stronger circadian rhythms. Sleep duration time was negatively influenced by greater activity, age, light (lux) exposure, and moon phase, and positively influenced by increased day length and mean nighttime temperature. The average daily nap ratio (i.e., the proportion of days where a nap was present) was 0.54 (SE = 0.05), with an average nap duration of 47.5 min (SE = 2.71; n = 139).

Discussion: This study showed that circadian rhythms in small-scale foraging populations are more entrained to their ecological environments than Western populations. Additionally, Hadza sleep is characterized as flexible, with a consistent early morning sleep period yet reliance upon opportunistic daytime napping. We propose that plasticity in sleep-wake patterns has been a target of natural selection in human evolution.

KEYWORDS
actigraphy, ecology, forager, napping, segmented sleep

1 | INTRODUCTION

The cross-cultural study of human sleep is in its infancy (McKenna, Ball, & Gettler, 2007; Worthman, 2008; Worthman & Melby, 2002). Researching sleep outside of post-industrialized Western context is critical to understanding the ways in which today's sleep patterns depart from our ancestral sleep patterns and any associated impacts on health in Western society (Nunn, Samson, & Krystal, 2016; Samson & Nunn, 2015). Despite an increase in our understanding of sleep mechanisms, physiology, and chronobiology (Campbell & Tobler, 1984;

Carskadon & Dement, 2005; Heller, 2005; Mistlberger & Rusak, 2005; Zepelin, Siegel, & Tobler, 2005), remarkably little is known about sleep in small-scale non-industrialized populations. The vast majority of human sleep data is generated from western, educated, industrialized, rich, and democratic participants—so called "WEIRD" populations (Henrich, Heine, & Norenzayan, 2010) from the United States, Europe, and Japan (Knutson, 2014).

Traditional populations largely practice subsistence patterns that include foraging, small-scale agricultural, horticultural, and pastoralist strategies, including combinations of these subsistence regimes. The

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activity patterns of traditional societies are assumed to be more closely linked to natural daily and seasonal rhythms, as such populations lack environmental barriers (common in post-industrial society) that are likely to influence sleep—such as environmentally controlled buildings with insulation that blunts noise. Notably, recent research on sleep in small-scale populations suggests that circadian rhythms may exhibit greater stability than in non-Western populations (Samson, Manus, & Nunn, 2016; Yetish et al., 2015). Thus, the investigation of sleep-wake activity—particularly among human foragers living in adaptively relevant environmental conditions—is critical to furthering our understanding of the ecology and evolution of human sleep.

Multiple approaches have been taken with the goal of describing the "natural" human sleep-wake pattern, with special focus on the timing of human sleep within the 24-hr circadian cycle. These approaches include studies conducted in laboratory conditions that experimentally manipulated photoperiod (Wehr, 1992, 1999), ethnographic studies of sleep timing and related cultural practices (Worthman, 2008; Worthman & Melby, 2002), investigations into the effects of artificial light on traditional human circadian patterns (de la Iglesia & Lee, 2014), historical reports of sleep (Ekirch, 2006, 2016), actigraphy based field work in traditional populations (Yetish et al., 2015), and comparative analyses on human and nonhuman primates (Samson & Nunn, 2015).

Laboratory studies revealed that, when exposed to an experimentally short photoperiod, human sleep became unconsolidated (Wehr, 1992, 1999). Ethnographers, working in a variety of cultures and across subsistence regimes, often characterize nighttime activity and daytime napping as common (Worthman, 2008; Worthman & Melby, 2002). Historical records document a segmented sleep pattern associated with European preindustrial populations (Ekirch, 2016). Sleep measured in an equatorial, small scale-agricultural society in Madagascar, without access to electricity, has been described as "segmented" or nocturnally biphasic with common noon-time napping (Samson, Manus, et al., 2016). For example, statistical analysis in this population suggests the existence of a post-midnight bump in activity, which has similarities to the "first" sleep and "second" sleep periods that have been suggested to exist in European societies before the availability of effective artificial light (Ekirch, 2016). These studies support the notion that ancestral human sleep was more flexible than typically experienced today by Western populations, suggesting perhaps even a biphasic, or polyphasic, pattern.

In contrast, clinical definitions of sleep describe it as a monophasic phenomenon, where "the normal young adult...is sleeping well and on a fixed schedule of about 8 hr per night," in an unbroken alternating pattern of NREM and REM until morning arousal (Carskadon & Dement, 2005, p. 20). In support of the "sleep consolidation hypothesis," which states that the natural human sleep pattern is monophasic, Yetish et al. (2015) recently reported that sleep patterns in three equatorial foraging societies is characterized by a low frequency napping and an absence of segmented, or bimodal sleep. Thus, the question of whether human sleep is naturally consolidated or unconsolidated is an active avenue of research, with evidence for both patterns.

The primary aims of the present study were to (1) expand the actigraphic dataset on Hadza sleep, (2) compare sleep duration, quality, timing and rhythmicity to previously reported post-industrial values and small-scale Malagasy agriculturalists, and (3) assess the ecological (i.e., meteorological, temporal, and social) predictors of sleep in the Hadza. If Hadza foragers are characterized by consolidated, non-segmented sleep, we predict low frequency napping (exemplified by no difference between nighttime sleep duration and 24 hr sleep duration), nighttime wake-bouts, and short wake after sleep onset (WASO). Additionally, if nocturnally bi-phasic sleep is found, we predict clear overlap with another small-scale society—Malagasy agriculturalists (Samson, Yetish, et al., 2016) —that are characterized by nocturnally bifurcated sleep-wake patterns.

2 | METHODS

2.1 | Subjects

The Hadza are considered to be "median" hunter-gatherers, as they lie near the median value for most ecological and life history traits among sub-tropical foragers (Marlowe, 2010). They live in an east African environment with an effective temperature of 17°C, which is close to the median for warm-climate hunter-gatherers (16.3°C). Their annual diet consists of approximately 43% hunted foods (game animals, birds, and honey) and 57% gathered foods (median value for African hunter-gatherers is 32% and 67%, respectively), with high variability between seasons and across years (Berbesque, Marlowe, & Crittenden, 2011). Their median local group home range is approximately 122 km^2, although range sizes are declining due to adjacent population pressure and globalization (Blurton Jones, 2016; Crittenden, 2014). The Hadza exhibit high levels of sexual division of labor, with males acting as primary hunters and females as primary gatherers. Importantly, the median local group size is approximately 30 for the Hadza (mean group size for warm-climate hunter-gatherers is 26), and groups are characterized by central-place provisioning, with individuals returning to a central place to distribute food (Marlowe, 2006). The most prominent material item used as a sleeping platform is a hardened impala skin and blankets. During some seasons, sleep is accompanied by the use of fire. Married couples sleep together with offspring, usually on the same bed. Average annual temperature varies little across the year (mean ~28°C), but varies considerably between day and night (mean min = 14°C, mean max = 35°C). Traditionally, the dry season occurs between June and November and the wet season runs from December to May, where short rains are followed by long rains. The habitat is primarily savanna-woodland, with the inclusion of rocky hills, brush, and marshland (Marlowe, 2010).

Hadza participants were recruited from a bush camp called Sengele, near Lake Eyasi in northern Tanzania (latitude: 03–04°S and longitude 34–36°E) and participated in the study during the rainy season between June 21 and February 11, 2016. We used a total of 22 actigraphs, which were deployed through two phases of the study to maximize sample size. A subset of individuals ($n = 8$), wore watches throughout the entire study period; thus accounting for three

individuals removed from the analysis based on exclusion criteria, the total number of subjects that generated data throughout the study was 33. Day length during this time of year ranged between 12.23 and 12.28 hr. Sunrise occurred between 06:43 and 6:46, and sunset occurred between 18:59 and 19:00. Lunar phase ranged from full moon to complete cover of lunar light—coded quantitatively as a proportion, with $0 =$ new moon with no light, and $1 =$ full moon. Day length and lunar phase (geographically dependent moon cycle times) were recorded from Astronomical Applications Department of United States Navy (http://aa.usno.navy.mil/data).

Participants were healthy adults above 18 years of age, residing in nomadic or semi-nomadic camps that engaged in daily foraging. Thirty-three subjects completed the study, representing 21 females (mean age: 34.9 ± 14.3 years) and 12 males (mean age: 35.6 ± 14.7 years). Exclusion criteria included self-reported insomnia or physical disability due to injury or infirmed status that prevented an individual from engaging in active foraging; three individuals were excluded based on these criteria. Research approval was obtained with an Authorization Agreement (IAA) between Duke University and the University of Nevada, Las Vegas; thus, all eligible subjects gave their verbal informed consent, as outlined by the Institutional Review Board for human subjects research. All research was approved by the Tanzanian Commission for Science and Technology (COSTECH) and the Tanzanian National Institute for Medical Research (NIMR).

2.2 | Protocol

Participants were given a sleep survey at the beginning of the study period (January 20 to February 11, 2016) to measure body size and composition and to ascertain general information of subjective sleep quality (reported in the Results section). In addition, participants answered daily questionnaires about the frequency of daytime sleep bouts (i.e., napping) and discrete nighttime wake bouts. Building upon refined methods from previous sleep research with the Hadza (Yetish et al., 2015), we used the Motionwatch 8 actigraph (CamNtech), with all watches configured to generate data in 1-min epochs. Subjects were asked to press the event marker preceding any sleep event throughout the study, including sleep after nighttime wake bouts and before initiating daytime naps (although it should be noted that relying solely at event markers for sleep onset can reduce accuracy in sleep latency values). Although polysomnography (PSG) is currently considered the gold standard for quantifying sleep, it remains cumbersome, expensive, and difficult to apply with ambulatory participants, especially in small-scale societies. Actigraphy, on the other hand, is a noninvasive, wrist worn device that has been increasingly adopted to investigate sleep in varying ecological settings—urban, peri-urban, and rural (Johnson et al., 2007; Kawada, 2008; Yoon, Kripke, Youngstedt, & Elliott, 2003).

Actigraph data were scored using the CamNtech MotionWare 1.1.15 program. The software has a sleep detection algorithm that generates sleep quotas based on actigraphic counts. The software also has a nap analysis function that detects periods of inactivity that are attributable to napping; specifically the software has adjustable parameters such as *nap activity threshold* and the *minimum–maximum nap length.*

We used segmented sleep parameters that have been validated for field environments using actigraphy to assess daytime sleep (i.e., napping) and nighttime wakefulness (i.e., wake-bouts), based on a study that compared reported, event marked events to actigraphy scored events using the Bland-Altman technique to determine concordance (Samson, Yetish, et al., 2016). *Nap activity threshold* is the level at which the epoch within the specified period must be less than or equal to the entered value for the period to be scored as a nap; here, we used 50 counts as the threshold. The *minimum nap length* sets the minimum period of inactivity required to be scored as a nap, and was here set to 15 min. *Max nap length* identifies the maximum period of inactivity required to be scored as a nap, and was set to 210 min. We identified a *wake-bout*, or "segmented sleep," as a period of 20 consecutive epochs categorized as "awake" from the beginning of sleep onset until sleep end. The algorithmic high-sensitivity settings are most reliable for determining sleep (Kanady, Drummond, & Mednick, 2011); therefore, we used the high-sensitivity setting throughout this study.

2.3 | Statistical analyses

We used *R* version 3.1.3 (Team RC, 2016) to conduct statistical analyses. To characterize sleep in the sample population we generated descriptive statistics. Female and male sleep quotas were compared using a Wilcoxon rank sum test. Daytime sleep (i.e., napping) and nighttime wakefulness (i.e., wake-bouts) were described using descriptive statistics; these values were compared using unpaired *t* tests against values from studies performed in post-industrial societies (Carnethon et al., 2016; Natale, Plazzi, & Martoni, 2009). Height, weight, and body mass index (BMI) were compared between sexes using *t* tests and tested for associations with sleep duration and quality using fitted linear models. Pearson product-moment correlation was performed on the nighttime wake-bout preceding the recorded nap frequency.

To characterize circadian rhythms, we used Nonparametric Circadian Rhythm Analysis (NPCRA) (Van Someren et al., 1999); these values were then compared using previously established methods (Calogiuri & Weydahl 2013; Calogiuri, Weydahl, & Carandente, 2013) against a community-based, adult control group without sleep-disorder symptoms in a post-industrial population (Rock, Goodwin, Harmer, & Wulff, 2014). NPCRA does not assume that the data fit any predefined distribution, therefore making it the preferred method to analyze several consecutive 24-hr periods of activity-rest data (which do not typically fit well with traditional Cosinor waveform analysis) (Van Someren et al., 1999). In addition to traditionally reported nighttime sleep duration *total sleep time* (TST), we also summed TST with the sleep scored during the daytime and define this measure as *true total sleep time* (TTST). Thus, TTST is the total sum of all sleep (both daytime naps and nighttime sleep) in a 24-hr period. To test whether TTST significantly differs from sleep duration, we ran a paired *t* test between it and TST. All tests performed were two-tailed (or where appropriate one-tailed) with significance set at the 0.05 level.

To assess the ecological predictors of sleep, we ran linear mixed effects models using the *lme4* package (Bates, Maecher, Bolker, & Walker, 2014) for each of our different response variables. These

TABLE 1 Study sample characteristics for full sample by sex (male $n = 12$, female $n = 21$). Data are presented as mean (standard deviation)

Sleep-wake measure	Men	Women	Significance
Sleep onset	22:15 (0:30)	22:13 (0:36)	$t = 0.23, p = .81$
Sleep end	06:52 (0:28)	06:54 (0:28)	$t = -0.29, p = .77$
Sleep latency (hr)	0.40 (0.30)	0.38 (0.28)	$t = 0.13, p = .90$
Time in bed (hr)	9.20 (0.77)	9.16 (0.72)	$t = 0.13, p = .90$
Sleep duration (hr)	6.20 (0.72)	6.25 (0.72)	$t = -0.19, p = .85$
Wake after sleep onset (hr)	2.45 (0.68)	2.44 (0.66)	$t = 0.04, p = .97$
Sleep efficiency (%)	68.7 (7.8)	68.9 (7.7)	$t = -0.07, p = .94$
Sleep fragmentation	46.0 (10.5)	46.2 (10.4)	$t = -0.05, p = .96$
Cumulative nighttime activity	16,188 (5,756)	16,427 (5,975)	$t = -0.11, p = .91$
Daily nap ratio	0.55 (0.32)	0.53 (0.31)	$t = 0.18, p = .86$
Segmented sleep ratio (Wake bouts > 20 min)	0.59 (0.37)	0.59 (0.38)	$t = 0.07, p = .94$

included *true total sleep time* (total sleep throughout the 24-hr circadian cycle) and two measures of sleep quality: *sleep efficiency* (actual sleep time expressed as a percentage of time in bed) and *sleep fragmentation* (two measures: the sum of the mobile time [i.e., total time categorized as mobile in epoch-by-epoch categorization] expressed as a percentage of the inferred sleep time, and the number of immobile bouts [i.e., number of contiguous sections categorized as immobile in the epoch-by-epoch categorization] less than or equal to 1 min expressed as a percentage of the total number of immobile bouts).

For sleep segmentation (i.e., *nighttime wake-bouts* and *napping frequency*), we used a generalized linear mixed model fit by maximum likelihood (Laplace approximation) due to the non-normally distributed response variables. In all models, we included sex, age, mean out of bed activity (the average activity count per epoch between the time the subject got out of bed and the time the subject went to bed the next sleep period), day length (the duration of time between sunrise and sunset), mean out of bed light exposure (the average lux count per epoch between the time the subject got out of bed and the time the subject went to bed the next sleep period), moon phase, temperature, wind and humidity. We standardized the coefficients using the R "scale" function to compare the effects of different variables. Controlling for meteorological variables, which may vary across the season, permits us to make broader interpretations of the effects of environment on sleep, despite only generating data for a single season. To control for repeated measures, we included "subject" as a random effect. We used the *MuMIn* package (Bartoń, 2014) to average models with $\Delta AIC < 10$ and obtained models using shrinkage (full model averaging), which improves less certain estimates by pooling information from more certain estimates (McElreath, 2016). We then made statistical inferences using a combination of standardized coefficients, *p*-values and confidence intervals.

Functional linear modeling (FLM) was used to characterize and illustrate 24-hr sleep-wake patterns. This approach, specifically designed for actigraphy time-series data analysis, measures raw activity counts within and between samples, and avoids summary statistics that can mask differences across groups (Wang et al., 2011). FLM was

used to compare activity patterns between the Hadza and an equatorial small-scale, natural-light, agricultural society in Madagascar that has previously been assessed as having nocturnally bi-phasic sleep (Samson, Manus, et al., 2016). To this end, we applied a non-parametric permutation test method in the R package "actigraphy" (Shannon et al., 2015), as it does not rely on distributional assumptions. The *p*-value was calculated by counting the proportion of permutation *F* values that are larger than the *F* statistics for the observed paring. Here, we used the point-wise test (with 500 permutations; bspline method). This test provides a curve that represents the proportion of permutation *F* values that are larger than the *F* statistic for the observed pairing at each point in the time series (Wang et al., 2011).

3 | RESULTS

Sleep quotas characterizing the Hadza were calculated for each sex (Table 1). Volunteers ($n = 33$) ranged from ages 18 to 65 years, with 21 females (mean age = 34.9; $SD = 14.3$) and 12 males (mean age = 34.2; $SD = 12.0$) participating. We found no significant sex difference in the age of participants (*t* test; $p = .88$) or in any of the sleep quotas reported, with a small effect size (Cohen's *d* range = 0.01–0.10). Compared with post-industrialized western populations, the Hadza were characterized by shorter, poorer quality sleep with strong effect sizes (Cohen's *d* range 0.65–1.75) by every measure (Table 2). Based on our surveys, however, they rarely identify their sleep as insufficient or unsatisfactory. Thus, when asked if they sleep "not enough," "just enough," or "too much," 35 of 37 respondents (95%) said "just enough." Thirty-four (92%) respondents said they fall asleep quickly. Thirty-six respondents (97%) reported that they find their bed comfortable, while none of the participants reported suffering from sleep problems.

As for body size and composition, males (mean = 160.5 cm, $SE = 1.57$) were taller than females (mean 154.3 cm, $SE = 1.13$; $p = .04$), but we found no significant difference in weight between males (mean = 49.3 kg, $SE = 0.83$) and females (46.3 kg, $SE = 1.03$;

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TABLE 2 Comparison of sleep quotas between Hadza and healthy postindustrial populations. All data for comparison are drawn from Western samples, including a healthy control group (age range: 7–65, total $n = 282$) based in Bologna, Italy (Natale et al., 2009) and healthy cross-ethnicity study including averages derived from Black, Asian, Hispanic, and White subjects (age range: 35–64, total $n = 496$) from Chicago, in the United States (Carnethon et al., 2016)

Sleep quota	Hadza	Italy	USA	Significance
Sleep onset	22:13 (0:36)	00:03 (1:59)	N/A	$t = 6.38$, $p < .001$
Sleep end	06:54 (0:27)	08:13 (1:19)	N/A	$t = -6.87$, $p < .001$
Time in bed (hr)	9.16 (0.72)	8.1 (1.02)	N/A	$t = 5.80$, $p < .001$
Sleep latency (hr)	0.38 (0.28)	0.16 (0.09)	N/A	$t = 9.67$, $p < .001$
Sleep duration (hr)	6.25 (0.72)	7.60 (0.96)	7.02 (1.05)	Italy: $t = 7.82$, $p < .001$; USA: $t = -4.15$, $p < .001$
Wake after sleep onset (hr)	2.44 (0.66)	0.31 (0.22)	0.71 (0.34)	Italy: $t = 3.90$, $p < .001$; USA: $t = 2.61$, $p < .001$
Sleep efficiency (%)	68.9 (7.7)	94.2 (3.1)	89.9 (4.6)	Italy: $t = -3.59$, $p < .001$ USA: $t = -2.41$, $p < .001$
Sleep fragmentation	45.9 (16.4)	N/A	20.0 (7.7)	$t = 1.70$, $p < .001$
True total sleep time (24 hr total sleep)	6.53 (0.71)	N/A	N/A	

$p = .120$). Additionally, BMI did not differ between males (mean = 19.1, $SE = 0.19$) and females (mean = 19.4, $SE = 0.38$; $p = .61$). We found no significant associations between sleep quotas and height or weight. However, subjects with higher BMI exhibited longer sleep durations ($t = 2.66$, df = 30, $p = .013$).

Every subject had at least one nap during the study period; the Hadza average daily nap ratio (i.e., the proportion of days where a nap was present) was 0.54 ($SE = 0.05$); in other words, an individual napped, on average, 54% of the days of the study period. Nap duration averaged 47.5 min ($SE = 2.71$; $n = 139$). The average sleep segmentation ratio (i.e., the proportion of nights where at least one wake-bout greater than 20 consecutive minutes occurred) was 0.59 ($SE = 0.66$). Additionally, naps and wake-bouts covaried, as more nighttime waking was associated with

greater next day napping ($r = 0.34$, $t = 3.53$, df = 95, $p < .001$). The day: night ratio (i.e., the *mean day activity* divided by the *mean night activity*) was 4.57 ($SE = 0.26$). Finally, TTST (393.0 ± 4.21 SE) was significantly greater than nighttime TST (376.2 ± 3.90 SE; $t = -10.41$, df = 389, $p < .001$), with a strong effect size (Cohen's $d = 0.75$).

The NPCRA revealed stronger circadian rhythms in the Hadza compared with post-industrialized populations, with less circadian fragmentation (Table 3). Specifically, the Hadza sample was characterized by less interdaily variability. Notably, the five least active consecutive hours (L5) and the most active consecutive 10 hr (M10) values were significantly greater in the Hadza, indicating that in both periods of light and heavy activity the Hadza are more active compared with their western counterparts.

TABLE 3 Nonparametric Circadian Rhythm Analysis (NPCRA) comparing Hadza and postindustrial samples. For the Hadza sample, the mean number of analysis nights was 11.25. Healthy, postindustrial sample from Rock et al. (2014)

Parameter	Hadza	Post-industrial	Significance	Definitions
Interdaily stability	0.41 (0.10)	0.44 (0.09)	$t = 1.13$ $p = .26$	Degree of resemblance between the activity patterns on individual days; ranges from 0 to 1 and may typically be about 0.6 for healthy adults
Interdaily variability	0.58 (0.20)	0.99 (0.19)	$t = 7.56$ $p < .001$	Quantifies the fragmentation of periods of rest and activity; ranges from 0 to 2 and typically is <1 for healthy adults, with higher values indicating a more fragmented rhythm
L5	2,153 (864)	1,354 (583)	$t = 3.75$ $p = .004$	All days of data are overlaid and averaged in 24-hr periods. The L5 average provides the mean activity level for the sequence of the least five active hours, indicating how inactive and regular sleep periods are.
M10	40,079 (15,309)	21,680 (4,463)	$t = 5.35$ $p < .001$	All days of data are overlaid and averaged in 24-hr periods. The M10 average provides the mean activity level for the sequence of the most active hours, indicating how active and regular the wake periods are.
Relative amplitude	0.89 (0.06)	0.88 (0.05)	$t = 0.64$ $p = .52$	Calculated by dividing amplitude by the sum of L5 and M10; ranges from 0 to 1, with higher values indicating higher amplitude of the rhythm
L5onset	02:23	02:21		Onset time of the five most restful consecutive hours
M10onset	08:56	11:19		Onset time of the 10 most active consecutive hours

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TABLE 4 Ecological predictors of 24 hr total sleep duration. Positive coefficients indicate greater sleep duration, while negative coefficients shorter sleep duration. *Male* is the reference category for sex

Predictor	β	SE	Confidence interval	z	p
Activity	−0.27	0.06	(−0.40, −0.16)	4.66	< 0.001
Age	−0.33	0.08	(−0.49, −0.18)	4.11	< 0.001
Day length	0.55	0.18	(0.19, 0.91)	2.98	0.003
Light exposure	−0.25	0.05	(−0.36, −0.13)	4.19	< 0.001
Moon phase	−0.46	0.16	(−0.78, −0.14)	2.84	0.004
Temperature	0.25	0.08	(0.08, 0.41)	2.91	0.004
Wind	−0.07	0.07	(−0.20, 0.06)	1.03	0.300
Sex	−0.07	0.08	(−0.23, 0.09)	0.84	0.400
Humidity	0.02	0.05	(−0.08, 0.13)	0.44	0.660

True total sleep time was influenced by several predictor variables in multivariate tests (Table 4 and Figure 1). Specifically, TTST was negatively influenced by greater mean out of bed activity, age, out of bed mean light exposure, and moon phase (i.e., full moon); in contrast, TTST was positively associated with increased day length and mean nighttime temperature. With respect to sleep quality, humidity was the sole, consistent predictor to influence both *sleep efficiency* ($\beta \pm SE = -0.20 \pm 0.05$, $p = .0002$, C.I. $= -0.30$ to -0.09) and *sleep fragmentation* ($\beta \pm SE = 0.24 \pm 0.06$, $p < .001$, C.I. $= 0.13$–0.35).

We also considered influences on metrics of segmented sleep, focusing on two measures: *nighttime wake-bouts* and *napping frequency*.
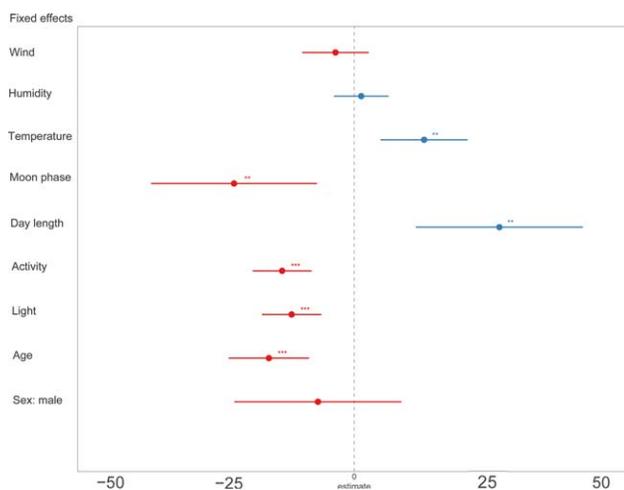

FIGURE 1 A standardized fixed effects plot illustrates that day length and temperature are positive predictors (indicated in blue) of 24 hr sleep duration whereas age, light exposure (during the out of bed period), mean activity per epoch (during the out of bed period), and moon phase are negative predictors (indicated in red) of total sleep duration. Asterisk indicate level of significance (**$p < .05$ to $p > .001$, ***$p < .001$). The units were scaled to permit comparability of the coefficients produces by the model [Color figure can be viewed at wileyonlinelibrary.com]

We found that average daily activity per epoch in between sleep periods reduced wake-bouts ($\beta \pm SE = -0.25 \pm 0.11$, $p = .02$). Additionally, and consistent with results from sleep quality analysis, humidity increased nighttime wake bouts ($\beta \pm SE = 0.24 \pm 0.08$, $p < .002$). Nap frequency was negatively influenced by age ($\beta \pm SE = -0.22 \pm 0.09$, $p = .02$), light exposure during the out of bed period in between sleep periods ($\beta \pm SE = -0.34 \pm 0.11$, $p = .001$) and average daily activity per epoch in between sleep periods ($\beta \pm SE = -1.11 \pm 0.18$, $p < .001$).

We applied functional linear modeling to actigraphy data from the Hadza and a previously studied small-scale agricultural population in Madagascar to assess differences in the timing of sleep-wake activity in the two groups. Figure 2 shows the group level circadian activity pattern, with red representing the Madagascar group and black representing the Hadza group. This plot shows a clear separation of the mean circadian activity and identifies the time periods when the curves differ between groups: (00:00–01:00, 02:30–03:30, 05:00–09:00, 12:00–13:00, 18:00–22:00). In general, differences in circadian activity were apparent, with the Hadza characterized by increased activity until noon and a steadily declining activity (with high count levels until after midnight) when the primary period of inactivity occurred. In contrast, the Madagascar group showed a clear decrease in activity around midnight, sandwiched by two relatively active periods, with pronounced high levels of early morning activity and a noontime decrease, which rebounded and then rapidly declined in the evening. Thus, we found that the Hadza are not generally characterized by a nocturnally bi-phasic sleep-wake pattern, such as that found in the Malagasy agriculturalists.

4 | DISCUSSION

This study examined the sleep-wake pattern of Hadza hunter-gatherers in relation to their ecology. We uncovered differences between the study population and previously reported values from post-industrial populations. Specifically, we report relatively short sleep time (i.e., a nighttime total sleep duration of 6.25 hr), despite longer durations of time in bed (9.16 hr), and longer sleep latency and greater WASO. Additionally, we demonstrated that this population has lower sleep efficiency. Intriguingly, despite the fact that Hadza daily energy expenditure is comparable with western populations (Pontzer et al., 2012), we found an association between greater BMI and longer sleep duration, suggesting a difference between the Hadza and Western populations, where high BMI is associated with short sleep duration (Cappuccio et al., 2008; Wirth et al., 2015). One factor that might account for this difference concerns the actual values of BMI: in the Hadza, high BMI indicated someone who was in the "normal" range, whereas in Western populations, high BMI was associated with obesity. Thus, the positive association between sleep duration and BMI may reflect opportunities for more sleep among better-nourished Hadza individuals.

We found strong linkage between environmental and demographic variables and sleep duration, quality, and circadian rhythms. Specifically, the Hadza have less fragmented circadian rhythms when compared with post-industrial populations, and they are characterized by greater
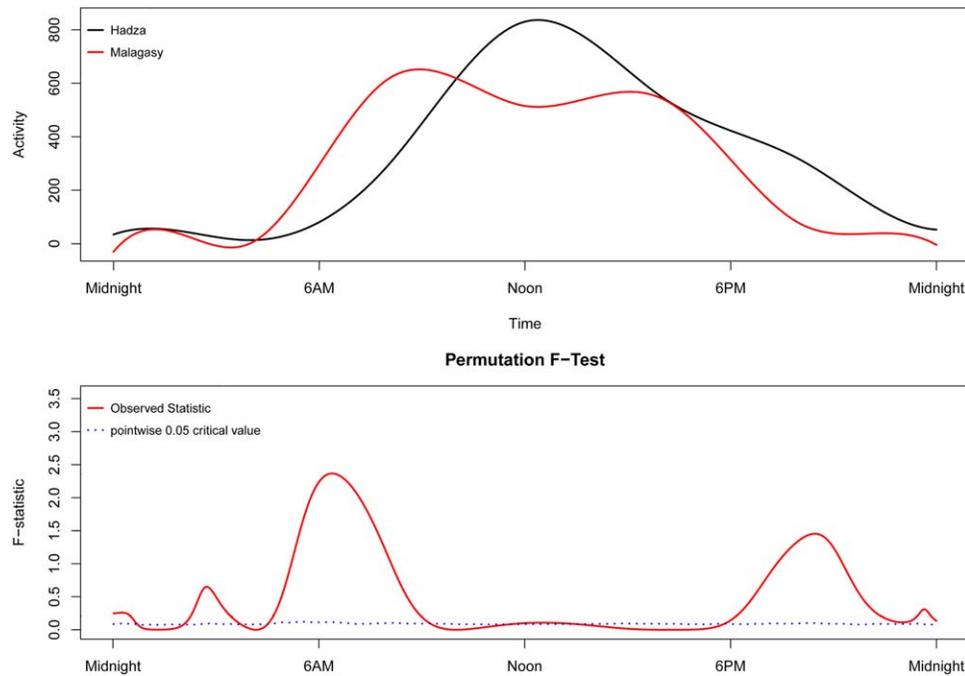
FIGURE 2 A functional linear modeling comparison between the 24-hr sleep-wake pattern of the Hadza and a small scale agricultural society in Madagascar characterized as nocturnally bi-phasic, segmented sleepers. The Madagascar population showed a pronounced increased activity after midnight and a pronounced decrease in activity around noon, whereas the Hadza showed continually increased activity from sleep's end until noon when activity showed a steady decrease until a prolonged consolidated bout of sleep in early morning. The bottom panel illustrates the point-wise critical value (dotted line) is the proportion of all permutation F values at each time point at the significance level of 0.05. When the observed F-statistic (solid line) is above the dotted line, it is concluded the two groups have significantly different mean circadian activity patterns at those time points [Color figure can be viewed at wileyonlinelibrary.com]

intensity of activity during their active periods (Table 3). Other results, such as higher-frequency daytime napping and nighttime wake-bouts, relatively higher WASO, and a longer duration of total sleep time relative to nighttime sleep time support the characterization of the Hadza as segmented sleepers. Interestingly, the FLM analysis indicated that when compared with a nocturnally bi-phasic segmented sleep-wake pattern characteristic of a small-scale agricultural society in Madagascar, the Hadza have a distinct segmented sleep-wake pattern, characterized by a primarily, monophasic, short nocturnal sleep bout supplemented by daytime napping (see Figure 3). Thus, both groups exhibit segmented sleep, but of different types: segmented sleep in the Hadza involves napping, while the Malagasy show evidence for segmented sleep during nighttime hours.

One limitation of our study concerns the comparability of the post-industrial groups and the Hadza dataset. The study performed by Natale et al. (2009) included a wide range of ages (7–65), and values reported by Carnethon et al. (2016) do not report all the variables we report with our Hadza sample. We suggest that future, multi-site studies should target demographically similar groups using similar equipment and methods.

Two principle *zeitgebers* (i.e., entrainment factors) that influence the timing of sleep in relation to circadian timing are light (via the master circadian clock known as the suprachiasmatic nucleus, Ibuka & Kawamura 1975; Ibuka, Shin-Ichi, & Kawamura, 1977), and temperature (via cold and warm sensing neurons, Siegel, 2011). Environmental

factors greatly influenced Hadza sleep duration and quality (Table 4). Controlling for age—which is known to decrease total sleep time in Western populations (Carskadon & Dement, 2005; Ohayon,
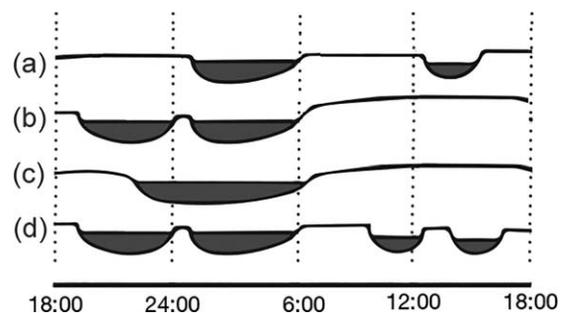

FIGURE 3 Flexible sleep-wake patterns may be a feature of human plasticity. (a) The Hadza reported in this study showed a monophasic nocturnal sleep pattern illustrated by a primary, early morning bout with supplemental daytime napping. (b) A biphasic, "first sleep, second sleep" pattern has been reported as common in preindustrial, agricultural societies in Western Europe (Ekirch, 2016). (c) A monophasic pattern is common in postindustrial economies with societal demands on activity from "9 am to 5 pm," and non-work related evening activity (Worthman, 2008). (d) A bifurcated pattern of nocturnal sleep bouts with supplemental daytime napping was the pattern evinced from a small scale, non-electric, agricultural society in Madagascar (Samson, Manus, et al. 2016). Image adapted from Miller, Matsangas, and Shattuck (2008)

Carskadon, Guilleminault, & Vitiello, 2004)—our model revealed that temperature and day length were positive influences on true total sleep time, whereas averaged activity during the out of bed period, light exposure during the out of bed period (including exposure to nighttime fires and ambient moonlight), and lunar cycle (i.e., greater ambient moonlight) negatively influenced true total sleep duration (Figure 1). Nighttime physiological equivalent temperature, calculated as an index of temperature, wind speed, and humidity (Matzarakis & Mayer, 1996; Matzarakis, Rutz, & Mayer, 2010), showed that subjects experienced cold stress at night (Samson *unpublished data*); thus, we infer that increased temperature improved sleep thermodynamics and comfort. Increased ambient light exposure has been shown to experimentally increase circadian rhythm and sleep duration (Ancoli-Israel et al., 2003; Campbell, Dawson, & Anderson, 1993). We interpret these data to suggest that Hadza experiencing longer days (and associated greater sunlight exposure) also experience longer sleep durations.

Intriguingly, lunar illumination has been shown to play a central role in regulating nocturnal behavior in primates (Colquhoun, 2006; Curtis, Zaramody, & Martin, 1999; Donati & Borgognini-Tarli, 2006), yet evidence that lunar phase impacts human physiology has been shortcoming (Foster & Roenneberg, 2008). Our study, coupled with similar results in Madagascar (Samson, Manus, et al., 2016), provides initial evidence that humans living with minimal barriers to their environments are more synchronized with circadian entrainment cues, and thus may experience less sleep in relation to nights with greater lunar illumination. Indeed, the evidence that moon phase predicts human activity in foragers highlights the potential importance of natural (i.e., lunar) and artificial (i.e., fire) light in fostering activity, including social activity. As for sleep quality, humidity was a strong predictor, with greater humidity being associated with increased sleep fragmentation and decreased sleep efficiency. The preferred relative humidity in controlled sleep environments has been shown to be 50% (Kim, Chun, & Han, 2010). Because nighttime relative humidity throughout the study period averaged 76%, increased relative humidity would have increased thermal stress and reduced sleep quality.

In sum, these data support the idea that changes from our ancestral sleep ecology, where physiology was in constant exposure to the environment, may have had significant consequences for sleep-wake patterns, with potential downstream effects on health (Nunn et al., 2016). For example, experiments have shown that circadian misalignment impairs autonomic function that enhances cardiovascular risk (Grimaldi, Carter, Van Cauter, & Leproult, 2016), while insulin sensitivity and inflammation increase markedly in circadian misaligned individuals, independently of general changes in sleep duration (Leproult, Holmbäck, & Van Cauter, 2014). In addition to links with negative health outcomes such as cancer, evidence is mounting that circadian misalignment is linked to psychiatric disorders such as depression, bipolar, schizophrenia, and attention deficit (Baron & Reid, 2014). Thus, the opportunity for evolutionary mismatch may have occurred as Western populations shifted to living in climate controlled, artificially extended photoperiods, resulting in multiple negative health outcomes.

Importantly, although in general our results support predictions from the sleep segmentation hypothesis, FLM analysis showed differences in expression of nocturnal sleep-wake patterns (Figure 3). For example, we did not find a nocturnal biphasic pattern (characteristic of the Madagascar population) among the Hadza, which is consistent with previous reports (Yetish et al., 2015). We do find a relatively consistent period of early morning sleep (03:00–06:00) in the Hadza, coupled with a highly variable sleep onset time (see also Yetish et al., 2015). Intriguingly, our data revealed that the Hadza nighttime wake-bouts and daytime napping are correlated. A longer nap likely provides a means to compensate for shorter sleep duration and poorer sleep quality on previous nights.

These results may shed light on why there have been many emerging and competing interpretations of "natural" circadian timing of human sleep. It may be that sleep phasing is not only a function of photoperiod (Wehr, 1999) or access to electrically produced illumination (Ekirch, 2016), but also the economic system and subsistence strategy that makes demands (via societal norms) on activity at specific times during the circadian period. We suggest that the underlying commonality illustrated by recent research is that human sleep is *flexible*. In other words, the relevant characteristic of "natural" human sleep is not the expressed timing, but the propensity for timing to be flexibly expressed in response to different ecological, social, and technological factors influencing sleep (Figure 3). Indeed, it has been suggested that a hallmark feature of human sleep is its efficiency in NREM-REM cycling, which ensures that homeostatic rebound meets the functional requirements of current cognitive demands in as short a time as possible (Halász, Bódizs, Parrino, & Terzano, 2014; Vyazovskiy & Delogu, 2014). Thus, a shift to less total sleep time and greater sleep intensity (i.e., deeper, more efficient sleep), coupled with plasticity in sleep timing, could have had important implications for early human evolution (Samson & Nunn, 2015).

Based on these findings, we propose that plasticity in sleep-wake patterns has been a target of natural selection in human evolution. There could have been favored frequency dependent selection for flexible sleep. For example, for example, in relation to effects of conspecific and predator threats on safety during terrestrial sleep (G. Yetish personal communication), which may be helped by light or fragmented sleep and the flexibility to catch up on sleep at a later time. Alternatively, there could have been relaxed selection on variation from monophasic sleep. Multiple predictions stem from the sleep flexibility hypothesis: (i) we predict that (after controlling for phylogeny) compared with other primates, humans would differ in their sleep-wake patterns and (ii) measuring sleep within traditional populations in high-latitude environments—where the ecological drivers of sleep (i.e., photoperiod and temperature) vary drastically from the blunted, relatively stable circadian entrainment factors associated with equatorial societies—would reveal high variability in sleep-pattern expression.

The success of *Homo sapiens*, attributed to a reliance on culture, technological innovation, and unparalleled cooperative networks, has been described as "a spectacular evolutionary anomaly" that has resulted in humans colonizing every terrestrial habitat. Humans have

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adapted to vastly different ecological systems—from equatorial latitudes with a *wet* and *dry* season characterized by stable temperature and photoperiod, to Arctic latitudes with extremely variable photoperiod and temperature relating to *winter* and *summer* seasons. Thus, a high degree of physiological plasticity—including in sleep—would have contributed significantly to this expansion and success (Hill, Barton, & Hurtado, 2009; Vitousek, 1997). Sleep research in populations with highly divergent environmental contexts can elucidate the plasticity inherent in these and other biological systems, ultimately informing how humanity spread across the globe.

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