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The evolution of human sleep: Technological and cultural innovation associated with sleep-wake regulation among Hadza hunter-gatherers

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ABSTRACT

Sleep is necessary for the survival of all mammalian life. In humans, recent investigations have generated critical data on the relationship between sleep and ecology in small-scale societies. Here, we report the technological and social strategies used to alter sleep environments and influence sleep duration and quality among a population of hunter-gatherers, the Hadza of Tanzania. Specifically, we investigated the effects that grass huts, sound levels, and fire had on sleep. We quantitatively compared thermal stress in outdoor environments to that found inside grass hut domiciles to test whether the huts function as thermoregulated microhabitats during the rainy season. Using physiological equivalent temperature (PET), we found that the grass huts provide sleep sites with less overall variation in thermal stress relative to outside baseline environments. We also investigated ambient acoustic measures of nighttime environments and found that sound significantly covaried with sleep-wake activity, with greater sound levels associating with less sleep. Finally, after controlling for ecological variables previously shown to influence sleep in this population, fire was shown to neither facilitate nor discourage sleep expression. Insofar as data among contemporary sub-tropical foragers can inform our understanding of past lifeways, we interpret our findings as suggesting that after the transition to full time terrestriality, it is likely that early *Homo* would have had novel opportunities to manipulate its environments in ways that could have significantly improved sleep quality. We further conclude that control over sleep environment would have been essential for migration to higher latitudes away from equatorial Africa.

1. Introduction

Sleep is a fundamental requirement for mammalian life (Horne, 1988; Kushida, 2004). All mammals studied, to date, experience some form of sleep and, if deprived, they suffer impairment of physiological function and cognitive performance (Rechtschaffen, 1998) – which, if prolonged, can ultimately result in death (Rechtschaffen and Bergmann, 2002). Sleep expression in primates is characterized by several distinct features relative to other mammals, including a more consolidated sleep pattern, general reductions in sleep times among diurnal primates, increased sleep intensity (i.e., depth of sleep staging) and the maintenance of social contact during sleep (Nunn et al., 2010). Comparatively, human sleep is unique in that it is shorter, deeper, and exhibits a higher proportion of REM (rapid eye movement) than expected when compared to other primates (Samson and Nunn, 2015). Moreover, it has been hypothesized that human sleep in post-industrialized countries is vastly different from the sleep of our hominin ancestors (Worthman and Melby, 2002; Worthman, 2008). Therefore, in order to determine the variability in human sleep patterns and attempt to make inferences about the past, it is necessary to study sleep in small-scale mobile and semi-nomadic populations whose ecological environment may more closely resemble that of our hominin ancestors.

A critical factor that influences sleep is the sleep site, which can function to reduce predation risk and thermodynamic stress, and facilitate social bonds (Kappeler, 1998; Lesku et al., 2006; Lima and Rattenborg, 2007; Capellini et al., 2008). Factors that acutely

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stimulate or inhibit sleep are known as “masking factors.” In other words, they are behavioral facilitators and inhibitors that either encourage or discourage sleep expression (Webb, 1988; Moore, 1990). Arguably, the most significant behavioral facilitator of sleep in human and non-human primates is the sleep site – that is, all aspects of the sleeping environment, which include photoperiod, thermal stress, noise, sociality, and familiarity of surroundings (Haskell et al., 1981; Libert et al., 1991; Epstein et al., 1997). Interestingly, non-human great apes in the wild not only sleep arboreally, but construct sleeping platforms on which to sleep (Fruth and Hohmann, 1996). Ape sleeping platforms have been found to improve sleep site safety (van Casteren et al., 2012; Samson and Hunt, 2014), repel insects (Samson et al., 2013), reduce thermal stress (Stewart, 2011), improve comfort (Stewart et al., 2007), and augment post-sleep cognitive ability (Martin-Ordas and Call, 2011; Shumaker et al., 2014).

Here, we quantitatively investigate the sleep sites among the Hadza of Tanzania, adding to previous qualitative descriptions of sleep sites among small-scale populations (Worthman and Melby, 2002; Hewlett and Roulette, 2014) and to recent cross-cultural analyses of sleep among foragers (Yetish et al., 2015; Samson et al., 2017a). To this end, we focus on the construction of sleeping sites and domiciles, sound levels, and the use of fire. The functional role of a shelter is often assumed to relate to the size, layout, and construction materials of a domicile. Shelters in small-scale societies vary across geography and subsistence strategy (Eibl-Eibesfeldt, 1989). For example, when they were still foraging, the !Kung of the Kalahari (southern Africa) slept in small, stick-framed, grass covered huts with few to no physical barriers to the environment (Worthman and Melby, 2002). The Lese horticulturalists (Democratic Republic of the Congo) and Swat Pathan mixed agriculturalists (Afghanistan/Pakistan border) sleep in shelters made of mud and branches that have constructed partitions that can extend to the ceiling (Barth, 1981), and the Gebusi highland horticulturalists (New Guinea) sleep in 20–30 m long communal long house structures with large internal partitions that provide visual but not acoustic separation from the other 20–100 other residents (Knauft, 1985).

Moreover, a wide range of sleeping platforms are observed across cultures, ranging from vertically raised bedsteads to thin floor mats (Beldegreen, 1991). Piles of vegetation constructed from branches, lianas, leaves, and grasses, which are sometimes interwoven or lashed together, have been observed among pastoralists and farmers (e.g., East African Maasai, Central African Tonga and Azande) and forest-dwelling hunter-gatherers (e.g., Central African Efe, South American Caingang, Jivaro in Ecuador, Thai Mrabri) (Métraux, 1946; Schlipp, 1956; Turnbull, 1962; Talbot, 1963; Reynolds, 1968; Hewes, 1994). Sleeping platforms are also constructed with animal hides, with or without a foliage base, such as those constructed by the Alaskan Alutiiq, who prepare the ground by first laying grass down and then layering mountain-goat and bear skins on top (Schlipp, 1956; Turnbull, 1962). Despite the cross-cultural variation seen in sleeping substrate, to our knowledge this is the first study to directly test how such variation in sleeping substrates influences sleep duration and quality.

The acoustic properties of sleeping sites (e.g., human voices, animal movement or calls, and weather-generated noises) can be influenced by the way individuals distribute themselves in their environment. For example, extreme ambient noise levels have been associated with low socioeconomic status among individuals living in post-industrialized economies (Tsai et al., 2009). These noisy environments may contribute to lower sleep duration and quality and may, in turn, generate negative health outcomes (Gangwisch, 2014), such as reported associations between living near traffic-heavy areas and an increased likelihood of dementia (Chen et al., 2017). Acoustic levels are particularly pertinent in small-scale populations that lack environmental barriers, such as insulated buildings that blunt noise, common in the post-industrialized west. Given that the majority of sub-tropical hunter-gatherer societies are not densely populated, with a camp on average consisting of approximately 30 individuals (Marlowe, 2006), sound may influence sleep-wake activity in novel ways compared to industrialized societies.

Fire, which acts as a source of light, heat, smoke, white noise, visual stimulation and/or psychological comfort, is another consideration when choosing a sleep site, as it can influence sleep in several significant ways (Worthman, 2008). Fire has been implicated as a predator deterrent (Wrangham and Carmody, 2010), a way to regulate thermal stress (Coolidge and Wynn, 2006), and a fumigant to repel biting insects (Moore et al., 2007). Additionally, in the cultural west, exposure to controlled fire has been empirically shown to reduce blood pressure and increase prosociality (Lynn, 2014). Several of these factors have led researchers to speculate that the controlled use of fire was important throughout early human evolution (Dunbar and Gowlett, 2014). Taken together, the characteristics of fire could positively influence sleep duration and quality. Alternatively, fire needs constant tending, is a source of light which could potentially suppress melatonin (i.e., sleep-wake regulating hormone) (Burton, 2011), and could increase nighttime activity by facilitating social engagement (Dunbar and Gowlett, 2014). Whether a facilitator or impediment to sleep, either outcome could lend credence to the hypothesis that the controlled use of fire was critical to early human evolution (Coolidge and Wynn, 2006; Wrangham, 2006; Wrangham and Carmody, 2010; Samson and Nunn, 2015).

Studying sleep among hunter-gatherers and other mixed-subsistence small-scale populations is important because forager populations continue to be used as referential standards for inferring evolutionary origins of behavior (Lee, 1992; Crittenden and Schnorr, 2017). Attempts to describe the adaptive sleep-wake pattern among humans have varied, including controlled experiments manipulating photoperiod (Wehr, 1992, 1999), investigations into the effects of artificial light on circadian patterns (de la Iglesia et al., 2015; Samson et al., 2017c), analysis of historical accounts of segmented sleep (Ekirch, 2006, 2016), and comparative analyses on non-human and human primates (Samson and Nunn, 2015). Importantly, activity patterns of non-industrial societies are assumed to be more closely linked to adaptive daily and seasonal rhythms, as such populations lack environmental barriers, such as environmentally controlled buildings with insulation that blunts noise (Yetish et al., 2015), that are likely to influence sleep. Therefore, while the Hadza are by no means analogs to the Paleolithic past, they do offer unique insight into the investigation of sleep-wake activity that might influence our understanding of past lifeways. They are semi-nomadic, live in close contact with their environment (e.g., soil, water, plants, animals), consume a diet that is largely composed of wild foods, and reside in temporary domiciles that do not have artificial light or climate control. Exploring sleep-wake patterns and sleep site construction among the Hadza offers relevant data on the evolution of human sleep, as they live in an environment that is most similar to the one in which our ancestors evolved.

The primary aims of the present study were to (1) characterize human-created environments that influence sleep, (2) assess sleep related social strategies, and (3) investigate how both factors function to influence sleep among the Hadza. We hypothesized that sleep duration and quality were influenced by the use of shelter, sleep substrate, sound, and use of fire. We used our data to test the following predictions: (a) if shelter functions to reduce thermal stress, then domicile constructions will regulate nighttime indices of temperature, wind, and relative humidity; (b) if sound influences sleep-wake patterns and individual camp level distribution throughout the campsite, then acoustics will differ between camps and predict sleep duration; and (c) if fire augments sleep, then duration and quality of sleep will increase when associated with fire.

2. Materials and methods

2.1. Participants

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 hunter-gatherers (Marlowe, 2010; Apicella and Crittenden, 2015). 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). Average annual temperature varies little across the year (mean ~ 28 °C), but considerably between day and night (mean minimum = 14 °C, mean maximum = 35 °C). Traditionally, the dry season occurs between June and November and the wet season occurs December—May, where short rains are followed by long rains; habitat is primarily savanna-woodland, with some rocky hills, brush and marshland (Marlowe, 2010).

Estimates of the annual Hadza diet suggest that it consists of approximately 43% hunted foods (game animals, birds, and honey) and 57% gathered foods, including fruits, legumes, tubers, nuts, and seeds (Crittenden, 2016). Marlowe has estimated the median value for the diets of other African hunter-gatherers to be approximately 32% hunted foods and 67% gathered foods, with high variability between seasons and across years (Marlowe, 2010). The median local group home range for the Hadza is 122 km^2, although range sizes are declining due to adjacent population pressure and globalization (Crittenden, 2014; Blurton Jones, 2016). The Hadza exhibit high levels of sexual division of labor, with males acting as primary hunters and females as primary gatherers (Berbesque et al. 2016). 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).

Hadza volunteers were recruited from Sengele, a bush camp located 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 January 21 and February 11, 2016. Sengele was broken up into two smaller camps, Sengele I and Sengele II, and treated as separate individual camps. The decision to do this was based on the residential groupings of the camp members (i.e., how they self-identified the camp in which they resided) and due to geographic distance between camps (127 m). Photoperiod (i.e., the period of time each day during which the environment is illuminated) ranged between 12.23 and 12.28 h. Sunrise occurred between 06:43 and 6:46 and sunset occurred between 18:59 and 19:00. Lunar phase ranged from full moon (0) to complete cover of lunar light (1). Photoperiod and lunar phase were recorded from The Astronomical Applications Department of the United States Navy (http://aa.usno.navy.mil/data).

Participants were healthy adults over 18 years of age, residing in nomadic or semi-nomadic camps that engaged in daily foraging. Thirty-three subjects completed the study, 21 females (mean age: 34.9 ± 14.3 years) and 12 males (mean age: 35.6 ± 14.7 years). Eight participants wore actigraphs throughout the entire study duration; to increase subject sample size, twenty-five individuals wore the actigraphs at either the beginning or end of the study for a minimum of 10 days. Exclusion criteria included self-reported insomnia or physical disability due to injury or infirmed status that prevented an individual from engaging in active foraging. Based on injury and infirmed status, three individuals were excluded from analysis (reducing the total number of individuals participating in the study from 36 to 33). All research was approved by the Tanzanian Commission for Science and Technology (COSTECH) and the Tanzanian National Institute for Medical Research (NIMR). All eligible subjects gave their verbal informed consent, as outlined by the Institutional Review Board for human subjects' research at the University of Nevada, Las Vegas and Duke University.

2.2. Equipment

We used the Motionwatch 8 actigraph (CamNtech). The MotionWatch 8 sensor logs motion data over a user-defined interval, or epoch, using a built-in tri-axial accelerometer. The sensor samples data at 50 Hz and accumulates data over the epoch, ultimately assigning it an integer value on a ratio scale. We collected data on the minute, as continuous one minute sampling is the most commonly used actigraphic method for measuring sleep--wake activity patterns in humans (Ancoli-Israel et al., 2003; Johnson et al., 2007) and non-human primates (Sri Kantha and Suzuki, 2006). Additionally, the MotionWatch 8 also records light via a lux sensor. Although polysomnography (PSG) is currently considered the gold standard for quantifying sleep, it remains cumbersome, expensive, and difficult to apply with ambulatory participants. Actigraphy, on the other hand, is emerging as a valuable approach to investigate sleep outside clinical or laboratory settings. The non-invasive, wrist worn device has been increasingly adopted to investigate sleep, not only in various populations living in the post-industrialized west (Yoon et al., 2003; Johnson et al., 2007; Kawada, 2008) but also in the developing world (Knutson, 2014; Samson et al., 2017c) and among small-scale foraging and mixed-subsistence populations (Yetish et al., 2015; Samson et al., 2017a).

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; moreover, the software has a nap analysis function that detects periods of inactivity that are attributable to napping or micro-sleeps. The algorithmic high-sensitivity settings are most reliable for determining sleep (Kanady et al., 2011); therefore, we used the high-sensitivity setting throughout this study.

Meteorological variables (temperature, relative humidity [RH], and wind speed) were recorded with Kestral 4000 pocket weather trackers. The weather trackers were set to record data at five-minute intervals. Baseline data (i.e., at the intersection between both camps) were recorded for 14 days. Comparative data, where Kestrals were placed in both an outside baseline and inside domicile environment, were generated for five nights ($n = 864$ meteorological samples) and four days ($n = 720$ meteorological samples). A different domicile was randomly chosen for each day and the weather trackers were hung 20 cm from the top of the domicile. Rainfall was measured daily.

Noise data were generated with Convergence Instrument's Noise Sentry RT. The outdoor sound level meter data logger has a digital microphone (with 128 Mb recording memory) that autonomously records sound levels (dB). Sound samples were generated at second intervals. Two sound level data loggers were placed in each of the two camps for the duration of the study to capture camp level sound dynamics. The number of adults and children in each camp, as well as the distance between the two camps (Sengele I and Sengele II distance = 127 m), were recorded. Data loggers were placed one meter above ground at the center of each camp.

2.3. Protocol

Participants were given a sleep survey at the beginning of the study period (January 20 – February 11, 2016) to screen for healthy sleep and ascertain general information of subjective sleep quality, including preference for sleep with or without fire and number of co-sleeping individuals per sleeping platform. Participants were asked to rank general perceived threats from greatest to least from among a list of five potential categories: (i) animals, (ii) disease, (iii) food insecurity, (iv) people, and (v) weather. Hadza participants ranked "food insecurity" as the most urgent primary threat (48.6%), "other people" (29.7%) as their second most urgent primary threat, with a tie between "animals" (10.8%) and "disease" (10.8%) for primary threats. "Weather" was perceived as the least dangerous, with 75.7% of respondents putting it in the least threatening category.

Participants were free to sleep within their grass hut domiciles or at an outside sleep site throughout the study. To determine sleep-related environmental factors, we interviewed every participant each morning and recorded the frequency of daytime sleep bouts (i.e., napping), discrete nighttime wake bouts, sleep site (indoor grass hut domicile versus outdoor sleep site), and whether they slept with or without a fire. Finally, those participants wearing actigraphs throughout the study were asked to press the actigraphy event marker preceding any sleep event, including sleep after nighttime wake bouts and before initiating daytime naps. They were asked daily if they had pressed the event marker or if there were any technical difficulties, including instances of watch removal, during the previous day. This protocol was also followed for the participants wearing actigraphs for part of the study. At no point during the study was a watch observed or reported to have been removed by a participant. The method of asking participants daily if they had used the event marker encouraged compliance as we showed that of the total wake events and sleep events, event markers were used for 0.88 (S.E. = 0.03) of the total sleep events (Samson et al., 2016). Consistent with validated actigraphic protocol (Stone and Ancoli-Israel, 2011), where event marking was absent, expert manual scoring (by DRS) was performed to assess "time in bed," and "time out of bed."

Throughout the study period, individual grass hut domiciles and sleeping platforms (i.e., beds) were measured for every study participant. The huts (see Fig. 1) are constructed exclusively by adult women and consist of interwoven tree branches (typically from the plants *Grewia bicolor* or *Acacia nilotica*) that are inserted into postholes in the ground and then covered in grass and/or large leaves (Marlowe, 2010; Crittenden, 2016). Every domicile at Sengele was measured ($n = 22$); the variables recorded are detailed in Table 1. Sleeping platforms measures were recorded as: number of layers, length, width, and thickness. Presence or absence of pillow (e.g., a balled blanket or shirt) was recorded. If present, length, width, and thickness were recorded.

To estimate individual energy balance and thermodynamic comfort levels, we applied a bioclimatic index using temperature, RH, and wind speed with the RayMan Pro (Matzarakis et al., 2007, 2010); this thermophysiological model calculates thermal stress using meteorological parameters and body proportions. The physiological equivalent temperature (PET) was the output from the model, and it used age (to assess metabolic rate), stature, body mass, clothing, and positional behavior to calculate an index of thermal comfort (Matzarakis et al., 2007). We derived individual measures for each sex by averaging values generated from the initial survey; additionally, previous work with the Hadza found that there are no differences between the sexes in any measure of sleep quotas (Samson et al., 2017a), further justifying the aggregation of the sexes for the purposes of this study. The average values for females were: age = 35, clothing = 80% of body, and body mass = 45.5 kg. The average values for males were: age = 35, clothing = 60% of body, and body mass = 48.0 kg. Both sexes were parameterized as lying down in a horizontal position, as it reflects positional behavior during sleep.

2.4. Statistical analyses

We used R. Core Team, 2016 to conduct statistical analyses. We compared the RayMan PET thermoregulatory comfort index between the simultaneously recorded inside domiciles and outside baseline values. We used a paired Wilcoxon test to assess significance. We provide the different grades of thermal sensation and physiological stress to compare with values generated in this study (Matzarakis and Mayer, 1996; Matzarakis et al., 1999). Moreover, we ran correlation tests (and associated power analyses) on the physical dimensions of sleeping platforms and total sleep time and wake-bouts.

Functional linear modeling (FLM) was used to characterize and illustrate 24 sleep-wake patterns relative to sound levels. The FLM approach, specifically designed for actigraphy time-series data analysis, measures raw activity counts within and between samples; summary statistics can mask differences across groups (Wang et al., 2011), making FLM a powerful analytical tool. Functional linear modeling was used to compare individual activity patterns, based on which camp they slept in, relative to the dB mean value experience by each volunteer. To this end, we applied a non-parametric permutation test method in the R package "actigraphy" (Shannon et al., 2015). A further advantage of this method is that it does not rely on distributional assumptions. The *p*-value is calculated by counting the proportion of permutation F values that are larger than the F statistics for the observed data. Here, we used the point-wise test (with 500 permutations) that provides a curve which is the proportion of all permutation F values at each point in the time series (Wang et al., 2011). We also used a simple linear regression to test for associations between sound level and sleep duration.

To assess the technocultural predictors of sleep, we ran linear mixed effects models for each of our different types of response variables (sleep duration: nighttime total sleep time, and sleep quality: sleep efficiency and sleep fragmentation) using the lme4 package (Bates et al., 2015). For sleep segmentation (i.e., nighttime wake-bouts), due to the non-normally distributed response variables, we used a generalized linear mixed model fit by maximum likelihood (Laplace approximation). In all models, we included variables known to influence Hadza sleep (Samson et al., 2017a), such as age, mean daylight activity (actigraphy counts), photoperiod, nighttime noise (dB), daily mean light exposure (lux), moon phase, temperature, sleep site (either inside their hut or somewhere outside the hut), rainfall (mm), humidity, wind, and the presence and absence of fire. Due to the fact that domiciles can be used to shield against rain and wind, we included interactions between sleep site and both rainfall and wind. These predictors were scaled to ensure comparability between coefficients. To control for repeated measures, we included "subject" as a random effect, and we obtained coefficients based on optimization of the log-likelihood using shrinkage. Shrinkage incorporates measurement error (i.e., standard error) into the regression model, which improves less certain estimates by pooling information from more certain estimates (McElreath, 2016). We used the MuMIn package (Bartoń, 2015) to average models with $\Delta\text{AIC} < 10$ and interpreted models. We then made statistical inferences using a combination of standardized coefficients, *p*-values and confidence intervals.

3. Results

Average domicile dimensions are reported in Table 1. Most domiciles were a single dome but 6/27 (22%) were characterized by

Figure 1. The most common domiciles were grass huts constructed by women; several women work together for up to two hours, gathering flexible branches that they bend into an inverted U shape and stick the ends into the ground (bottom right). Once braced in the ground, they crisscrossed several branches to form an upside-down bowl-shaped structure that is then stuffed with grasses (bottom left) (Marlowe, 2010). Larger, two-domed domiciles (top) were made by intertwining two huts together. Participant consent for photograph was given to DRS.

Table 1
Grass hut domicile averaged for each dimension.[a]

Dimension	Mean ± standard deviation
Steeple	1.22 ± 0.42
D1	285.4 ± 38.3
D2	256.0 ± 32.6
C1	188.9 ± 17.7
H1	284.2 ± 31.8
H2	270.7 ± 17.9
H3	267.5 ± 20.7
H4	274.2 ± 29.6
T	21.2 ± 4.0

[a] Variables measured were as follows: number of steeples (i.e., either one or two domes), diameter one (D1 = from domicile entrance to its back), diameter 2 (D2 = perpendicular distance from D1), center (C = the intersection between D1 and D2, from ground to top of dome), height 1 (H1 = starting clockwise from entrance, the length of the curve of the dome from the ground to the center of the dome), height 2 (H2 = 90° clockwise turn from entrance, length from the ground to the center of the dome), height 3 (H3 = 180° clockwise turn from the entrance, length from the ground to the center of the dome), height 4 (H4 = 270° clockwise turn from the entrance, length from the ground to the center of the dome), thickness (T = thickest point in the domicile from inside to outer surface).

two interconnected domes (see Fig. 1). Average sleeping platforms dimensions (cm) were as follows (Fig. 2): number of layers = 2.45 ± 1.46, length = 181.2 ± 17.5, width = 126.9 ± 24.1, thickness = 0.75 ± 1.1, surface area = 2.30 m^2 ± 0.6. The Hadza used bunched up textiles, or mounded earth as pillows, yet 41% reported not using a pillow (Fig. 2). Pillow dimensions (cm) were as follows: length = 28.8 ± 12.0, width = 86.0 ± 41.0, thickness = 13.7 ± 4.8.

Sleeping platform thickness ($F = 0.32$, $df = 29$, $p = 0.57$), number of layers ($F = 0.06$, $df = 29$, $p = 0.80$), and use of pillow ($U = 1.08$, $p = 0.56$) were not significantly associated with total sleep duration. However, sleeping platform surface area showed a trend towards significance for both total sleep time ($n = 31$, F = 2.96, $p = 0.090$) and wake-bouts ($n = 31$, F = 2.9, $p = 0.099$), and power analysis showed that a sample size of 42 and 43 (respectively) would have produced sufficient power to detect statistical significance at the 0.05 level. The median for the number of co-sleeping individuals that slept in the same nightly sleeping platform was 2 (range: 1–6).

Throughout the study duration, mean night temperature was 23.16 ± 3.6 °C and mean daily rainfall was 2.06 ± 3.13 mm. Table 2 shows PET grades (°C) of thermal sensation and physiological stress to the human body. Female average PET was 25.71 (standard error

Figure 2. Sleeping platforms. Traditionally, the Hadza used skinned animal (often impala) hides as mattresses (bottom right), and they occasionally still do, but more often bedding materials are procured from trading with neighboring pastoralists; bedding materials used were: textile blankets and sheets, linen sacks, woven grass matts, and mosquito nets (top). A pillow is not always used, but when present it is often rolled up clothing or a dirt mound under the bedding layers (bottom left). Participant consent for photograph was given to DRS.

[S.E.] = 0.37) and male average PET was 25.70 (S.E. = 0.37), thus all analyses comparing PET between inside and outside microhabitats were performed using sex averaged PET. The baseline outside condition for 24 h, day–night averaged PET was 25.70 ± 10.69, whereas the domicile inside condition was 29.20 ± 9.13 (Wilcoxon paired test = $p < 0.001$). Daytime, baseline outside PET was 34.75 ± 9.06 (moderate heat stress) and nighttime PET was 18.18 ± 4.03 (slight cold stress). Daytime, domicile inside PET was 37.65 ± 6.81 (moderate to strong heat stress) and nighttime PET was 22.16 ± 2.24 (slight cold stress to comfortable). Figure 3 illustrates the significant differences between domicile and baseline PET between day and night. Moreover, a variance F test showed significant differences between the variance of nighttime domicile and baseline (F = 3.24, df = 863, $p < 0.001$) and daytime domicile and baseline (F = 1.77, df = 863, $p < 0.001$), where the inside domicile conditions had less variance than outside.

Simple linear regression showed that nighttime total sleep time was predicted by sound level (F = 27.97, $p < 0.001$) with an R^2 of 0.15. Additionally, controlling for environmental variables, increasing sound level negatively correlated with nighttime total sleep time (see Table 3). There were differences between mean nighttime sound at both camps, with a mean difference of 5.06 dB (camp 1 = 49.11 ± 3.76; camp 2 = 44.81 ± 2.39; Wilcoxon test = $p < 0.001$). Functional linear modeling applied to actigraphy data ($n = 32$ nights, with a multi-day average for each volunteer) and night averaged sound level (dB) showed that nighttime noise predicted greater activity in the morning (08:00–09:00) and evening (19:00–23:30) (Fig. 4).

After controlling for all covariates, nighttime total sleep time (TST) was influenced by several predictor variables (Table 3). Specifically, TST was negatively influenced by greater mean age, sound level, outdoor sleep site (not within a hut), moon phase, active period activity, and active period light exposure (lux); in contrast, TST was positively influenced by longer photoperiod and greater temperature. With respect to sleep quality, sleep associated with fire did not influence either sleep efficiency (β ± SE = −0.06 ± 0.08, p = 0.50, C.I. = −0.24–0.11) or sleep fragmentation (β ± SE = −0.03 ± 0.09, $p < 0.77$, C.I. = −0.21–0.15). Furthermore,

Table 2
Physiological equivalent temperature (PET) for different grades of thermal sensation and physiological stress in humans (Matzarakis et al., 1999).

PET (°C)	Thermal sensation	Physiological stress level
4	Very cold	Extreme cold stress
8	Cold	Strong cold stress
13	Cool	Moderate cold stress
18	Slightly cool	Slight cold stress
23	Comfortable	No thermal stress
29	Slightly warm	Slight heat stress
35	Warm	Moderate heat stress
41	Hot	Strong heat stress
>41	Very hot	Extreme heat stress

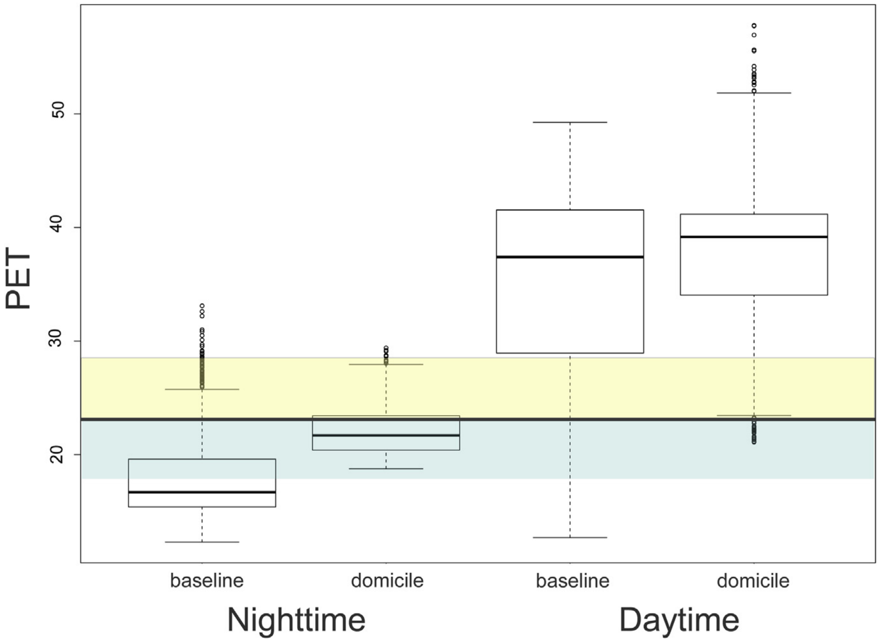

Figure 3. A comparison between nighttime and daytime sleep site thermal comfort measured with physiological equivalent temperature (PET, °C) illustrating the differences between baseline (outside normal ambient temperature) and domicile (inside grass hut) thermal sensation and physiological stress on individual sleepers. Interestingly, the variation inside the domicile is not as large as the variation outside. Note the black, horizontal line that represents ideal thermal comfort, where individuals experience no thermal stress; the only condition where this occurs is in the nighttime domicile microhabitat. The light, transparent yellow highlights the zone where there is slight heat stress and the light, transparent blue highlights the zone where there is slight cool stress. The middle band represents the median and the top and bottom of the box are the 25th and 75th percentile, respectively. The whiskers represent the minimum–maximum 1st and 3rd quartile plus 1.5× the interquartile range. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Predictors of 24-h total sleep duration, including environmental factors.[a]

Predictor	β	SE	Confidence interval	z	p
Activity	−0.21	0.07	(−0.36, −0.07)	2.95	=0.003
Age	−0.37	0.09	(−0.55, −0.20)	4.23	<0.001
Photoperiod	0.99	0.33	(0.33, 1.64)	2.97	=0.003
Nighttime noise	−0.28	0.10	(−0.48, −0.08)	2.66	=0.007
Light exposure	−0.30	0.07	(−0.42, −0.16)	4.36	<0.001
Moon phase	−0.87	0.33	(−1.51, −0.23)	2.66	=0.007
Temperature	0.39	0.10	(0.21, 0.58)	4.13	<0.001
Sleep site: outdoor	−0.15	0.07	(−0.28, −0.01)	2.14	=0.033
Rainfall	0.11	0.08	(−0.06, 0.27)	1.28	=0.199
Humidity	0.02	0.07	(−0.10, 0.15)	0.37	=0.713
Wind	0.04	0.09	(−0.13, 0.22)	1.50	=0.620
Fire: present	0.04	0.08	(−0.12, 0.19)	0.45	=0.652
Sleep site*rainfall	−0.03	0.06	(−0.16, 0.10)	0.50	=0.620
Sleep site*wind	0.02	0.07	(−0.11, 0.15)	0.37	=0.713

[a] Positive coefficients indicate greater sleep duration, while negative coefficients shorter sleep duration. Outdoor is the reference category for sleep site. Fire present is the reference category for fire. We included interactions between sleep site and both rainfall and wind. Fire did not influence sleep duration. SE = standard error.

segmented sleep was also unaffected by the fire association, given wake-bouts were not significantly influenced ($\beta \pm SE = 0.20 \pm 0.28$, $p = 0.48$). In sum, the presence or absence of fire at a sleep site had no significant effect on sleep (Fig. 5) although it was present 67% of the time (295 out of 436 nights as reported by individual daily surveys) and reported as being helpful to sleep by 88% (32/36) of respondents to our surveys. Additionally, males slept outside 32% (37/117) of nights whereas females slept outside 25% (46/187) of nights and the difference between sexes was not significant (Pearson's Chi-squared = 1.06, $df = 2$, $p = 0.58$); indoor sleep site TST averaged 433 min (SD = 53 min) and outdoor sleep site TST averaged 424 min (SD = 56 min). Sleeping within a grass hut versus outdoors was predicted by rainfall and wind. Individuals were more likely to sleep inside with increased rainfall ($\beta \pm SE = -1.65 \pm 0.59$, $p = 0.006$, C.I. = −2.81 to −0.48); individuals were more likely to sleep outside with increased wind ($\beta \pm SE = 1.75 \pm 0.56$, $p = 0.003$), C.I. = 0.59–2.90).

4. Discussion

We analyzed technological and social strategies used by the Hadza to alter sleep environments in ways that influence sleep duration and quality. In particular, we found that the grass hut domiciles used by the Hadza likely function as microhabitats — with comparatively less overall variation in thermal stress relative to outside baseline environments. This may be particularly critical during the rainy season, when the data were collected, as more people are likely to sleep inside (Marlowe, 2010). Overnight, when temperatures drop to a point of thermal discomfort (as measured by PET), the shelters are warmer and can be significantly more comfortable than sleeping outside. To our knowledge, we report the first ambient acoustic measures of nighttime environments of hunter-gatherers. These data illustrate that sound greatly influenced sleep, with greater sound levels being associated with less sleep. Finally, after controlling for ecological variables previously shown to influence sleep in this population (Samson et al., 2017a), fire was found to neither facilitate nor discourage sleep expression. Overall, our findings lead us to support the hypothesis that sleep is influenced by the use of sleep site, shelter, and acoustics but, in general, not by sleeping platform or fire.

Specifically, our findings support the prediction that shelter functions as a microhabitat construction that can be strategically used to reduce thermal stress. The PET comparative analysis of baseline outside and inside the domicile revealed significant differences in microhabitat thermal stress. The outside condition had greater variation in thermal stress and nighttime PET median was

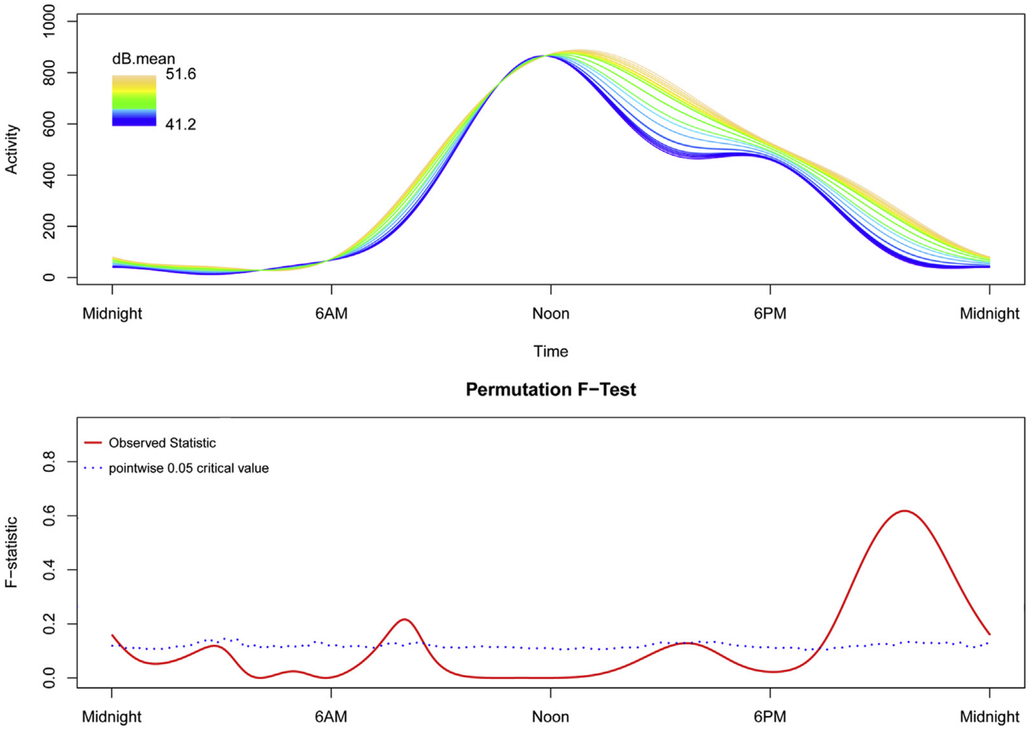

Figure 4. A nonparametric permutation *F* comparing activity (y-axis) and the average nightly sound level (x-axis) within each camp. The point-wise critical value (dotted line) is the proportion of all permutation *F* values at each time point at the significance level of 0.05. When the observed *F*-statistic (solid line) is above the dotted line, it is concluded the continuous measures have significantly different mean circadian activity patterns at those time points.

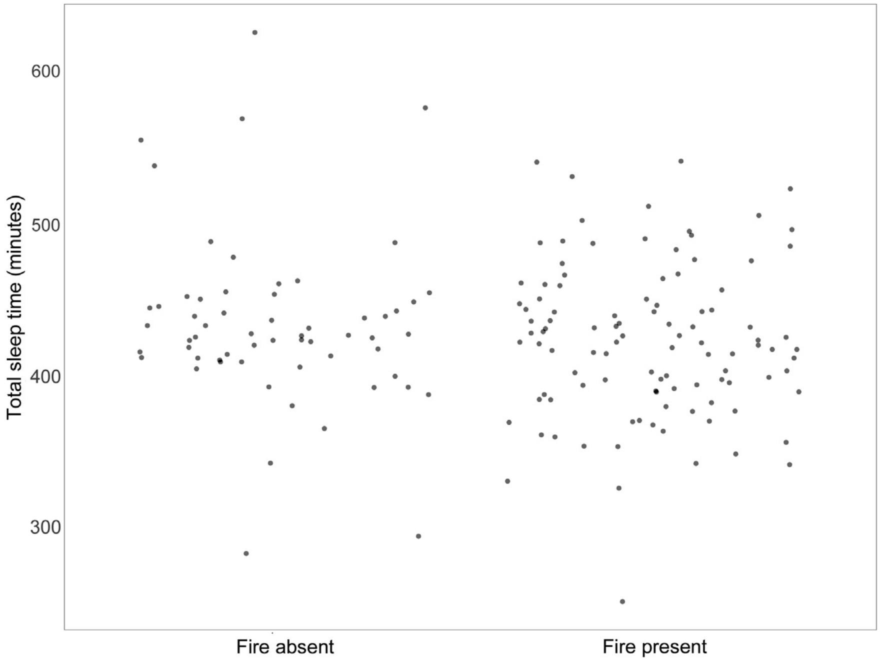

Figure 5. A plot for each standardized fixed coefficient (i.e., each predictor regressed on the response) illustrates there is no influence of the presence or absence of fire at the sleep site and total sleep time.

in the moderate cold stress range; in comparison, the PET median inside the domicile microhabitat was in the comfortable grade, with the 24th–75th percentile range within the slight cold to slight warm gradients (Fig. 3). The finding that there was less variation in PET in the microhabitat also serves as evidence that this structure is what Shumaker et al. (2011: 204) have called an “architectural construction” (i.e., composite function structure consisting of two or more physically linked tools and/or objects) that can be used to reduce thermoregulatory stress during sleep. As a comparative example, ape sleeping platforms on average take five minutes to build and are considered to be complex architectural constructions that also provide thermoregulatory buffering (Stewart, 2011); the architectural constructions manufactured by Hadza women are much more labor intensive and can take up to four hours to construct (Marlowe, 2010).

Additionally, our model showed that increased rainfall was predictive of individuals sleeping inside their domicile whereas greater wind was predictive of individuals sleeping outside. In other words, we interpret these results to suggest that individuals sought the most comfortable sleep site by modulating when they slept indoors or outdoors; specifically, individuals could choose to sleep within grass huts to avoid the rain and reduce cold stress, whereas they could choose to sleep outdoors to gain access to open airflow on nights with exceptional heat stress. Yet, temperature, rain, and wind may not be the only reasons to modulate inside versus outside sleep, as the survey responses on threat perception highlight that Hadza consider conspecifics and animals to be a noteworthy threat.

Within the domiciles are sleeping platforms. Traditionally, the Hadza used skinned animal (often impala) hides as mattresses (Marlowe, 2010), and they occasionally still do, but more often bedding materials are procured from trade relationships with neighboring ethnic groups or through exchange with missionaries, tourists, or researchers. These bedding materials include textile blankets, linen sacks, woven grass mats, and mosquito nets (see Fig. 2). Although bed dimensions were not associated with sleep duration or quality, the surface area of the sleeping platform approached significance. Intriguingly, pillows made of balled shirts or textiles were used by only 59% of the population, and when used they were not found to affect duration or quality of sleep. Limitations to our study include lack of seasonal variation, as our analysis here is restricted to the rainy season. Future work could experimentally test whether sleeping platforms (or fireside sleep) have a role in sleep physiological and post-sleep cognitive function in small-scale societies or in controlled laboratory settings.

An additional limitation to our study is that sounds were measured only by decibel level and not analyzed for qualitative meaning. Despite this, our findings nevertheless support the prediction that sound is linked with sleep-wake patterns and the distribution of individuals throughout both Sengele I and Sengele II camps. Throughout the night, the camp with the greater number of individuals was the louder camp; comparatively, the acoustic levels at the larger camp were, on average, 5.06 dB greater. Interestingly, when asked why there were two separate camps in relatively close proximity, rather than one large location, people often cited noise as justification. Furthermore, 69% of surveyed respondents claimed that noise negatively affected their sleep. Moreover, mean dB was negatively associated with nighttime total sleep duration and our model confirmed this trend when controlling for covariates. There were two periods of the day when increased noise levels were associated with increased activity: 8:00–9:00, and 19:00–23:30 (see Fig. 4). The early morning was characterized by sex-specific gatherings before initiating primary foraging periods, while the evening was often associated with fire-side social activity. This pattern is similar to the one described by Wiessner (2014) of the Ju/'hoansi, where fireside night talk plays an important role in transmitting cultural information that generates regularity of behavior, trust, and cooperation at the regional level. As an example, the epeme dance, a sacred Hadza ritual, was often timed during this period. The function of the ceremony is to act as a social adhesive and bring fortune to future hunting expeditions (Woodburn, 1964). The dance usually occurs every night when there is no moon in the sky and is acted out between the hours of full darkness and midnight, as the ritual requires the surrounding area to be dark (Marlowe, 2010).

Our findings did not support fire as a predictor of sleep. After controlling for covariates, sleep associated with and without fire did not differ in duration or quality (Fig. 5). In addition, fire associated sleep did not affect segmentation (wake-bouts > 20 min). Given that fire can either act as a behavioral facilitator or inhibitor of sleep, it may be that these factors cancel each other out. Our initial survey showed that fire is considered by 89% of the population to be helpful to sleep and 86% responded that they used it as a light source at night. A full moon emits exposure value to illuminate the human figure at 0.131 lux and firelight emits enough lux to illuminate the human figure at 80 lux. When the actigraphy lux sensor detected occurrences of light exposure between dusk and dawn throughout the study period, it was most likely from proximity to fire given that the watches were set to detect light at 1 lux (Fig. 6). Interestingly, the half-maximum effects for dose-dependent light exposure for suppression of melatonin is 50–130 lux (Cajochen et al., 2000); additionally, firelight also emits a wide spectrum of light intensity, ranging from long wave light (red and yellow) to short wave light at its base (blue) (Burton, 2011). Short waves are known to suppress melatonin and negatively impact sleep (Chang et al., 2015). Therefore, there is the intriguing possibility that moonlight may not suppress melatonin, but firelight – in the proper dose – could. Future work in controlled settings could experimentally determine the linkage between fire association and melatonin production. While fire may not influence sleep-wake activity, its use could serve other, essential functions such as cooking (Wrangham and Conklin-Brittain, 2003). Whether fire is critical to controlling thermodynamic stress among Hadza sleepers is a question for future research. This issue is particularly intriguing, given its important implications for early humans dispersing out of equatorial Africa (where temperatures and photoperiod remain relatively constant throughout the year) into higher latitudes with greater cold stress.

4.1. Evolutionary implications

The data presented here can be further used to make predictions about sleeping behavior in human evolution. Within primates, the evolution of increased body mass (over 30 kg) coincided with the innovation of ape nest construction, suggesting that larger body mass made sleeping directly on branches less viable for larger-bodied apes (Samson and Hunt, 2012). A further transition, from nest-building in trees to sleeping on the ground, has also occurred at some point in human evolution. Given its obligate bipedality (Wood and Collard, 1999) and mass and stature estimates that are comparable to modern humans (McHenry, 1991; Anton and Snodgrass, 2012), *Homo erectus* can be inferred to be the first fully terrestrial, ground sleeping hominin (Samson and Nunn, 2015); in contrast to the more arboreal earlier hominins, including the *Australopithecus* lineage (Hunt, 1996), the body and limb proportions of *H. erectus* would make arboreal sleep difficult to facilitate.

With the advent of full-time terrestriality, we propose significant evolutionary shifts in human sleep environments. Due to preservation bias of organic materials, direct prehistoric archaeological evidence of sleep related technology is relatively recent and rare. For example, grass beds (consisting of stems and leaves covered by compacted clay) dating to 23, 000 ka were uncovered at the Israeli site of Ohalo II (Nadel, 2004). Other evidence has been found in a Mousterian Neanderthal cave site where bedding near hearths was uncovered (Cabanes et al., 2010) and the oldest evidence of bedding discovered in situ was found at Sibudu, South Africa and dates to approximately 77,000 years ago (Wadley et al., 2011). Despite the recent dates for bedding in the archaeological record, it is likely that early *Homo* used sleeping platforms, given

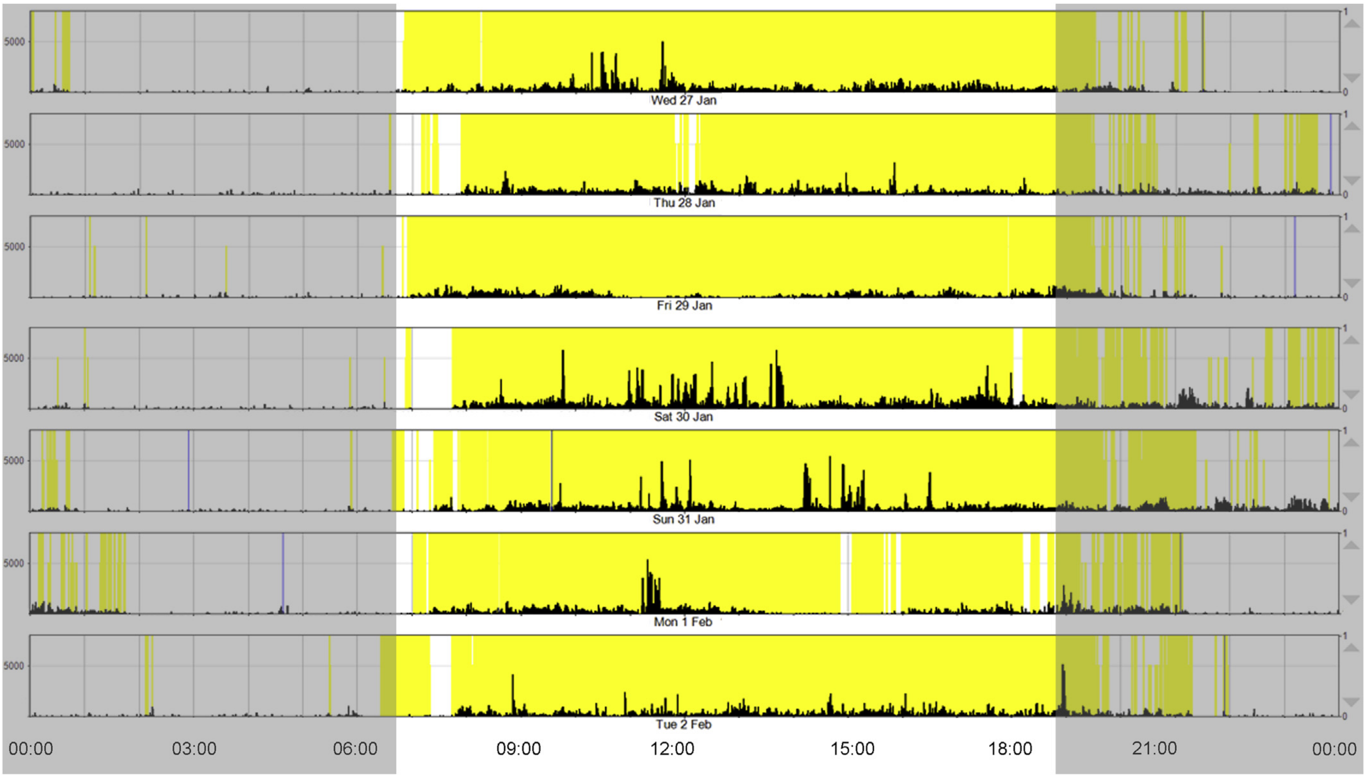

Figure 6. An actogram with associated recorded light throughout a week span for a 26 year old male. The shaded area represents the maximum dusk–dawn interval during the study period. Black represents raw activity and yellow represents lux exposure. The light sensor records white light with a response optimized to match the human eye. The light is sampled once per second and averaged over the epoch. The results are stored as lux values. This graph illustrates that light exposure is common during the night and fire or moonlight are the only sources of light available to the Hadza. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

their universal application in the great apes (Fruth and Hohmann, 1996). Once fully terrestrial, early *Homo* most likely combined the innovative use of stable ground substrates with shelter technology to provide sleep sites with less overall variation in thermal stress than previously possible for a primate. These technological and social innovations to sleep sites coupled with group level social cohesion and variation in chronotype (driven by mixed age groups) may have also facilitated sentinel-like behavior and thus more secure and safe sleep sites (Samson et al., 2017b). In sum, novel sleep site conditions could have been an important prerequisite to derived human-unique sleep architecture (Samson and Nunn, 2015) that contributed to the evolutionary success of our species.

5. Conclusions

The success of *Homo sapiens*, attributed to a reliance on culture, technological innovation, and unparalleled cooperative networks, has been described (Boyd and Richerson, 2005: 11) as “a spectacular evolutionary anomaly,” that has resulted in humans colonizing terrestrial habitats worldwide in a variety of ecosystems (Hill et al., 2009). Our study has shown that the domicile huts used by the Hadza serve as a method of providing a barrier to biotic and abiotic environmental factors that also increase thermal consistency in an often unpredictable environment. Mastery of such technology, including the controlled use of fire in cold environments, would have been a prerequisite for early hominin expansion out of Africa. Humans have 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 (Refinetti, 2006). Importantly, a high degree of physiological plasticity, including flexibility in the timing, duration, and quality of sleep permitted by secure, temperature regulated sleep sites would have been a unique human adaptation. Future research in populations with highly divergent environmental contexts across varying latitudes could elucidate the plasticity inherent in these and other biological systems, ultimately informing how humanity spread across the globe.

Acknowledgments

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