Natural Sleep and Its Seasonal Variations in Three Pre-industrial Societies

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Natural Sleep and Its Seasonal Variations in Three Pre-industrial Societies

Highlights

- Preindustrial societies in Tanzania, Namibia, and Bolivia show similar sleep parameters
- They do not sleep more than "modern" humans, with average durations of 5.7–7.1 hr
- They go to sleep several hours after sunset and typically awaken before sunrise
- Temperature appears to be a major regulator of human sleep duration and timing

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In Brief

Yetish et al. find that hunter-gatherers/horticulturalists sleep 6.4 hr/day, 1 hr more in winter than in summer. Onset is about 3.3 hr after sunset, and sleep occurs during the nightly period of falling temperature. Onset times are irregular, but offset time is very regular. Little napping is seen. Light exposure is maximal in the morning, not at noon.

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Current Biology
Report

Natural Sleep and Its Seasonal Variations in Three Pre-industrial Societies

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SUMMARY

How did humans sleep before the modern era? Because the tools to measure sleep under natural conditions were developed long after the invention of the electric devices suspected of delaying and reducing sleep, we investigated sleep in three preindustrial societies [1–3]. We find that all three show similar sleep organization, suggesting that they express core human sleep patterns, most likely characteristic of pre-modern era *Homo sapiens*. Sleep periods, the times from onset to offset, averaged 6.9–8.5 hr, with sleep durations of 5.7–7.1 hr, amounts near the low end of those industrial societies [4–7]. There was a difference of nearly 1 hr between summer and winter sleep. Daily variation in sleep duration was strongly linked to time of onset, rather than offset. None of these groups began sleep near sunset, onset occurring, on average, 3.3 hr after sunset. Awakening was usually before sunrise. The sleep period consistently occurred during the nighttime period of falling environmental temperature, was not interrupted by extended periods of waking, and terminated, with vasoconstriction, near the nadir of daily ambient temperature. The daily cycle of temperature change, largely eliminated from modern sleep environments, may be a potent natural regulator of sleep. Light exposure was maximal in the morning and greatly decreased at noon, indicating that all three groups seek shade at midday and that light activation of the suprachiasmatic nucleus is maximal in the morning. Napping occurred on <7% of days in winter and <22% of days in summer. Mimicking aspects of the natural environment might be effective in treating certain modern sleep disorders.

RESULTS

It has been argued that the invention of the electric light, followed by the development of television, the Internet, and related technologies, along with increased caffeine usage, has greatly shortened sleep duration from “natural” levels and disrupted its evolved timing. The purported reduction in sleep duration has been linked to obesity, mood disorders, and a host of other physical and mental illnesses thought to have increased recently (http://www.healthypeople.gov/2020/topics-objectives/topic/sleep-health#eight), although complaints about reduced sleep time in the “modern world” were made at least as far back as the 1880s [8, 9].

In the current paper, we examine sleep duration, timing, and relation to natural light, ambient temperature, and seasons in three preindustrial human societies (Figure 1A). The Hadza live in northern Tanzania, 2° south of the equator, in woodland-savannah habitats around Lake Eyasi. The Hadza in this study were wholly dependent on hunting and gathering each day for wild foods. Until the recent past, the Kalahari San were also nomadic hunter-gatherers. The Ju/’hoansi (Ju/’hoan language group) San that we studied live in the Den/ui village, 20° south of the equator, are currently not migratory, but they are isolated from surrounding villages and continue to live as hunter-gatherers. Genetic studies indicate that the Kalahari San genome is the most variable of those yet sequenced, being much more variable within this group than in the descendants of the small groups that migrated out of Africa to populate Europe, Asia, and the Americas [2]. The Tsimane, living near the furthest reaches of the human migration out of Africa, close to the Maniqui River in Bolivia and 15° south of the equator, are hunter-horticulturalists. Extensive health studies of the Tsimane have found that although child mortality is higher than in “modern” societies, largely due to infectious diseases, adults have lower levels of blood pressure and atherosclerosis and higher levels of physical fitness than industrial populations [10]. Many live into their 60s, 70s, 80s, and beyond. Similar health findings have been reported among Hadza [1, 11] and San [12, 13].

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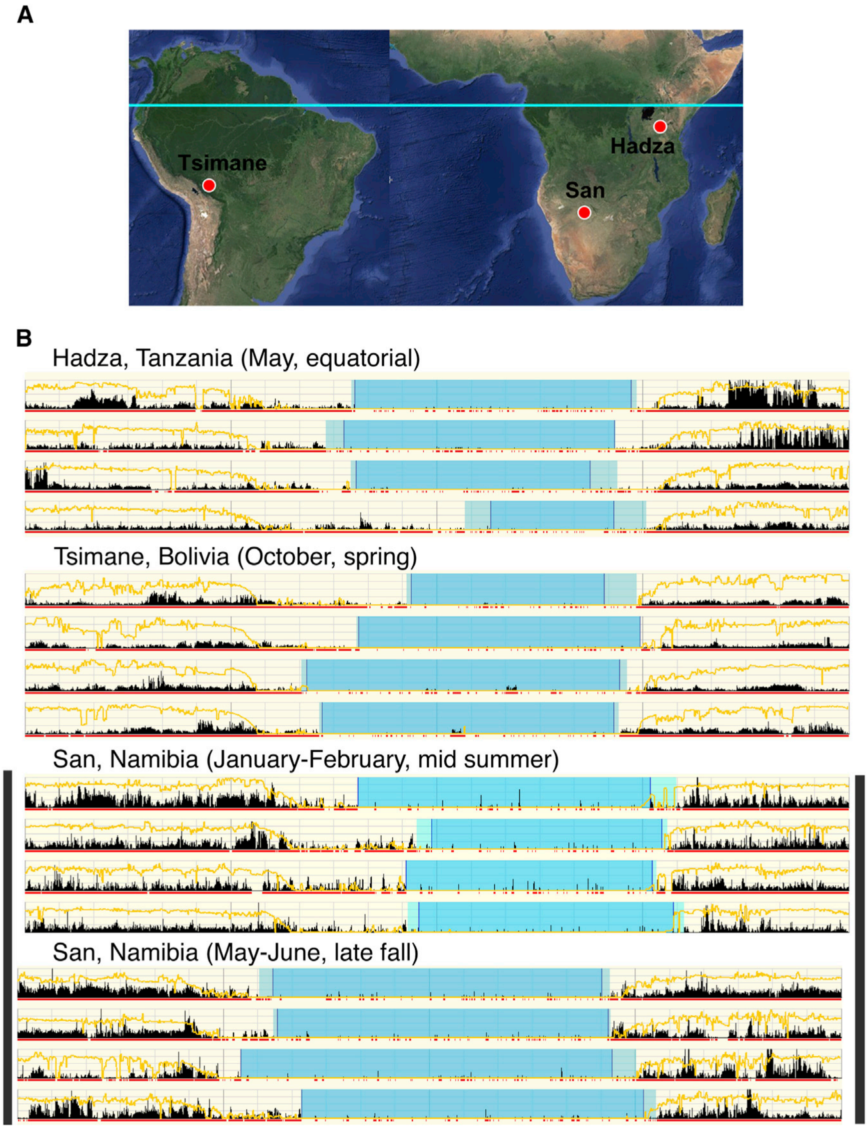

Figure 1. Recording Sites and Representative Actograms

(A) Location of recording sites (left to right: Tsimane, San, and Hadza).

(B) Representative Actograms from Hadza, Tsimane, and San subjects (the bottom two sets show the same San participant in summer [upper set] and winter [lower set]). Sleep onset time is highly variable and occurred several hours after sunset in all groups. Awakening time was relatively regular and occurred before sunrise, except in the San in summer. Naps may have occurred on up to 7% of days in winter and up to 22% of days in summer. Extended periods of nocturnal waking were rare. Yellow, log plot of light level; red, 1 min intervals with movement; black, number of movements in each 1 min interval; light blue, Actogram-scored rest; and dark blue, Actogram-scored sleep period. Sleep period, defined as the interval between sleep onset and offset, is greater than sleep time, defined as the sleep period minus waking after sleep onset (WASO). Sleep efficiency (sleep time divided by "bed" time) was between 81% and 86%, similar to that in industrial populations. See Table S1).

In these societies, electricity and its associated lighting and entertainment distractions are absent, as are cooling and heating systems. Individuals are exposed, from birth, to sunlight and a continuous seasonal and daily variation in temperature within the thermoneutral range for much of the daylight period, but above thermoneutral temperatures in the afternoon and below thermoneutrality at night. By examining three such groups in two continents over long periods of time, we were able to evaluate common elements and differences that provide insights into the nature of human sleep under natural conditions.

Sleep Duration

Sleep time in the Hadza, San, and Tsimane groups (Figure 1B) was similar, between 5.7 and 7.1 hr, with the sleep period duration (time between sleep onset and offset) of from 6.9 to 8.5 hr (Table S1). Sleep parameters were determined with Actiwatch-2 devices, which have been extensively validated with polysomnography (Figure 1B; see the Supplemental Experimental Procedures). The SD of sleep onset times exceeded the SD of sleep offset times in all San individuals (N = 27, p = 7.4E-5, binomial test) and in all Tsimane individuals (N = 45, p = 2.0E-08), with a similar trend in the more limited dataset from the Hadza. Therefore, sleep duration was much more strongly correlated with sleep onset time than with sleep offset time in both summer and winter. Sleep onset and offset times were very weakly correlated with each other (Table S1).

BMI

Mean body mass indices (BMIs) of the three groups were between 18.3 and 26.2 (Table S2), with none of the participants having BMIs >30, in keeping with prior anthropological observations of a lack of obesity in these populations [11].

Summer versus Winter Durations

The Tsimane and San live far enough south of the equator to have substantial seasonal changes in day length and temperature. Tsimane participants recorded in the winter slept 56 min longer than those in summer (Figure 2A) (t = 2.1, degrees of freedom [df] = 19, p = 0.05). In the San, we recorded the same group of 13 participants in winter and summer. Sleep times in the winter were longer than in the summer by an average of 53 min (Figure 2B and Table S2) (t = 3.7, df = 20, p = 0.001).

Napping

It has long been known that "modern" humans experience an extended dip in midafternoon alertness, which is not due to food intake [14, 15]. It has been speculated that under "natural"

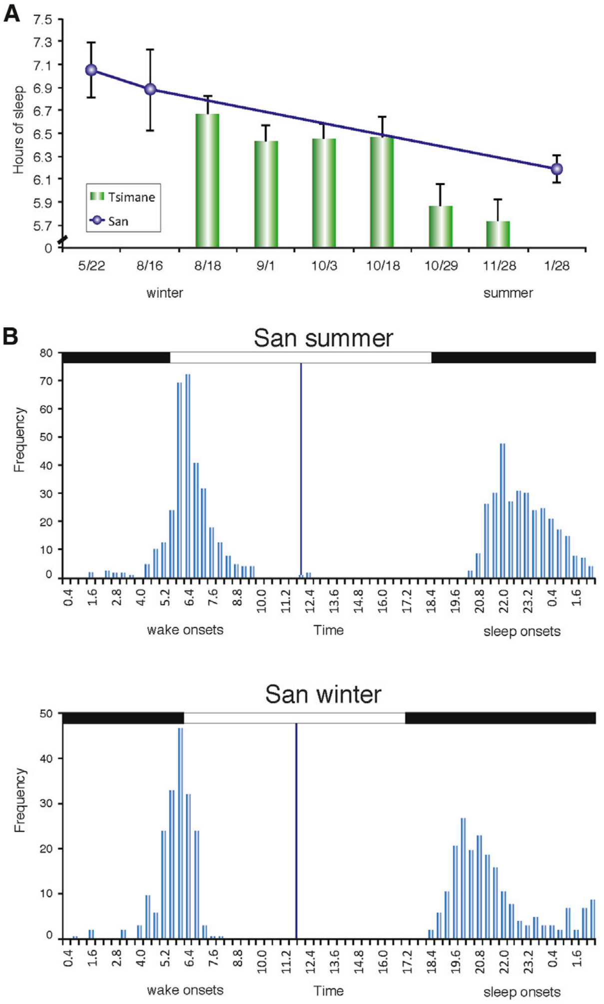

Figure 2. Seasonal Effects on Sleep

(A) Sleep duration decreased from winter to summer. (Note that the Hadza, San, and Tsimane live in the southern hemisphere.) The Tsimane data were from six separate groups recorded over the 4-month period. Each group consisted of seven to 12 individuals recorded for 7 days. A parallel study in the San recorded from ten individuals, each for 21 days in May–June. An additional five San individuals were recorded for 11 days in August, and 13 of the initial 15 were recorded for 28 days in Jan–February of the next year (two of the original ten participants had migrated out of Den/ui).

(B) Change in sleep onset and offset times across the seasons. The same San individuals were sampled for a 28-day period in summer and a 21-day period in winter (a total of 1,260 sleep onsets and offsets). Note the much later sleep onset in the summer and the later wake onset in the summer relative to winter, despite the shorter sleep times. Bin size is 0.4 hr (24 min). The blue vertical line marks solar noon.

conditions, a nap would occur during this period and that this nap has been suppressed by industrial lifestyles. An automated Actogram analysis using the Actogram program (see "Actiwatch-2 devices" in the Supplemental Information) on the data from the San scored no afternoon naps in 210 days of recording in the winter. It scored ten naps on 364 days in the summer (3% of days) (see Table S3). Nocturnal awakenings were also infrequent (see Table S3). The Actograms of the Tsimane and Hadza participants showed a similar dearth of potential napping and nocturnal waking intervals (Figure 1B). Because Actiwatches have not been as thoroughly validated against polygraphic recording for naps as they have for nighttime sleep [4, 16–18], we conducted a second quantification of naps using visual scoring of the Actiwatch records to identify periods with motor activity reduced to levels seen within the nighttime sleep for periods of 15 min or longer. We saw such episodes in only 7% of the recording afternoons in the San winter data. This should be considered the maximum incidence of napping, since we cannot exclude the possibility that some or all of these were waking rest periods. In the summer, 22% of days had potential naps (comparing summer and winter frequencies: t = 3.5, df = 25, p = 0.0007) (Figure 1B). Nap duration using the longer summer visually scored putative nap periods averaged 32 min. Thus, if all potential napping time was considered sleep time, it would raise the average daily sleep duration in summer by 7 min. It remains possible that naps shorter than 15 min occur, but electroencephalogram recording would be necessary to identify them.

Insomnia

Since insomnia is a complaint and does not closely correspond to sleep time [19, 20], we investigated the prevalence of this complaint in the Tsimane and San groups. At the time of application of Actiwatches on the Tsimane, G.Y. and a Tsimane translator visited the participants in their homes early in the morning to conduct an interview on fatigue and sleep quality. A similar interview was done by J.M.S. on the San group. Neither group has a word for insomnia in their language, so we explained the concept in terms of sleep onset insomnia and sleep maintenance insomnia not due to illness. Five percent of the participants said they sometimes had sleep onset problems and 9% sometimes had sleep maintenance problems. Less than one-third of these participants said that they had these problems regularly, i.e., more than once a year (1.5% and 2.5% of the total number of participants). These numbers are far lower than the 10%–30% chronic insomnia rate reported in industrial societies [19, 20].

Light

Average sleep onset across groups occurred between 2.5 and 4.4 hr after sunset (mean = 3.3 hr) (Table S2 and Figure 3). At the latitudes of the participant populations, the duration of evening and morning civil twilight ranges from 24–28 min. Therefore, the participants remained awake long after darkness had fallen. The three groups often had small fires, but the Actiwatch-measured light levels remained below 5.0 lux (the lower limit of the Actiwatch-2 sensor) throughout the night (Figure 3). Awakening occurred on average 1 hr before sunrise in the Tsimane and Hadza, well before civil twilight (Table S2), but awakening was much closer to sunrise than sleep onset was to sunset. Awakening was also well before civil twilight in the winter in the San (Table S2). But in the summer, awakenings in the San participants occurred 1 hr after sunrise, on average (t = 2.4, df = 20, p = 0.02) (Figures 2, 3, and 4). The shorter sleep duration in the summer was completely a result of later sleep onset, not of earlier awakening (mean sleep onset time = 22:44 summer versus 21:16 winter) (t = 5.0, df = 20, p = 6.8E-5]. So, neither sleep onset nor offset were tightly linked to solar light level. A striking feature of the light exposure in all three groups was that it decreased from a maximum level at approximately

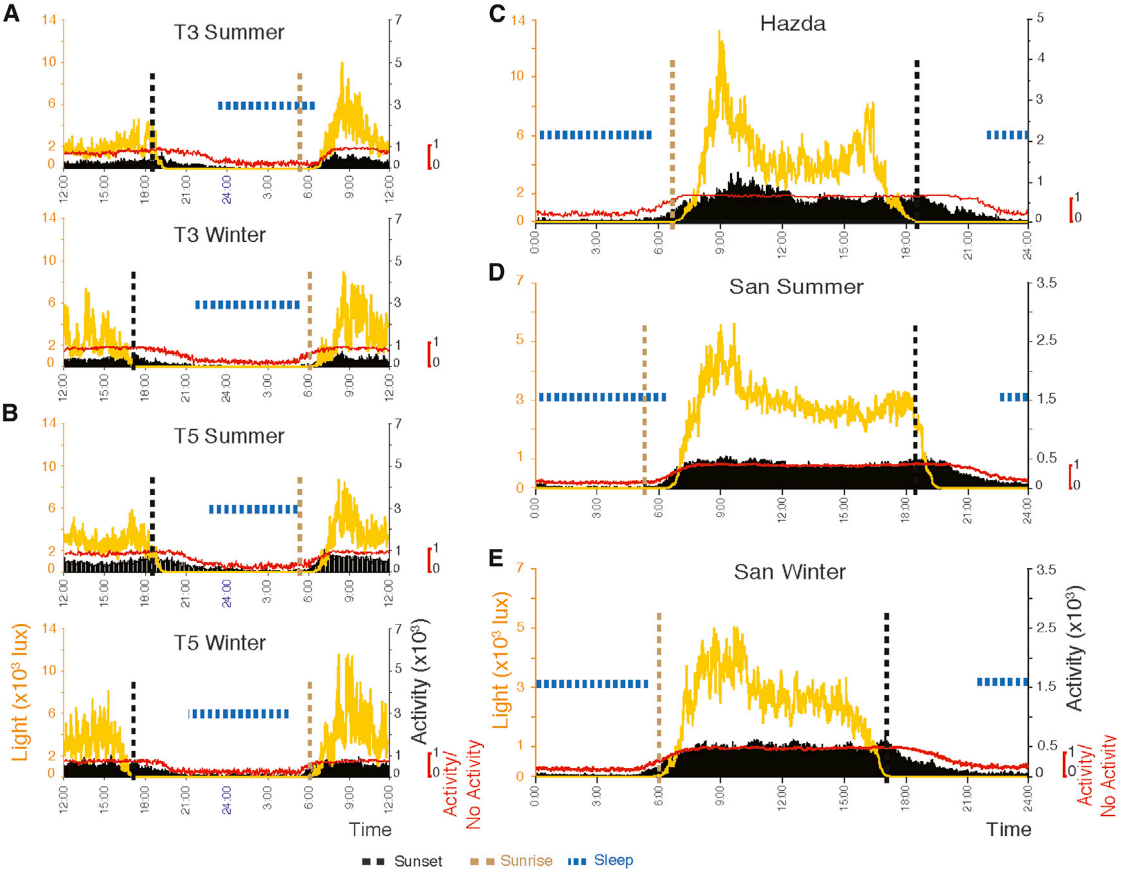

Figure 3. Light and Activity Plots

(A and B) Average light and activity level in plots centered at midnight. Two San participants (T3 and T5) are shown. Both have shorter sleep time in the summer despite later awakening. Participant data are the average sleep parameters over the summer or winter recording periods. The yellow line indicates subject light exposure as measured by the Actiwatch. Sunset, identifiable by the vertical interrupted black line, is not tightly linked to sleep onset. Interrupted blue bars indicate sleep periods. The red line at the bottom of each graph plots average of 1 min epochs with (+1) and without (0) activity. Note the maintained and even increased activity (black) with sunset, location of inactivity linked to sleep at the end of the dark period, awakening before dawn in winter, lack of period of activity within sleep, and differences between the duration of summer and winter nighttime inactivity period. The durations of these inactivity epochs are used in the algorithm that identifies sleep (Figure 1). Sleep onset occurs from 2.5 to 4.4 hr after sunset in all of the groups examined (mean = 3.3 hr).

(C) Staying out of the midday sun. Plots are centered at noon. Light levels recorded by the Actiwatch drop steeply and consistently at midday, despite the increase of the ambient light level from morning (9 a.m.) to noon levels. The figure shows the average of 60 days of data from the ten Hadza recorded in Tanzania. It shows the reduction in light exposure during the afternoon; a lack of reduction in afternoon activity to sleep levels, consistent with the lack of regular napping; and the reduction in activity throughout the sleep period. No regular period of activity was seen in the night, consistent with the lack of a "second sleep" scored by the algorithm (see also Figure S1).

(D and E) Averaged data across all San recorded in summer and winter. Note the consistent pattern across groups and seasons. Time is local clock time.

9 a.m. to a lower level at noon, despite the doubling of ambient light levels over this period. This occurred in winter as well as in summer, indicating that all three groups sought shade from the midday sun (Figure 3).

Temperature

Because we noticed that the Hadza, Tsimane, and San did not initiate sleep at sunset and that their sleep was confined to the latter portion of the dark period, we investigated the role of temperature. We found that the nocturnal sleep period in the Hadza was always initiated during a period of falling ambient temperature (Figure S1), and we saw a similar pattern in the Tsimane. Therefore, we precisely measured ambient temperature at the sleeping sites along with finger temperature and abdominal temperature in our studies of the San [21]. Figures 4 and S1 show that sleep in both the winter and summer occurred during the period of decreasing ambient temperature and that wake onset occurred near the nadir of the daily temperature rhythm. A strong vasoconstriction occurred at wake onset in both summer and winter (Figures 4 and S2), presumably functioning to aid thermogenesis in raising the brain and core temperature for waking activity. See the Supplemental Experimental Procedures for a discussion of the use of iButtons to measure vasoconstriction and vasodilation. The presence of vasoconstriction at awakening indicates that the subjects were not vasoconstricted prior to awakening.

Among Tsimane, summer wake times were earlier and sleep onset times were later than in the winter, accounting for their reduced sleep duration; however, in the San, despite their shorter sleep duration in the summer, as in the Tsimane, the

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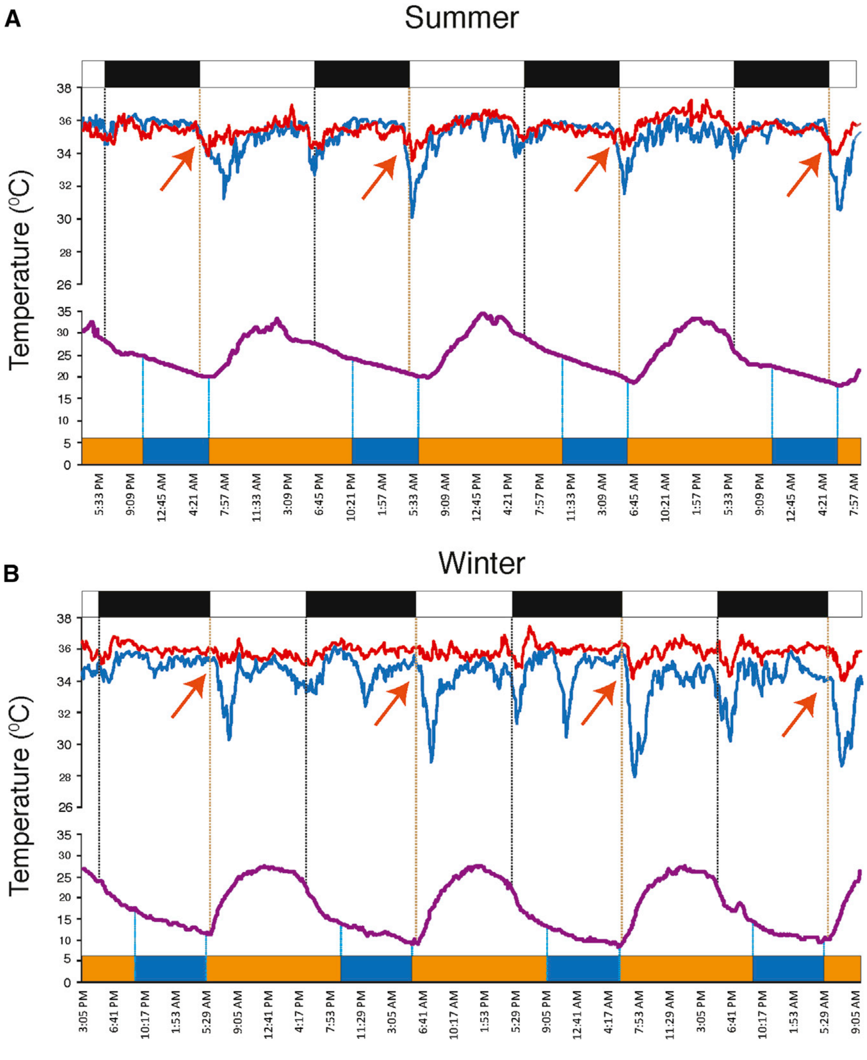

Figure 4. Relation of Sleep to Ambient Temperature and Skin Temperature

Sleep offset, averaged across all subjects and all days, consistently occurs near the nadir of daily environmental temperature, in both summer (A) and winter (B). For the San recorded in the summer, the temperature nadir occurred after sunrise, as did awakening. In the winter, the nadir occurred near sunrise with awakening preceding sunrise. Note that the ambient temperature has a gradual fall at night and a rapid rise starting at sunrise, with sleep occurring during the period of slowly falling temperature. Vasoconstriction is seen upon awakening in both summer and winter. In the winter, there are additional vasoconstrictions occurring during the day. These are most likely related to food preparation or other similar activities exposing the hands to cold. Violet lines, environmental temperature; red lines, abdominal temperature; and blue lines, finger temperature. See also Figure S2 for an example of individual subject data. All temperatures recorded by iButtons are synchronized to the Actiwatch time ±2 min. Black bars, night; orange bars, waking; and blue bars, sleep. Vertical lines at top of the figures indicate light-dark transitions; those at bottom indicate sleep-wake transitions. Sleep measures are the averages of the 15 participants recorded in the summer and the 13 of these participants recorded in winter (see Figure 1 and Table S1). Red arrows indicate onset of drop in finger temperature starting near the temperature nadir, indicative of peripheral vasoconstriction, serving to warm proximal regions with awakening. See also Figure S1.

time of awakening was significantly later, with the decreased sleep times being entirely the result of later sleep onset. The San the participants awakened, on average, 1.0 hr *after* sunrise in the summer. The Tsimane awakened 1.4 hr *before* sunrise in the summer (Table S2). The 2.4 hr difference in awakening times, with respect to sunrise, was significant (t = 8.4, df = 22, p = 1.2E-08). This was not due to differences in day/night length at the two recording locations. The summer observation period in the San had 11 hr nights and 13 hr days. The summer observation period in the Tsimane had 11.1 hr nights and 12.9 hr days. The difference between the sleep offset times in these two populations, despite the similar light conditions, may be due to the much cooler morning temperatures (by 6°C on average) and the shifting of the temperature nadir into the light period (Figure 4) in the San's environment, paralleling the effect of winter on changes in sleep duration.

DISCUSSION

A striking finding is the uniformity of sleep patterns across groups despite their ancient geographic isolation from each other. This suggests that the observed patterns are not unique to their particular environmental or cultural conditions but rather are central to the physiology of humans living in the tropical latitudes near the locations of the San and Hadza groups, where our species evolved.

In some ways, the sleep in these traditional human groups is more similar to sleep in industrial societies than has been assumed. They do not sleep more than most individuals in industrial societies [1, 4–7, 22]. The traditional groups do not regularly awaken for extended periods in the middle of the night (see the Supplemental Experimental Procedures), despite anecdotal reports [23]. Sleep is strongly modulated by the seasons, averaging 53–56 min longer in the winter, coincident with a 1.2 or 2 hr increase in the night duration in the San and Tsimane, respectively (Table S2 and Figure 2). In contrast, no seasonal effect on sleep durations has been reported in most studies in industrial societies. Kleitman [24] summarizes some of the early, conflicting data on seasonal changes in sleep (p. 192). A recent large-scale study of seasonal sleep changes reported an 18 min difference between summer and winter. This study investigated participants in Berlin (latitude +53°), where night duration changes from 7 hr 39 min in summer to 16 hr 21 min in winter) [25]. Of course, the Berlin participants were not as directly exposed to changes in light and temperature as were our participants.

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Light has been shown to be a major factor in human sleep and circadian rhythm control, partially mediated by light's effects on the melanopsin system [19, 26–28]. Consistent with this, we show here that sleep occurs almost entirely during the dark period in these traditional societies. In contrast, sleep typically continues well after sunrise in industrial populations [27]. A recent study has shown a striking difference in the sleep onset and offset times as a function of light exposure in a comparison of two closely related traditional Argentinian hunter-gatherer populations [26]. Three other studies showed the rapid regularization of human sleep patterns created by moving "modern" subjects into more natural lighting situations [28–30].

Our finding that hunter-gatherers get maximal light exposure in the morning, rather than at noon, is consistent with behavioral thermoregulation to avoid afternoon heat. It also may explain the greater effectiveness of morning light [31, 32] in the reversal of depression, since such treatments tend to restore the evolved pattern of human exposure to light.

Of the ten groups we studied, the only group in our study that awakened after sunrise was the San in the summer. The Tsimane always arose before dawn. At the end of November to the beginning of December (2 weeks from the summer solstice), they awakened more than 1 hr 20 min before sunrise, whereas the San, at approximately the same season with nearly indistinguishable seasonal light levels (13 versus 12.9 hr of light), awakened nearly 1 hr after sunrise. Our data suggest that ambient temperature might be responsible for the difference between these groups and might be a major determinant of sleep timing and duration, independent of light level.

Historical evidence suggests that "until the close of the early modern era, Western Europeans experienced two major intervals of sleep bridged by up to an hour or more of quiet wakefulness" [33] (see also [30]). Our results suggest that the bimodal sleep pattern that may have existed in Western Europe is not present in traditional equatorial groups today and, by extension, was probably not present before humans migrated into Western Europe. Rather, this pattern may have been a consequence of longer winter nights in higher latitudes. In this view, the "recent" disappearance of bimodal sleep was not a pathological development caused by restricted sleep duration, but rather a return to a pattern still seen today in the groups we studied, enabled by the electric lights and temperature control that restored aspects of natural conditions in the tropical latitudes.

We found that nocturnal sleep in all groups occurred toward the end of the night, during the period of lowest ambient temperatures. In nature, the daily rhythm of environmental temperature is tightly locked to the rhythm of sunset and sunrise. However, in most industrial societies, the seasonal and circadian temperature rhythms are greatly attenuated by insulated buildings and artificial heating and cooling. The synchronization that we observed between the reduction in ambient temperature at night and sleep under traditional conditions, with its associated decline in core temperature [34], may have evolved to save energy by reducing the temperature differential between body and environment and consequent heat loss. Being active during the late night period of lowest temperatures would be metabolically costly. Individuals in groups like those we observed may be less vulnerable to insomnia because they are exposed to a falling ambient temperature at the time of sleep onset and do not have to actively shed heat to achieve the body temperature reduction that accompanies sleep onset [35–37]. The daily reduction in light is followed by the daily reduction in temperature. The delayed melatonin response to darkness is adaptive in facilitating sleep after darkness [27], bringing the entire sleep period in synchrony with the lowest nighttime temperatures.

Our findings indicate that sleep in industrial societies has not been reduced below a level that is normal for most of our species' evolutionary history. Recreating aspects of the environments that we observed in preindustrial societies might have beneficial effects on sleep and insomnia in industrial populations.

EXPERIMENTAL PROCEDURES

Methods Summary

Institutional review board (IRB) approval for the San studies was obtained through the IRB of Witwatersrand University in Johannesburg, for the Hadza through Yale University, and for the Tsimane through the University of New Mexico. Informed consent in the San was made with the supervision of the Nyae Nyae Development Foundation of Namibia. Sleep was quantified with Actiwatch-2 devices worn for 6–28 days. Sleep states were scored by the Actogram program. We extracted the light and acceleration data and statistically compared these data with temperature, solar, and seasonal variables. The San participants wore iButton temperature recorders on the middle fingers of both hands and on the abdomen for 4 days at the start of recording periods in the summer and winter periods. iButton devices were also placed near the participants' sleeping sites to accurately measure environmental temperature and humidity at 4 min intervals. (See the Supplemental Experimental Procedures for details.)

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, and four tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.09.046.

AUTHOR CONTRIBUTIONS

G.Y., J.M.S., P.M., M.G., and H.K. conceived the study; G.Y. collected the data in Bolivia; B.W. and H.P. collected the data in Tanzania; J.M.S. and P.M. collected the data in Namibia; G.Y., C.W., R.M., and J.M.S. analyzed the data; and all authors assisted in writing the manuscript.

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Current Biology

Supplemental Information

Natural Sleep and Its Seasonal Variations in Three Pre-industrial Societies

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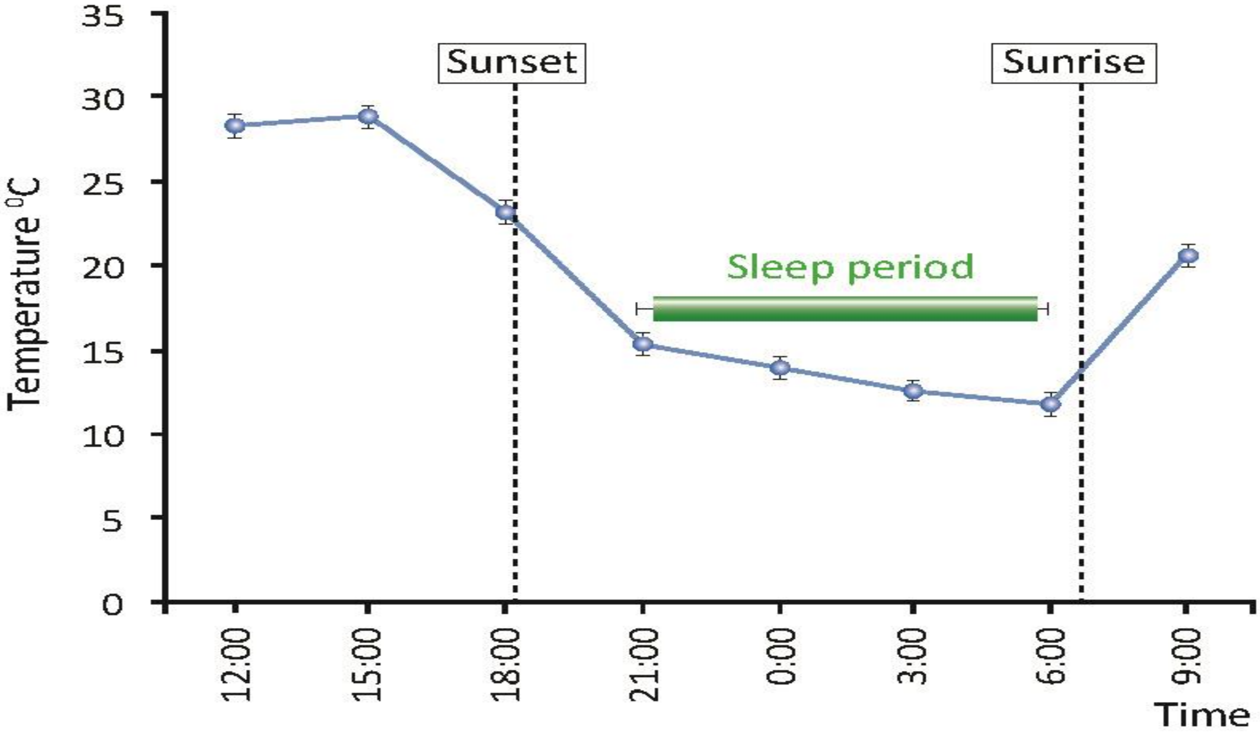

Fig. S1. Data from Hadza in Tanzania. Sleep onset and offset occur in the dark. Sleep periods averaged over 60 nights, 10 participants (onset and offset SEMs are indicated). Average sleep onset is 3.4-h after sunset and offset is 1-h before sunrise. Temperature measurements are from Serengeti station near the Hadza encampment. The Hadza, at latitude -4 are the closest to the equator of the three groups examined, the San are the furthest (latitude -20) and the Tsimané fall in between (at latitude -15). In the Hadza, we can see the same temperatures excursion across the 24-h period and the same general relation of sleep and awakening with respect to this temperature cycle as in the other two groups. Supplement to figure 4.

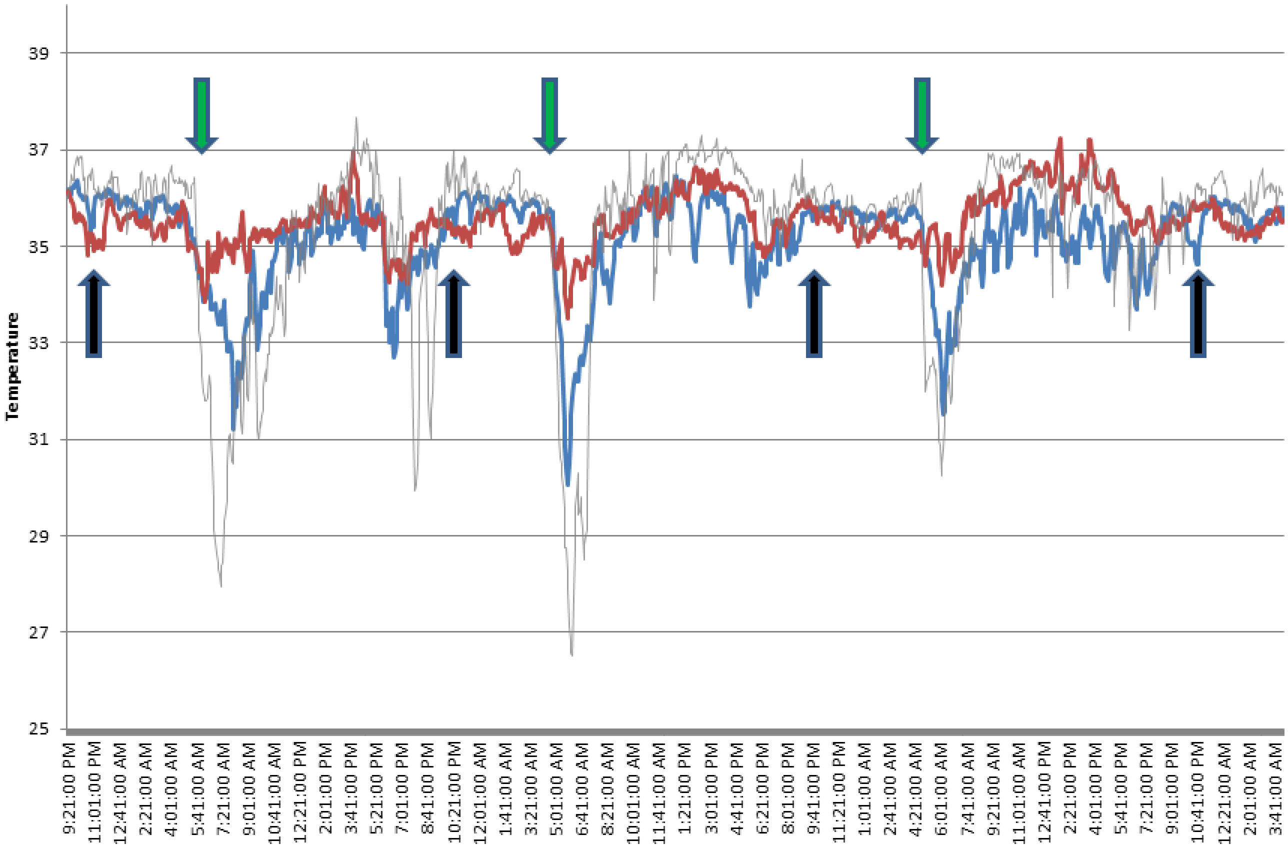

Fig. S2. Abdominal and finger temperatures from Fig 4 on an expanded scale. Sleep offset times are indicated with green arrows and onset times are indicated with black arrows. Red and blue traces illustrate group averages of abdominal and finger temperatures. The light gray trace shows representative finger temperature from an single participant. This is useful in illustrating that vasoconstriction is seen in individual, daily data. The data also shows that no vasodilation is seen in the individual raw data or in the averaged data, i.e. it has not been obscured in the averaged data by asynchronous occurrence of sleep onsets relative to sleep offset times. Smaller vasoconstrictions, not time-linked to wake onset, may be related to food preparation. Supplement to figure 4.

Table S1. Sleep duration in decimal hours (h), standard deviation (SD) of sleep duration in each subject, correlation between sleep duration and sleep onset and offset values A table is provided for each of the three groups examined that contained at least 6 days of recording. Seven subjects recorded for 4-5 days were used for mean values but not for correlation studies because samples with fewer than 6 pairs of value are not suitable for correlation studies. Sleep onset values are strongly correlated with sleep duration, such that earlier sleep onset is linked to longer sleep duration. However, sleep offset values are relatively weakly correlated with sleep duration. The San (and the other groups-see Fig. 1) do not often “sleep in” in the morning to compensate for delayed sleep onset. Significant relations are highlighted with yellow. Statistical analysis shows that the correlations between sleep onset time and sleep duration are significantly and substantially larger than those between sleep offset and sleep duration. Sleep onset and offset times are not strongly correlated. The binomial test shows that there is a significant difference in the number of significant correlations between sleep onset and sleep duration and sleep offset and duration in all 3 groups [Hadza p=0.01, Tsimane p=3.3E-10, San p=0.0006]. Values listed as 0.0000 have p values less than 0.0001 or r values of more than 0.99. See main manuscript sleep duration. [**see spreadsheet for data]**

Table S2. Information about participant groups

Night duration is from sunset to sunrise, clock time and times relative to solar noon are given, high and low temperatures are in °C. WASO (wake after sleep onset) amounts were comparable to those recorded in “modern” populations with the same devices (see refs. in main text), BMI=Body Mass index, Total days is the number of participant-24-h days recorded (recording duration x participants). Each group had equal number of females and males, except for groups with an odd number of participants. The Hadza were recorded from May 13-20, 2013. Overall there were 47 female and 47 male participants. ± indicates standard deviation between individual averages across recording period in each group. All groups are south of the equator, so northern seasonal timing is reversed. The Hadza are in the equatorial zone, so summer-winter designations do not apply. We label winter (W), spring (SP), summer (S). and fall (F) according to standard southern hemisphere designations. The Tsimane groups used different subjects at each time point. The San recordings used 8 of the same subjects in both the 5/14 and 1/15 recordings. Two the 10 subjects recorded during the 5/14 run had migrated out of Denui and could not be located for the summer recording. To keep the statistical treatments uniform and conservative, we used unmatched t tests in both the Tsimane and San groups in the body of the paper. See main manuscript: sleep duration, summer vs winter, BMI, light and temperature headings

GROUP/ MIDPOINT OF RECORDING	LATITUDE degrees	LONGITUDE degrees	NIGHT DURATION h	SLEEP TIME h	WASO (wake after sleep onset)	SLEEP EFFICIENCY =sleep time/time in “bed”	ENVIRONMENTAL TEMPERATURE RANGE	AGE	BMI	PARTICIPANTS	TOTAL DAYS
HADZA	-3.7315	35.1946	12.1	6.3±0.63	81±25	82±5.8	12-29	36.6±11.8	21.4±2.5	10	60
TSIMANE											
8/18/13-W	-14.875	-66.7282	12.4	6.6±0.93	82±17	83±6.0	14-29	38.0±10.7	26.1±3.9	9	63
9/1/13-W-SP	-14.875	-66.7282	12.2	6.4±1.03	92±16	81±4.6	15-33	35.2±14.3	22.8±3.3	9	63
10/3/13-SP	-14.875	-66.7282	11.7	6.4±1.12	72±13	85±5.54	18-28	32.2±10.7	26.2±3.5	10	70
10/18/13-SP	-14.875	-66.7282	11.5	6.5±0.32	64±17	86±4.2	22-31	44.4±23.7	25.4±4.8	7	70
10/29/13-SP	-14.875P	-66.7282	11.4	5.9±1.39	82±17	81±7.5	22-30	34.2±11.3	24.9±4.1	7	70
11/29/13-S	-14.875	-66.7282	11.1	5.7±1.15	86±8	82±5.5	23-34	37.0±15.1	24.2±3.3	12	84
SAN											
5/14-F-W	-19.803	20.6872	12.9	7.1±0.52	77±15	85±3.9	10-26	45.3±11.1	18.6±1.4	10	210
8/14-W	-19.803	20.6872	12.6	6.9±0.97	95±22	81±5.4	15-29	23.4±3.5	19.3±2.9	5	55
1/15-S	-19.803	20.6872	11.0	6.2±0.60	72±10	84±3.7	20-33	38.5±14.0	18.3±2.2	15	420
			AVERAGES→	6.4	80.3	83		36.5	TOTALS→	94	1165

Table S2: Information about participant groups (continued)

GROUP START DATE	SUNSET	ONSET CLOCK	OFFSET CLOCK	SUNRISE	SOLAR NOON	ONSET -SOLAR	ONSET - SUNSET	CENTER OF WAKE PERIOD	SOLAR NOON-OFFSET	SUNRISE - OFFSET	CENTER OF WAKE-SOLAR NOON
HADZA	18.57	21.98±0.6	5.68±0.41	6.63	12.60	9.38	3.41	16.30	6.92	0.95	3.70
TSIMANE											
8/18/13-W	18.33	21.36±0.76	5.55±0.48	6.68	12.52	8.84	3.03	15.81	6.97	1.13	3.29
9/1/13=W	18.37	21.03±0.85	5.01±0.42	6.53	12.45	8.58	2.66	16.02	7.44	1.52	3.57
10/3/13	18.40	22.13±1.8	5.68±0.46	6.13	12.27	9.86	3.73	16.45	6.59	0.45	4.18
10/18/13	18.43	21.60±1.8	5.14±0.55	5.97	12.20	9.40	3.17	16.46	7.06	0.83	4.26
10/29/13	18.48	21.16±0.4	4.93±0.85	5.87	12.17	8.99	2.68	16.23	7.24	0.94	4.06
11/29/13-S	18.72	21.26±0.97	4.39±0.72	5.78	12.25	9.01	2.54	16.87	7.86	1.39	4.62
SAN											
5/14 LF-W	18.12	21.27±0.41	5.61±0.41	6.02	11.57	9.70	4.15	15.66	5.96	0.41	4.09
8/11-W	17.42	21.38±0.61	5.85±0.51	5.97	11.70	9.68	3.96	15.52	5.85	0.11	3.82
1/15-S	18.35	22.74±0.56	6.22±0.73	5.21	11.83	10.91	4.39	16.52	5.61	-0.90	4.69

Table S3. Napping and nighttime awakening scored by Actogram program. See main manuscript: napping.

		NAPS		NIGHTIME AWAKENING	
SUBJECT	DAYS/ SUBJECT	#	duration h	#	duration h
			WINTER		
TS 11 DEN	21	0	0	0	0
TS 12 DEN	21	0	0	2	1.5, 2
TS 13 DEN	21	0	0	0	0
TS 14 DEN	21	0	0	0	0
TS 15 DEN	21	0	0	0	0
TS 16 DEN	21	0	0	1	1.3
TS 17 DEN	21	0	0	3	1.5, 2.5, 1.5
TS 18 DEN	21	0	0	3	1.5, 3.5, 4.5
TS 19 DEN	21	0	0	1	2
TS 20 DEN	21	0	0	0	0
			SUMMER		
DEC 13A	28	4	4, 3.5, 3.0, 3.0	1	2.5
DEC 14A	28	0	0	0	0
DEC 15A	28	0	0	0	0
DEC 16A	28	0	0	0	0
DEC 17A	28	0	0	1	0.5
DEC 18A	28	2	2.0, 2.5	3	2.5, 1.0, 5.0
DEC 19A	28	0	0	0	0
DEC 20A	28	0	0	0	0
DEC 11B	28	0	0	0	0
DEC 12B	28	0	0	0	0
DEC 13B	28	1	3	0	0
DEC 14B	28	0	0	0	0
DEC 15B	28	3	4, 3.5, 2.5	0	0

Table S4. Higher standard deviation of sleep onset times than sleep offset (wake) times in 3 representative subjects. AVG=Average, SD=Standard Deviation. See main manuscript: sleep duration.

Subject #→	San Dec 19A	
SLEEP ONSET	DATE (+ next AM)	wake onset
24.93	Thursday 1/15/2015	5.63
22.32	Friday 1/16/2015	5.80
24.08	Saturday 1/17/2015	5.80
23.77	Sunday 1/18/2015	5.05
24.13	Monday 1/19/2015	5.97
20.98	Tuesday 1/20/2015	5.70
20.87	Wednesday 1/21/2015	5.27
20.93	Thursday 1/22/2015	6.55
25.58	Friday 1/23/2015	6.07
21.93	Saturday 1/24/2015	5.87
21.72	Sunday 1/25/2015	6.40
22.20	Monday 1/26/2015	4.83
21.67	Tuesday 1/27/2015	5.48
22.95	Wednesday 1/28/2015	5.48
23.50	Thursday 1/29/2015	6.82
22.32	Friday 1/30/2015	7.40
24.23	Saturday 1/31/2015	6.43
22.48	Sunday 2/1/2015	6.65
22.48	Monday 2/2/2015	6.60
12.30	Tuesday 2/3/2015	6.33
25.32	Wednesday 2/4/2015	5.80
21.95	Thursday 2/5/2015	6.55
24.67	Friday 2/6/2015	7.35
24.93	Saturday 2/7/2015	7.03
25.52	Sunday 2/8/2015	6.87
21.20	Monday 2/9/2015	7.78
23.12	Tuesday 2/10/2015	6.82
24.23	Wednesday 2/11/2015	5.70
22.73	AVG	**6.22**
2.52	SD	0.73

San Dec 20A		
SLEEP ONSET		wake onset
23.42		5.73
22.07		6.40
23.88		6.47
23.22		5.73
24.50		5.98
21.32		5.98
24.87		6.63
20.67		5.82
25.90		6.02
21.98		6.77
21.53		6.68
21.53		5.37
24.25		5.85
21.45		7.18
22.32		7.47
21.37		7.88
20.42		7.38
23.47		6.35
23.33		6.63
27.22		7.30
24.98		5.73
21.98		6.77
25.45		6.93
24.03		5.90
23.38		6.88
21.12		7.72
21.73		7.63
22.27		6.40
22.95	AVG	**6.55**
1.70	SD	0.68

San Dec 12B		
SLEEP ONSET		wake onset
20.88		6.75
23.05		6.42
23.98		5.97
21.87		6.38
24.38		5.28
22.80		5.85
24.72		6.38
21.00		6.67
22.92		7.12
21.05		2.47
22.97		6.87
22.55		5.93
20.88		6.22
21.33		6.13
20.88		6.05
21.65		7.23
21.40		7.77
21.50		6.30
22.60		6.67
23.37		6.22
22.38		6.87
21.22		6.75
23.17		6.05
25.37		6.22
23.93		6.37
21.37		6.17
22.43		6.67
21.13		6.87
22.45	AVG	**6.30**
1.30	SD	0.88

Supplementary Experimental Procedures

Sleep was quantified with Actiwatch-2 devices worn for 4-28 days. Sleep states were scored by the Actogram program. We extracted the light and acceleration data and statistically compared these data with temperature, solar and seasonal variables. The San participants wore iButton temperature recorders on the middle fingers of both hands and on the abdomen for 4 days at the start of recording periods in both the summer and winter periods. iButton devices were also placed near the participants' sleeping sites to accurately measure environmental temperature and humidity at 4 min intervals.

Supplementary methods and discussion

Participants: The populations studied did not have electricity, generators or battery powered devices. All participants were interviewed with the assistance of indigenous translators. Those who were ill were excluded. Villages in which caffeine or alcohol use occurred were excluded and this was always confirmed in the individual participant interviews. Beyond this requirement, participants between 20 and 55, with equal numbers of males and females in each group, were randomly selected. Age and height were recorded using a portable stadiometer and BMI calculated. We do not see significant correlations between BMI and any other the other sleep variables. This may be because the BMI ranges were rather narrow, as were the range of sleep durations. But it is worth noting that even though a large portion of the sleep durations were at a level associated with obesity in the US populations [S1], none of the subjects were obese.

Each participant provided verbal consent to the research. The participants were informed of the goals of the study and were paid $30 USD in gifts for their participation in the month long San studies. In case of Tsimane, they were given gifts for participation, with a value of 70 Bolivianos or about 10 US Dollars. The Hadza participants were provided gifts for their participation, with a value of 15,000 Tanzanian Shillings, or 10 US Dollars.

Each population eats locally acquired foods. The San eat meat from local game, baobab fruit, fish and berries. The Hadza eat game meat, baobab fruit, honey, tubers, and berries. The Tsimane eat a mix of hunted game, fish, and cultivated plant foods, primarily rice, manioc and plantains.

Sleep conditions: The Hadza sleep on animal skins on the ground, with Maasai style 'shuka' blankets. They sleep upon flat, circular sleeping spaces that are 2-2.5 meters in diameter. To make such a sleeping space, they clear the ground of thorns and rocks, and then place down either a kudu skin or an impala skin (both of which are prized for their soft hair), upon which they sleep. The Hadza data were collected during the wet season, and during such times, sleeping spaces are inside huts. The simple domed huts, open to the outside, are framed with tree branches and thatched with grass. In the dry season, sleeping spaces are often open air. After sunset, a fire is usually set just at the entryway to a hut, or next to an open air sleeping area. Families sleep close together, 2-6 people often sharing a single sleeping space. They sleep either naked or with very little clothing. They cover themselves with light blankets, often made of cotton or cotton-nylon blends. San participants slept on a blanket on the ground, covered by an additional blanket, without pillows in the winter and without a blanket or much clothing in the summer. They sometime slept in grass huts with 1 meter wide openings, always completely exposed to the environment, and at other times outside the huts. The environmental iButtons were placed above ground at their sleeping sites. The Tsimane participants slept on beds above-ground made of tree-bark slats inside thatch-roofed houses with walls made of bamboo, other tree boles, or occasionally wood tablets. Most Tsimane beds have thin blankets.

Elevations:
Hadza, 1030 meters (Lake Eyasi, Tanzania)
San, 1150 meters (Tsumkwe, Namibia)
Tsimane; 197 meters (San Borja, Bolivia)

Actiwatch-2 devices: (Philips Respironics, Bend Oregon), were placed on the wrist of participants studied, in most cases remaining for at least 6 days to a maximum of 28 days (Table S2). Each record was visually inspected to identify and exclude instances of artifact. All collected data were scored by the "Actogram" program (Phillips Respironics) using the default 1-min setting that has been used in many prior studies. The sleep period analyzed was automatically selected by the software and not modified or selected by the investigators in >97% of cases. But all days of data were visually scanned for any discrepancies in the data selection of the major sleep period and corrected by defining the major sleep interval.

A Medline search for "(actigraphy or actiwatch or actigraph) and sleep" brings up 2,132 papers. Many papers have compared actigraphy to polysomnography as an indicator of sleep [S2, S5-S13]. It should be borne in mind that whereas polysomnography (PSG) is often considered the "gold standard" for identifying sleep it has long been known that when participants are in PSG defined sleep and are "awakened" they will frequently say they are not asleep [S14] This cognitive mismatch can occur in all sleep stages.

Conversely, when an actiwatch is used, and continuous movement is identified in a neurologically normal individual, it is highly likely that the participant perceives that they are awake. The main source of error in actigraphy is in somewhat overestimating sleep time. When no movement is occurring the participant need not be asleep, just immobile.

A recent comparison of the Actiwatch with simultaneous polysomnography concluded that the Actiwatch and its companion Actogram software, as used in the current study, had "a 97% sensitivity for sleep, a 96% specificity for wakefulness and an overall accuracy of 96%." It further found that overall, "Actiwatch sleep time overestimated PSG sleep time by 26.4-min per sleep period (95% CI 18.0-34.8 min; P < 0.0001)"[S11], consistent with some periods of inactive waking being scored as sleep. Marino et al. [S2] reported "Overall, sensitivity (0.965) and accuracy (0.863) were high. They “conclude that actigraphy is overall a useful and valid means for estimating total sleep time and wakefulness after sleep onset in field and workplace studies.”

In our study of the Hadza and in all our studies of the Tsimané, conventional Actiwatch wrist bands were used. Such bands can easily be removed, although we instructed the participants not to do this. In the Tsimane participants we found a few periods of inactivity that contained an abrupt onset and zero or invariant light levels, as might be obtained when the Actiwatch was off the wrist. Therefore, in our studies of the San, which were done after the Hadza and Tsimane, we attached the Actiwatches with hospital bands (Wristband LLC, Atlanta) recommended by Respironics. They cannot be removed except by cutting the band. Repaired bands are obvious. In the few cases when bands were found to be cut, we discarded the data. The results in the San were qualitatively and quantitatively similar to those in the Hadza and Tsimane, in terms of nighttime sleep duration, sleep onset-offset and wake after sleep onset (WASO); however, somewhat fewer periods of abrupt interruptions of daytime activity were seen in the San Actiwatch data, consistent with our goal of preventing removal, so we focused our nap evaluations on the San. The number of days in each long duration recording was determined by travel and logistical constraints. All collected data are presented, with the exception described above.

Although nighttime actogram scoring has been extensively validated against polygraphic scoring, there have not been many validations studies for Actogram scored napping. A recent study concluded that Actogram scored haps were accurate, but that “Discrimination of sleep and wake during periods of waking quiescence is not as robust as during periods of mainly daytime sleep” [S3]. In our initial analysis, naps were automatically scored with a second automated analysis of the Actograms. This second analysis was done after the initial analysis of sleep parameters using the default Actogram settings that have been extensively validated using polygraphic recording. To do this second analysis, we used the Tools/Options/auto intervals/Automatically set major Rest intervals/uncheck detect only one rest interval per day/minimum minor rest interval size 15 min (the most sensitive setting for nap detection)/medium. This feature also served to identify periods of nighttime waking interrupting sleep. We find very low rates of napping (Table S3). In a second analysis, naps were scored visually by looking for periods of >15 min with activity rates at or below that in actigraphically detected sleep in the same subject. This produced somewhat higher rates of napping (see results), but this analysis also indicated very low levels of napping.

The Actogram analysis indicates that nighttime awakenings occurred on 10 of 210 recording days during the winter and 5 of the 364 days of recording during the summer.

In summary, most subjects sored visually (see Results) or by the Actogram program (see below) did not regularly nap during the winter or summer periods, although more napping occurred in the summer in the minority of subjects that showed any naps. The few subjects that did nap, did not do so regularly. Most subjects did not awaken during the nightly sleep period, with nighttime awakenings occurring on 10 of 210 recording days in summer and 5 of the 364 days of recording during the summer (Table S3). Future studies should do polygraphic recording combined with perceptual tests to more accurately identify nap intervals. However, since active, continuous movement is incompatible with napping, the current work sets an upper limit on how frequently such episodes occur. Overall we find that naps and nighttime awakenings are uncommon occurrences in all three groups.

References for actiwatch validation studies against polygraphic recording: see S2, S5-S13

iButtons: In addition to the Actiwatch, each participant in Namibia had iButton temperature recording devices taped to both middle fingers and a third such device taped to the abdomen. A description of iButtons can be found at: http://www.maximintegrated.com/. The use and interpretation of iButton data as an indication of vasoconstriction and vasodilation is reviewed in [S4]. We used Ds1821H iButton for skin temperature monitoring. We used Ds1922 for monitoring environmental temperature, with a resolution of 0.0625° C. Both types of iButtons are stainless steel disks 15 mm wide and 6 mm thick. They were attached with Fixomull medical tape to the middle finger of both hands, and to the midline of the abdomen, 2 cm above the umbilicus(*28*). The two iButtons placed on the middle finger were averaged for the analyses presented here. Ds1922 iButtons were placed off the ground and out of direct sunlight, adjacent to the customary sleeping sites, to measure ambient temperature. The temperature at these sites typically closely tracked the ambient temperature reported by the nearby Tsumkwe weather station, but with much higher temporal resolution. The iButtons were set at a 4-min sample interval and were removed after 4 days. Skin temperature data were analyzed according to clock hour and not sleep period, and thus any skin temperature associations with sleep was not directly determined by our analytic method. We present both average time of awakening in fig 2 and 4 and average vasoconstriction data in fig 4 and we present individual vasoconstriction data in figure S2. The iButton data was also used to exclude any data from a subject with a fever. Only one such participant was seen.

Calculation of solar variables: Precise latitude and longitude coordinates were determined with a Garmin Montana 650 device with microSD™/SD™ card TOPO Southern Africa 2013 Pro 010-11982-00, for the San recording site, and Google maps for the Hadza and Tsimané sites. Coordinates were used with the National Oceanic & Atmospheric Administration Solar Calculator at: http://www.esrl.noaa.gov/gmd/grad/solcalc/ to determine the times of sunrise, sunset and solar noon.

Statistics: All p values are indicated for two tailed probabilities.

Morning light: The marked dip in light exposure at midday may have implications for the control of circadian rhythms. Our results indicate that in both summer and winter in the San and Tsimane, as well as in the Hadza, who do not experience a large seasonal variation in light exposure, the light that participants are exposed to is at its peak in the morning and diminishes to approximately half this value at noon, despite the much greater intensity of sunlight at noon. In retrospect this makes sense from a thermoregulatory standpoint, preventing overheating at midday. Our findings suggest that the beneficial effect of morning light may be at least partly a result of the evolved adaptation of the melanopsin-suprachiasmatic system to morning light because this is the time our ancestors would receive their strongest light stimulus.

Sex differences: We tested for difference in sleep duration between males and females in the Tsimane, the group with the largest N (20 males, 26 females) of any of our groups. We did not see significant differences in sleep duration between males and female sleep durations (average sleep time in males, 6.20 ±1.06h, females 6.54±1.30h), p=0.311 2 tailed t test.

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