Current Biology

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

Authors

Gandhi Yetish, Hillard Kaplan, Michael Gurven, ..., Charles Wilson, Ronald McGregor, Jerome M. Siegel

Correspondence

jsiegel@ucla.edu

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

Gandhi Yetish,¹ Hillard Kaplan,¹ Michael Gurven,² Brian Wood,³ Herman Pontzer,⁴ Paul R. Manger,⁵ Charles Wilson,⁶ Ronald McGregor,⁷ and Jerome M. Siegel^{7,8,9,*}

¹Department of Anthropology, University of New Mexico, MSC01-1040, Albuquerque, NM 87131, USA

²Department of Anthropology, University of California, Santa Barbara, 1210 Cheadle Hall, Santa Barbara, CA 93106, USA

³Department of Anthropology, Yale University, 10 Sachem Street, New Haven, CT 06511, USA

⁴Department of Anthropology, Hunter College, 695 Park Avenue, New York, NY 10065, USA

⁵School of Anatomical Sciences, University of the Witwatersrand, 7 York Road, Parktown, Johannesburg 2193, South Africa

⁶Department of Neurology and Brain Research Institute, University of California, Los Angeles, 10833 Le Conte Avenue, Los Angeles, CA 90095, USA

⁷Department of Psychiatry and Biobehavioral Sciences, University of California, Los Angeles, Los Angeles, CA 90095, USA

⁸VA Greater Los Angeles Healthcare System, 16111 Plummer Street, Los Angeles, CA 91343 USA

⁹Brain Research Institute, University of California, Los Angeles, Los Angeles, CA 90095, USA

*Correspondence: jsiegel@ucla.edu

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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/topicsobjectives/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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San, Namibia (May-June, late fall)	

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, Actogramscored 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).

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 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

Summer versus Winter Durations

obesity in these populations [11].

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).

in keeping with prior anthropological observations of a lack of

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 Actiwatchmeasured 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



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.

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

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 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.

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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