

NEUROPHYSIOLOGY

Moonstruck sleep: Synchronization of human sleep with the moon cycle under field conditions

Leandro Casiraghi¹, Ignacio Spiouzas², Gideon P. Dunster^{1*}, Kaitlyn McGlothlen¹, Eduardo Fernández-Duque³, Claudia Valeggia³, Horacio O. de la Iglesia^{1†}

Before the availability of artificial light, moonlight was the only source of light sufficient to stimulate nighttime activity; still, evidence for the modulation of sleep timing by lunar phases is controversial. Here, we use wrist actimetry to show a clear synchronization of nocturnal sleep timing with the lunar cycle in participants living in environments that range from a rural setting with and without access to electricity in indigenous Toba/Qom communities in Argentina to a highly urbanized postindustrial setting in the United States. Our results show that sleep starts later and is shorter on the nights before the full moon when moonlight is available during the hours following dusk. Our data suggest that moonlight likely stimulated nocturnal activity and inhibited sleep in preindustrial communities and that access to artificial light may emulate the ancestral effect of early-night moonlight.

INTRODUCTION

Timing and duration of sleep have changed vastly throughout human evolution and history, following changes in social organization and subsistence. Human beings, with reduced vision capabilities in low-lit environments, are mostly diurnal, and it is believed that nomadic groups timed their sleep onset to the time after dusk when it became too dark to be safe hunting and gathering (1). The establishment of industrial societies, with widespread availability of artificial light sources, allowed humans to accommodate their sleep and wake patterns to modern society demands by creating well-lit—or darkened—environments that isolated them considerably from natural cycles. These artificially lit environments, which can acutely inhibit sleep, also entrain the central body clock in the brain that controls the timing of sleep leading to a delayed onset of sleep and a shorter nocturnal sleep bout (1–4).

While the sun is the most important source of light and synchronizer of circadian rhythms for almost all species, moonlight also modulates nocturnal activity in organisms ranging from invertebrate larvae to primates (5). Moonlight is so bright to the human eye that it is entirely reasonable to imagine that, in the absence of other sources of light, this source of nocturnal light could have had a role in modulating human nocturnal activity and sleep. However, whether the moon cycle can modulate human nocturnal activity and sleep remains a matter of controversy. Some authors have argued against strong effects of moon phase on human behavior and biological rhythms (6–8), but recent studies have reported that human sleep and cortical activity under strictly controlled laboratory conditions are synchronized with lunar phases (9, 10). The controversy generated by these studies has underscored the need for longitudinal studies that can assess the potential effects of moon cycle on sleep (11).

To examine the hypothesis that the lunar phase affects sleep, we conducted a study with three Western Toba/Qom communities of the Argentinian province of Formosa. Once exclusively hunter-gatherers,

these geographically spread indigenous communities share a recent historical past and live under very different levels of urbanization (12). We tested the prediction that in communities without access to electricity, moonlit nights would be associated with increased nocturnal activity and decreased sleep. We worked with three Toba/Qom communities (see detailed information in Materials and Methods and table S1): one in an urban setting with full access to electricity (Ur) and two rural communities, one with access to limited electric light (Ru-LL) and another with no access to electric light at all (Ru-NL).

RESULTS

Consistent with previous studies (3), shorter sleep duration and a delayed onset of sleep were associated with increased access to electric light (fig. S1 and table S2). Moreover, both the duration and the time of sleep onset showed a clear modulation throughout the moon cycle that was evident in the whole population, as well as in the individual communities. The peak in sleep onset time and trough of sleep duration took place 3 to 5 days before the night of full moon (Fig. 1). Times of sleep offset suggested a negligible variation across the moon cycle (fig. S2).

The modulation of sleep duration and onset across the moon cycle was evident at the individual level for most participants in the three communities (Fig. 2 and figs. S3 and S4). We fitted individual data to sine waves with a 30-day period through a nonlinear least squares approach and analyzed the parameters of the best-fitting participants (i.e., the three best quartiles according to the standard error of the regression, S ; $n = 51$). The individual phases of sleep duration and onset showed a consistent clustering of the troughs of sleep duration and the peaks of sleep onset on the days before the full moon (Rayleigh z tests, mean phase in days before the full moon [fiducial limits]: duration, 2.8 [5.0 to 2.5], $P = 6 \times 10^{-4}$; onset: 3.3 [4.4 to 2.2], $P = 3 \times 10^{-7}$; fig. S5 and Supplementary Text). Changes in each participant's sleep duration across the lunar cycle ranged from 20 to more than 90 min and did not differ considerably between groups {mean duration change in minutes [95% confidence interval (CI)]: Ru-NL, 46 [36 to 56]; Ru-LL, 52 [41 to 63]; Ur, 58 [50 to 67]}. Changes in the onset of sleep varied from 30 to 80 min (Ru-NL, 29 [17 to 41]; Ru-LL, 32 [20 to 43]; Ur, 32 [24 to 40]). Thus,

Copyright © 2021
The Authors, some
rights reserved;
exclusive licensee
American Association
for the Advancement
of Science. No claim to
original U.S. Government
Works. Distributed
under a Creative
Commons Attribution
NonCommercial
License 4.0 (CC BY-NC).

¹Department of Biology, University of Washington, Seattle, WA, USA. ²Sensorimotor Dynamics Lab (LDSM), CONICET, Universidad Nacional de Quilmes, Bernal, Argentina. ³Yale University, New Haven, CT, USA.

*Present address: National Institute of Mental Health, Bethesda, MD, USA.

†Corresponding author. Email: horacioid@uw.edu

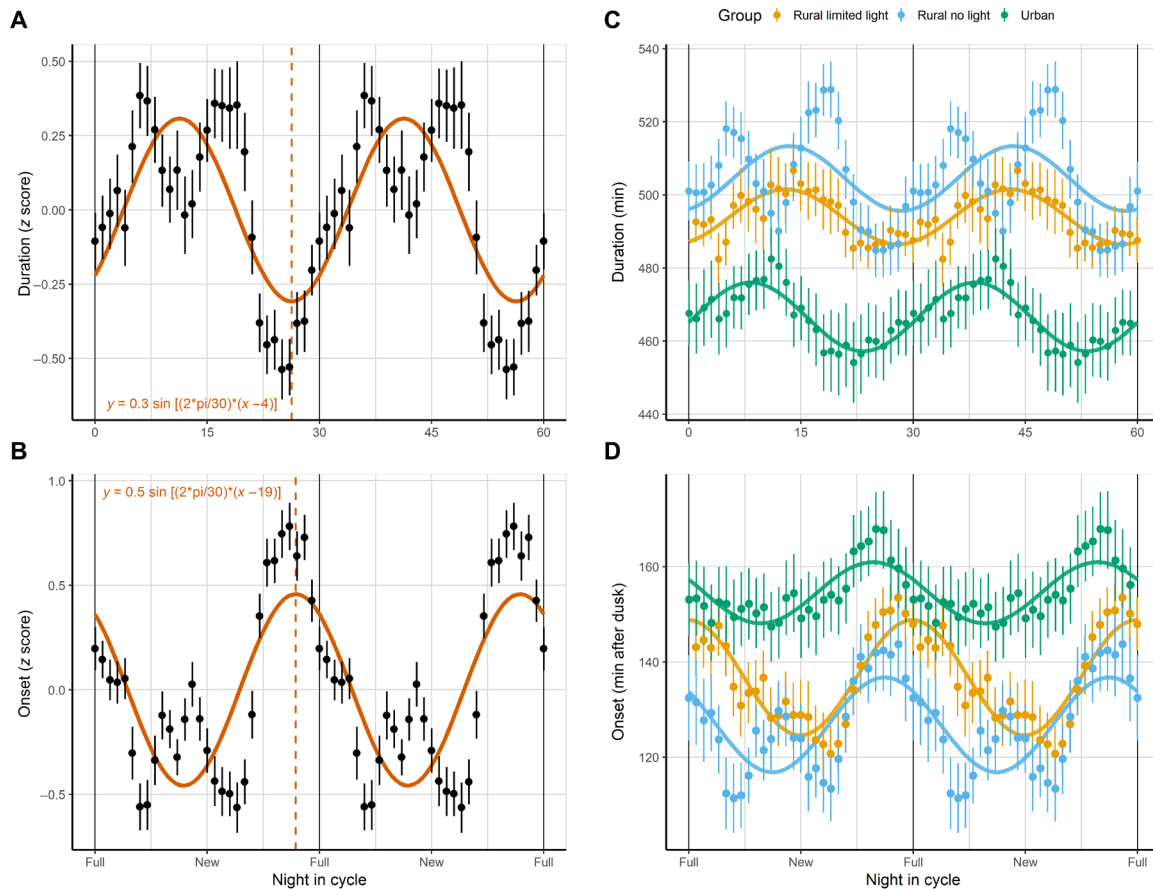


Fig. 1. Sleep timing changes through the moon cycle. (A and B) Double plots of the average duration and onset of sleep in the Toba/Qom population across the moon cycle expressed as average z scores (\pm SEM; $N = 69$ participants). Solid lines represent the best fit of the complete dataset to sinusoidal curves with a 30-day period from a nonlinear least squares fit (see Materials and Methods), and the vertical dashed lines indicate the trough of sleep duration (i.e., the shorter sleep events) and the acrophase of sleep onset (i.e., the latest sleeping times). Best-fit equations are indicated for each variable. Fitted sine wave amplitudes mean and 95% confidence intervals (CIs): duration: 0.31 [0.25 to 0.37]; onset: 0.46 [0.40 to 0.51]. (C and D) Double plots of the average values (\pm SEM) of duration (in minutes) and onset of sleep (in minutes after the astronomical dusk) by community. Solid lines represent best fits for each community data subset. Fitted sine wave amplitudes mean and 95% CIs: duration: Ru-NL, 8.8 [4.9 to 12.8]; Ru-LL, 7.5 [4.0 to 11.0]; Ur, 9.4 [4.6 to 14.2]; onset: Ru-NL, 10.0 [6.2 to 13.7]; Ru-LL, 12.1 [9.1 to 15.1]; Ur, 6.4 [2.5 to 10.3]. Amplitude and phase parameters for all fits are summarized in table S9. Individual data series for participants with records for at least 80% of the moon cycle were filtered through moving average with a window of 7 days before summarizing the data. Number of participants: Ru-LL, 20; Ru-NL, 23; Ur, 26.

moon phases were associated with predictable and biologically relevant changes in daily sleep timing.

The moon is responsible for several environmental cycles, but its lighting power during the night is arguably the most relevant cycle to humans in natural conditions. Humans typically start their daily sleep bout some hours after dusk but rarely wake up before dawn, a pattern we also documented earlier among the Toba/Qom (3). Moonlight intensity is sufficient to allow outdoor activities, and it is likely to prevent sleep initiation; in contrast, and importantly, it is unlikely to wake somebody who has already fallen asleep. In this context, it is primarily moonlight available during the first hours of the night that is more likely to drive changes in the onset of sleep. In contrast, moonlight late in the night, when most individuals are typically asleep, should have little influence on sleep onset or duration. The hours of available moonlight change predictably through the moon cycle according to the time of moonrise, approximately 50 min later every day (fig. S6); under a mostly symmetrical photoperiod like that of the spring season, moonlight becomes less avail-

able during the early night on the nights that follow the full moon night. We hypothesized that the adaptive value of the synchronization between sleep and the moon cycles is to stimulate wakefulness on nights when moonlight is available during the early night, which are the nights that precede the night of full moon but not the ones that follow it, when the moon rises much later than dusk.

To test predictions derived from this hypothesis, we determined the availability of moonlight during the first 6 hours of every night recorded in the study and classified them into three categories of “moonlight phases” (see Materials and Methods and fig. S6): full moonlight (F-ML), no moonlight (No-ML), and waning/waxing moonlight (W-ML). Figure 3 shows the change in sleep timing between F-ML and No-ML for the different communities. Within-subject averaged data comparing the two phases are shown in Fig. 3 and the summarized data are presented in table S3. Linear mixed-effects models (LMEMs) considering community, moonlight phase and the interaction between these, age and sex as fixed effects, and subject identity as a random effect were fit to analyze the associations

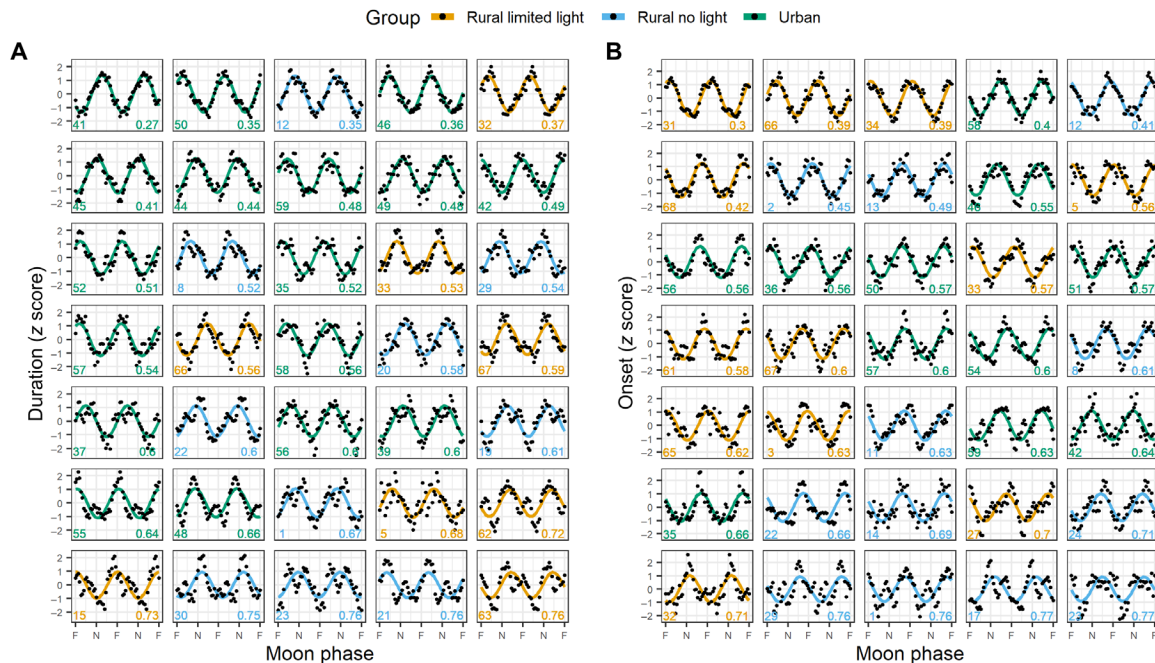


Fig. 2. Individual patterns of sleep timing across the moon cycle. Double plots of (A) sleep duration and (B) onset of sleep, expressed as z scores, of the 35 best-fitting participants (as evaluated by the standard error of regressions, *S*) in the study for each variable. Dots indicate the data on a given night in the cycle, and colored lines represent the best fit of a sine wave with a 30-day period through a nonlinear least squares approach. Individual data series for participants with records for at least 80% of the moon cycle were filtered through moving average with a window of 7 days before summarizing the data. The numbers on the bottom of each plot identify the participant (left) and the *S* value for the fit (right). The data for the complete set of participants are presented in figs. S3 and S4.

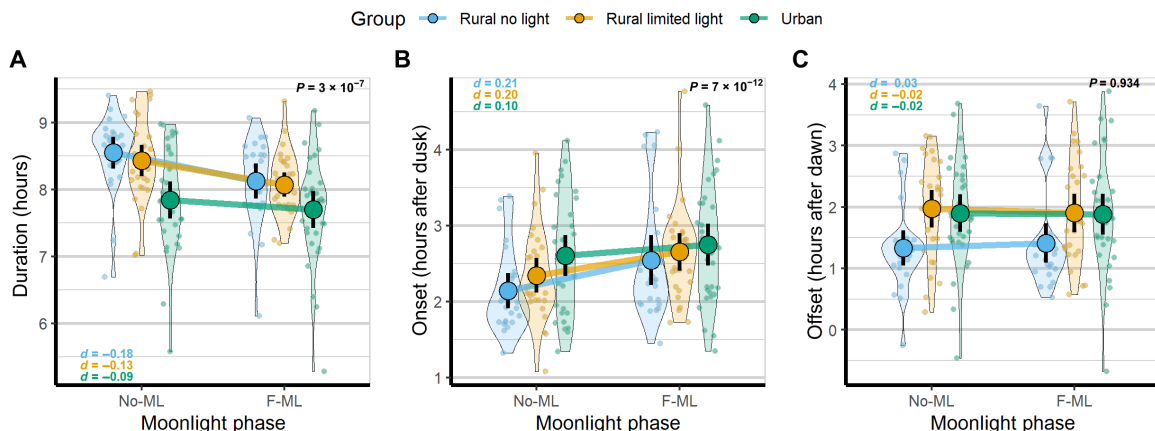


Fig. 3. Analysis of changes in sleep variables according to the No-ML (no moonlight) and F-ML (full moonlight) phases. (A) Duration of sleep (hours), (B) sleep onset (hours after dusk), and (C) sleep offset (hours after dawn). Smaller dots represent each individual's mean, while the bigger dots represent the means for each community and are connected by color lines. Vertical black error bars represent the 95% CI of the mean. The reported *P* values correspond to the main effect of moonlight for the type III analysis of variance (ANOVA); Cohen's *d* values are for Tukey contrasts between moonlight phases in each community in the linear mixed-effects models. Only participants with at least four nights recorded in each phase were considered. Number of participants: Ru-NL, 25; Ru-LL, 25; and Ur, 32.

between changes in sleep variables and moonlight phase [the full description of the estimates and effects sizes are presented in table S4, and type III analysis of variance (ANOVA) evaluation of fixed factors is shown in table S5; see Supplementary Materials for a description of the model and R syntax]. According to the models, the duration of sleep for the three communities was 25 [95% CI: 13 to 37], 19 [7 to 32], and 11 [0 to 21] min longer during No-ML than

F-ML nights for the Ru-NL, Ru-LL, and Ur groups, respectively. Accordingly, participants fell asleep 22 [13 to 30], 22 [12 to 31], and 9 [2 to 17] min earlier on No-ML nights for the Ru-NL, Ru-LL, and Ur groups, respectively (table S6). Time of sleep offset did not show consistent differences between phases. Contrasts suggested a differential effect of the moonlight availability on the sleep variables, with larger effects for groups with less access to electric light (table S6). It

is worth noting that even a change of about half hour in the duration and time of sleep, which was the lesser change across the cycle found for individuals, is biologically relevant. Both field studies using daily sleep logs during 6 weeks (13) and a retrospective analysis of sleep recordings from a sleep laboratory (9) found that people slept about 20 min less on full moon than on new moon nights, an effect size similar to the one found in our study. Earlier sleep offsets did not coincide with nights in which moonlight was available during the late night, before dawn (fig. S2 and tables S7 and S8), suggesting that late-night moonlight did not drive changes in sleep offset.

Beyond moonlight phases within the ~29.5-day synodic month, the gravitational pull of the moon on the Earth surface is maximal twice as frequently (every ~14.75 days), during full or new moons. Recent evidence indicates that bipolar patients can show mood (14, 15) and sleep [one reported case (16)] changes synchronized with these ~15-day semilunar phases. If a similar synchronization pattern exists with the sleep parameters of our Toba/Qom participants, we would expect that some individuals have bimodal peaks or the opposite phase relationship in their sleep parameters. The distribution of sleep duration and onset in the Toba/Qom communities (Fig. 1) and the inspection of the individual recordings (Fig. 2 and figs. S3 and S4) suggest that the two parameters show a second trough and peak, respectively, within the lunar month. To further examine this possibility, we fitted sleep duration and sleep onset data with a periodic function with two sinusoidal components (30- and 15-day periods; see Materials and Methods). This approach led to more informative models than those of single 30-day sine waves for 68 of 69 and 62 of 66 participants for duration and onset, respectively [figs. S7 to S9; differences between Akaike information criterion (AIC) values of $\Delta AIC_{\text{median}} = -61.6$ for duration and $\Delta AIC_{\text{median}} = -49.2$ for onset]. This result indicates that, for the vast majority of participants, sleep timing is associated with both the ~30-day (lunar) and ~15-day (semilunar) lunar phases. While the 15-day period component was evident for single participants in every community, we were not able to detect it at the population level in the urban community for neither sleep duration nor sleep onset patterns (table S10). This result indicates that the 15-day component in the urban community is weaker than in the other communities.

All three communities of Toba/Qom, including those in the urbanized setting, showed a strong association of sleep timing with the moon cycle. To explore whether a similar modulation of sleep across the moon cycle occurs in people living in large modern urban environments, we analyzed sleep recordings obtained from 464 University of Washington undergraduate students. Unexpectedly, the changes in sleep duration and onset throughout the moon cycle resembled those of the Toba/Qom people, with sleep events starting later and becoming shorter in the week before the full moon (Fig. 4). Even with the limitations inherent to nonlongitudinal studies, the data suggest that sleep changes across the moon cycle may still be present in completely urbanized environments, where individuals may have little awareness of the synodic moon phases. Light pollution measurements in the highly urbanized areas of Seattle where students typically live reveal values that are above our full moonlight measurements in the Toba/Qom rural environments. Our results are also in line with two retrospective analyses of electroencephalographic recordings of sleep, obtained in the controlled conditions of sleep laboratories, which found that both polysomnographic sleep and cortical activity were synchronized with lunar phase (8, 9); these results point to the importance of longitudinal studies to determine

the extent to which the modulation of sleep by the moon cycle prevails under modern living conditions. Studies of this nature may also reveal a semilunar component as the one we report for the Toba/Qom.

DISCUSSION

Our results show that sleep timing is synchronized with the moon cycle under a range of living environments. Toba/Qom participants slept less and stayed up later on the days previous to full moon nights, when moonlight is available during the early night. This pattern could represent a response to the availability of moonlight during the first half of the night for communities with limited or no access to electric light. The amplitude of the lunar phase effect on sleep parameters appears to be stronger the more limited the access to electric light is. However, we were able to corroborate this modulation both in a Toba/Qom community living with full access to electricity and in a sample of college students living in a modern city. Together, these results strongly suggest that human sleep is synchronized with lunar phases regardless of ethnic and sociocultural background, and of the level of urbanization.

Increased level of access to artificial light in the Toba/Qom communities correlated with later sleep onsets and shorter duration of sleep. These findings are consistent with previous work from several laboratories including ours (3, 17–19), as well as with the hypothesis that electric light allowed humans to extend their evening activity and push sleep times later into the night, therefore reducing the total amount of night sleep (20). The availability of electric light during the evening mimics the sleep-inhibiting effects of moonlight. This is particularly evident during nights with high moonlight availability during the early hours of the night, in which the timing of sleep is most similar across the Toba/Qom communities with and without access to electric light (Fig. 3). This finding may indicate that the effect that electric light has—delaying sleep onset and shortening sleep—could be emulating an ancestral effect of moonlit evenings, although the light intensities we are typically exposed to in our artificially lit environments are much higher.

While some studies have found minimal, or no association, between the moon cycle and sleep parameters (6, 8, 21, 22), they compared sleep during nights around the full moon to sleep during the nights of both the waxing/waning phases and the new moon, which may not correspond to the peaks and troughs of sleep duration and onset. Inspection of the college students' data according to full and new moon phases, as these previous studies did, shows no clear association with sleep duration or onset (Fig. 4). In contrast to these studies and in line with our findings, two other studies found an association between sleep parameters and moon phases. Rösli *et al.* found an effect of moon phase on subjective sleep duration as measured by sleep diaries with shorter sleep durations around full moon nights. Similarly, in a retrospective analysis of polysomnographic sleep in a sleep laboratory, Cajochen *et al.* (8) found a pattern of sleep duration through moon phases similar to what we found for our population, as well as on the percentage of time spent on specific sleep stages. Last, a recent study reported that nocturnal activity appears to be higher during new moon nights in a group of hunter-gatherer Hadza, but this result is based on a small sample, a sampling window of less than a full moon cycle, and is confounded by the fact that the group has rituals during nights without moonlight (23).

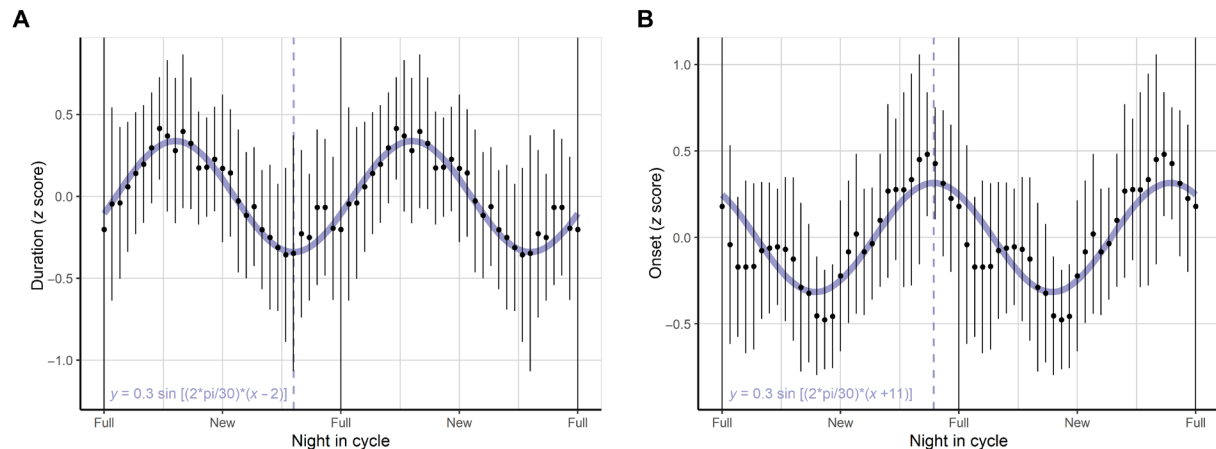


Fig. 4. Association of sleep duration and onset with the moon cycle in a highly urban setting. Double plots of (A) sleep duration and (B) sleep onset expressed as z scores (\pm SEM) on weeknights recorded on 463 college students in different quarters from 2015 to 2018. The differences between individual data points and the mean values in each season were calculated for over ~4300 sleep events. The solid lines represent the best fits to sine waves with a 30-day period to the data from nonlinear least squares fits (see Materials and Methods); wave equations are printed at the bottom left. The dashed vertical lines indicate the phase of shorter (A) and later (B) sleep events. Fitted sine wave amplitudes and 95% CI: duration, 0.34 [0.13 to 0.55]; onset, 0.32 [0.10 to 0.53]. The average data summaries were filtered through a moving average with a window of 7 days. Participants/sleep events per quarter: spring, 173/1729; summer, 66/619; fall, 136/1240; and winter, 88/796.

What could be the potential adaptive value of increased activity during moonlit nights? Our interviews with Toba/Qom individuals indicate that moonlit nights are particularly rich in social activities. Toba/Qom elders report that, at times when food was obtained from the forest, moonlit nights had particularly high hunting and fishing activity. Furthermore, mythological stories associate the moon with the female reproductive cycle and sexual relations. The moon in the Toba culture is represented as a man who has sexual relations with women, it induces the first menstruation and regulates the timing of the following menstruations (24). Interestingly, stories told by elder Toba/Qom point to moonlit nights as nights of higher sexual activity. These latter stories suggest the possibility that ancestrally moonlight-associated encounters could have synchronized reproductive activity with women's fertility (25). Although the true adaptive value of human activity during moonlit nights remains to be determined, our data seem to show that humans—in a variety of environments—are more active and sleep less when moonlight is available during the early hours of the night. This finding, in turn, suggests that the effect of electric light on modern humans may have tapped into an ancestral regulatory role of moonlight on sleep.

Although our results point to moonlight availability during the early night as a likely determinant of later sleep onset and shorter sleep duration, the presence of similar lunar rhythms in sleep parameters in Seattle college students who may not be aware of the availability of moonlight, together with the presence of semilunar (~15-day long) components on the sleep parameters of the Toba/Qom communities, suggests that other physical phenomena associated with the moon cycle could influence sleep. It is thus conceivable that although the ultimate cause—which confers adaptive value—for nocturnal activity in synchrony with the moon cycle is to display activity during moonlit nights, the proximal cause—which induces changes in sleep parameters—for sleep modulation by the moon cycle is the gravitational pull by the moon, which is a more reliable indicator of moon phase than its associated nocturnal illuminance. This hypothesis predicts that both semilunar oscillations—respectively associated with new and full moons—should have the same am-

plitude. However, although the new and full moon gravitational pulls may be indistinguishable, they consistently occur at different times of the solar day; namely, full moons but not new moons exert their gravitational pull during the night. This raises the possibility that moon gravity could have a time-of-day specific effect on sleep.

A limitation of our observational study is that we cannot establish causality. It would be difficult to manipulate human exposure to the light the moon reflects and virtually impossible to manipulate the exposure to the gravitational pull it exerts on Earth. Nevertheless, it is hard to conceive that the conserved synchronization between sleep and the moon cycle that we report occurred by chance.

MATERIALS AND METHODS

Participants and study groups

All described study procedures were approved by the Internal Review Board of University of Washington's Human Subjects Division and were in agreement with the Declaration of Helsinki. Oral consent was obtained from every participant from the Toba/Qom communities after a verbal explanation of all procedures in Spanish. All participants were bilingual (Toba/Qom/Spanish). Parental oral consent was obtained for participants under 18 years old, who also gave their assent to participate. University of Washington participants (undergraduate students) were all over 18 years of age and provided written consent.

Toba/Qom participants were aware that we were interested in studying the relationship between the moon cycle and sleep but were unaware of any of our specific predictions, e.g., that moonlit nights would be associated with less sleep. University of Washington participants were unaware of any relationship between their sleep study and moon phases.

Toba/Qom participants

Toba/Qom participants [$N = 98$, females 56%, mean age (range) = 24.1 (12 to 75)] lived in one of three Toba/Qom communities in the

Formosa province, north of Argentina. Each community had different levels of access to electric light:

1) A community located in the outskirts of Ingeniero Juárez (23°47' S, 61°48' W), a town with 19,000 inhabitants. All the participants in this community had 24-hour access to electric light at home and outside through streetlights, as well as to other urban features (consolidated roads, public leisure spaces, and commercial premises). This community is referred to as the Urban group (Ur, $n = 40$).

2) A community located in Vaca Perdida (23°29' S, 61°38' W), a small rural settlement of approximately 300 people 50 km north of Ingeniero Juárez. These participants had 24-hour access to electricity at their homes, and light fixtures were limited at most to one light bulb per room. In contrast to the Urban community, this community had no electric light poles in outside areas during dark hours. This community is referred to as the Rural, limited light group (Ru-LL, $n = 33$).

3) A group of participants living in sparsely distributed houses in a region known as Isla García, approximately 3 km away from Vaca Perdida. These participants lived in small extended-family groups, without any organized settlement features and no access to electric light. While children and some adults may have been exposed to artificial light at school or other settings away from their home location, this could have only occurred during natural daylight times. This community is referred to as the Rural, no light group (Ru-NL, $n = 25$).

The three communities share the same ethnic and historical past (12). The community at Ingeniero Juárez originated from a group of Toba people who migrated from the northern region in the 1990s. Housing, daily chores, and social behavior are very similar between the communities, and the vast majority of adults are typically unemployed and rely on government subsidies.

Age and sex characteristics of the three study communities are presented in table S1. The three study communities were similar with regard to sex [$\chi^2(2) = 0.686$, $P = 0.710$] and age [ANOVA $F(2,96) = 0.774$, $P = 0.464$]. As expected, women displayed onset times that were 15 [95% CI: 0 to 30] min earlier than men (Cohen's $d = 0.432$) (26). Age was associated with shorter sleep duration ($d = -1.411$) and later sleep onset times ($d = 0.429$), which would be expected for the age range of our participants (table S2) (27, 28).

Data were recorded during field campaigns in three consecutive years: September to October 2016 and 2017 and October to November 2018. The three campaigns were carried out during the spring (September to November in the Southern Hemisphere) to keep environmental factors (including weather, sunrise and sunset times, and sunlight intensity) as stable as possible.

University of Washington participants

We also analyzed sleep data from 464 college students [mean age (range) = 21.5 (18 to 38), 62% females; 41% Caucasian, 26% Asian, 8% Hispanic, and 15% others/nonidentifying] at the University of Washington (Seattle, WA) that were recorded across different quarters between 2015 and 2018 as part of a separate study. The data from one subject who did not wear the watch consistently were discarded.

Locomotor activity and sleep recording

Participants were equipped with Actiwatch Spectrum Plus wrist locomotor-activity loggers (Respironics, OR) for 1 to 2 months in the case of the Toba/Qom participants and from 1 to 3 weeks for the college students. The data acquisition interval was set to 1 min. Recorded data were downloaded and exported using the Philips

Respironics Actiware software V.6.0.9. Participants also completed a sleep log throughout their participation, indicating times and locations of sleep events (including naps), and whether they left their home community on any given day. These logs were used for the validation of the data and to discard data from time ranges when the subjects were under different conditions to those in their main study group. The Actiware software was set to determine sleep onsets whenever 10 consecutive minute bins were classified as of immobility (<4 activity counts) and sleep offsets after the last 10 consecutive minutes of immobility in a sleep bout. Minute bins were labeled as “wake” when they surpassed the 40 activity counts.

Data treatment and analysis

Preparation and treatment of raw recordings, as well as the statistical analysis and plotting of data, were performed in R (29) unless otherwise indicated.

Astronomical data

Sun and moon data for the Ingeniero Juárez region through the dates of recording were obtained from NASA's Jet Propulsion Laboratory HORIZONS Web-Interface (<https://ssd.jpl.nasa.gov/horizons.cgi>) with a 1-min precision. The synodic moon cycle that determines the well-known “full,” “new,” and “waning” or “waxing” moon phases has an approximate average duration of 29.5 days. All nights in our study were numbered according to their position in the synodic cycle: Full moon nights were considered as “night zero” with all previous and subsequent nights ordered from 1 to 29 or 30, depending on the day of the next full moon, when nights numbering was restarted. In short, a night in position “1” in the cycle represents the night immediately after a full moon.

We use a second classification of phases through the moon cycle according to the availability of moonlight during the early night hours, which we refer to as “moonlight phases.” We calculated the time in the first 6 hours after astronomical dusk—the time that marks the disappearance of natural daylight—during which the moon was above the horizon for every night of recording, rounded this time to the nearest hour, and classified nights into three moonlight phases: (i) nights in which there was no moonlight through the first 6 hours of the evening (no moonlight, No-ML); (ii) nights during which there was moonlight available throughout the whole 6 hours (full moonlight, F-ML); and (iii) all other nights in which the moon either rose after astronomical dusk or set before 6 hours after astronomical dusk (waning/waxing moonlight, W-ML). The distribution of these moonlight phases shows correspondence with the standard moon phases, with the F-ML nights preceding the full moon by 1 week (fig. S6).

Sleep measurements

Actograms from individual recordings were visually inspected to check for data integrity before any analysis. Low-quality criteria included fragmented recording or very frequent missing-data periods, sustained saturated Actiwatch counts, or total lack of activity counts during extended periods of time. Seven Toba/Qom participants who displayed very low quality recordings, due to noncompliance wearing the watch or to Actiwatch malfunction, were removed from the sample at this point.

To detect and discard very long and very short sleep events (artifacts from Actiwatch recording or the software algorithm), as well as irregular sleep events (long daytime siestas, naps, all-nighters), we analyzed our sleep databases for outliers in two steps: first, looking at values of duration, and then at times of sleep onset according

to the time of dusk. We performed the analyses through the median absolute deviation (MAD) method setting a threshold of three MADs, using the Routliers package for R (30).

To explore the patterns of sleep duration and timing through the moon cycle in the Toba/Qom communities, we selected the participants with data for at least 80% of the nights in the cycle. Sixty-nine participants met this condition: 20 in Ru-LL, 23 in Ru-NL, and 26 in Ur. Each participant's data points were first averaged by night in the cycle (for those with data for over a whole cycle), and data for any missing nights were completed by linear interpolation. Data were then run through a moving-average filter with a seven-night window to eliminate low-frequency noise. The data were fitted through a nonlinear least squares approach to the best possible sine curve with a 30-day period using the nls tool from the stats package (29). Because recent literature has pointed to the possibility of semilunar month (~15 days) rhythms in mood and sleep (14–16), alternative fits were performed considering the combination of a sine wave with a 30-day period along a 15-day period wave. The equations for these curves were

$$y = A_{30} \sin [(2\pi/30) * (\text{night} - P_{30})] + M \quad (1)$$

$$y = A_{30} \sin [(2\pi/30) * (\text{night} - P_{30})] + A_{15} \sin [(2\pi/15) * (\text{night} - P_{15})] + M \quad (2)$$

where night represents the night order in the moon cycle, A_{30} and A_{15} represent the sine amplitudes, P_{30} and P_{15} represent the phase angles of the 30- and 15-day components, respectively, and M represents the center value (which was not included in fits of z-scored data). For the evaluation of population data fits, 95% CIs of the estimated parameters were calculated from complete datasets to determine nonzero amplitude values (i.e., a nonnegligible sinusoidal pattern).

Goodness of fit of individual data fits was measured by the standard error of the regression (S), a proper measure for nonlinear equation fits. When analyzing group differences in parameters obtained from individual fits, we only included subjects within the best three quantiles of S values for their z-score fits for each variable (that is, 51 of the abovementioned 69 participants with enough data). For comparing modeling alternatives, we calculated the AIC for the individual fits and considered a more informative model when it was reduced by more than 2 units. For sleep duration patterns, in 68 of 69 participants, the two-component models were more informative, while for the sleep onset patterns, that was the case for 62 of 66 individuals. The single-component model did not converge in a fit for the sleep onsets of one participant, while the same happened with the two-component model for the sleep onsets of two participants in the sample.

Rayleigh z tests were used to analyze phase clustering and were performed and plotted with El Temps software v1.311 (University of Barcelona, Spain). Fiducial limits were used as a measure of CIs of the mean phases, due to the nonnormal nature of the circular distribution. Circular distributions were compared by Watson-Wheeler tests for homogeneity of phases using the circular package for R (31).

Because we did not count with longitudinal recordings for college students throughout the moon phases, these data were analyzed as follows. We first calculated the average and SD of sleep duration and sleep onset on school nights (Sunday to Monday, excluding

nights before a holiday) for each season. Then, we normalized each sleep variable by subtracting the season average and dividing it by the season SD. We then averaged these population data according to the day on the moon cycle and smoothed it by running a moving average with a seven-night window. The data were then fitted to a sine wave with a 30-day period through the nonlinear least squares approach described above.

Statistical analysis

To estimate the associations between the moonlight phases and demographic variables on sleep features, we applied LMEMs using the lme4 package (32). Only participants who presented data for at least four nights within each moonlight phase were considered for these analyses. QQ plots for every LMEM fit were visually inspected to check normality of residues; these are presented in the “Statistical model definitions and diagnostics” section in the Supplementary Text. All the random effects (intercepts by subject) of the best-fitted models were normally distributed. To estimate the predicted difference of sleep duration, onset, and offset with moonlight phase, we calculated Tukey contrasts using the estimated marginal means of each group [via the emmeans R library (33)]. The syntax used for LMEMs is also presented in the Supplementary Text.

Cohen's d effect size for each fixed effect of the best-fitted models and the above-defined contrasts was calculated using the lme.dscore function of the EMATools R package (34). This package calculates the Cohen's d using the following equation

$$d = \frac{2\beta / \text{Std. Error}(\beta)}{\sqrt{df}}$$

The degrees of freedom of the model (df) were calculated using the Satterthwaite approximation [via the lmerTest R library (35)]. CIs for the fixed effect estimations were calculated using the confint function of the stats R library with alpha level set at 5% and using the Wald method. For the CIs of the effect size, we followed the lme.dscore methodology but using the beta estimates limits of the CI instead of the beta estimate itself.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/7/5/eabe0465/DC1>

[View/request a protocol for this paper from Bio-protocol.](#)

REFERENCES AND NOTES

1. N. C. Rattenborg, H. O. de la Iglesia, B. Kempnaers, J. A. Lesku, P. Meerlo, M. F. Scriba, Sleep research goes wild: New methods and approaches to investigate the ecology, evolution and functions of sleep. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* **372**, 20160251 (2017).
2. L. P. Casiraghi, S. A. Plano, E. Fernández-Duque, C. Valeggia, D. A. Golombek, H. O. de la Iglesia, Access to electric light is associated with delays of the dim-light melatonin onset in a traditionally hunter-gatherer Toba/Qom community. *J. Pineal Res.* **69**, e12689 (2020).
3. H. O. de la Iglesia, E. Fernández-Duque, D. A. Golombek, N. Lanza, J. F. Duffy, C. A. Czeisler, C. R. Valeggia, Access to electric light is associated with shorter sleep duration in a traditionally hunter-gatherer community. *J. Biol. Rhythm.* **30**, 342–350 (2015).
4. D. B. Boivin, J. F. Duffy, R. E. Kronauer, C. A. Czeisler, Dose-response relationships for resetting of human circadian clock by light. *Nature* **379**, 540–542 (1996).
5. N. Kronfeld-Schor, D. Dominoni, H. de la Iglesia, O. Levy, E. D. Herzog, T. Dayan, C. Helfrich-Forster, Chronobiology by moonlight. *Proc. R. Soc. B* **280**, 20123088 (2013).
6. J.-P. Chaput, M. Weippert, A. G. Le Blanc, M. F. Hjorth, K. F. Michaelsen, P. T. Katzmarzyk, M. S. Tremblay, T. V. Barreira, S. T. Broyles, M. Fogelholm, G. Hu, R. Kuriyan, A. Kurpad, E. V. Lambert, C. Maher, J. Maia, V. Matsudo, T. Olds, V. Onywera, O. L. Sarmiento, M. Standage, C. Tudor-Locke, P. Zhao, A. M. Sjödin, Are children like werewolves? Full

- moon and its association with sleep and activity behaviors in an international sample of children. *Front. Pediatr.* **4**, 24 (2016).
7. R. G. Foster, T. Roenneberg, Human responses to the geophysical daily, annual and lunar cycles. *Curr. Biol.* **18**, R784–R794 (2008).
 8. M. Cordi, S. Ackermann, F. W. Bes, F. Hartmann, B. N. Konrad, L. Genzel, M. Pawlowski, A. Steiger, H. Schulz, B. Rasch, M. Dresler, Lunar cycle effects on sleep and the file drawer problem. *Curr. Biol.* **24**, R549–R550 (2014).
 9. C. Cajochen, S. Altanay-Ekici, M. Münch, S. Frey, V. Knoblauch, A. Wirz-Justice, Evidence that the lunar cycle influences human sleep. *Curr. Biol.* **23**, 1485–1488 (2013).
 10. M. Smith, I. Croy, K. Persson Wayne, Human sleep and cortical reactivity are influenced by lunar phase. *Curr. Biol.* **24**, R551–R552 (2014).
 11. V. V. Vyazovskiy, R. G. Foster, Sleep: A biological stimulus from our nearest celestial neighbor? *Curr. Biol.* **24**, R557–R560 (2014).
 12. E. Miller, *Peoples of the Gran Chaco* (Bergin & Garvey, 1999).
 13. M. Rössli, P. Jüni, C. Braun-Fahrlander, M. W. G. Brinkhof, N. Low, M. Egger, Sleepless night, the moon is bright: Longitudinal study of lunar phase and sleep. *J. Sleep Res.* **15**, 149–153 (2006).
 14. T. A. Wehr, Bipolar mood cycles associated with lunar entrainment of a circadian rhythm. *Transl. Psychiatry* **8**, 151 (2018).
 15. T. A. Wehr, Bipolar mood cycles and lunar tidal cycles. *Mol. Psychiatry* **23**, 923–931 (2018).
 16. D. H. Avery, T. A. Wehr, Synchrony of sleep-wake cycles with lunar tidal cycles in a rapid-cycling bipolar patient. *Bipolar Disord.* **20**, 399–402 (2018).
 17. C. R. C. Moreno, S. Vasconcelos, E. C. Marqueze, A. Lowden, B. Middleton, F. M. Fischer, F. M. Louzada, D. J. Skene, Sleep patterns in Amazon rubber tappers with and without electric light at home. *Sci. Rep.* **5**, 14074 (2015).
 18. L. K. Pilz, R. Levandovski, M. A. B. Oliveira, M. P. Hidalgo, T. Roenneberg, Sleep and light exposure across different levels of urbanisation in Brazilian communities. *Sci. Rep.* **8**, 11389 (2018).
 19. A. N. Smit, T. Broesch, J. M. Siegel, R. E. Mistlberger, Sleep timing and duration in indigenous villages with and without electric lighting on Tanna Island, Vanuatu. *Sci. Rep.* **9**, 17278 (2019).
 20. C. A. Czeisler, Perspective: Casting light on sleep deficiency. *Nature* **497**, S13 (2013).
 21. A. Sjödin, M. F. Hjorth, C. T. Damsgaard, C. Ritz, A. Astrup, K. F. Michaelsen, Physical activity, sleep duration and metabolic health in children fluctuate with the lunar cycle: Science behind the myth. *Clin. Obes.* **5**, 60–66 (2015).
 22. J. Haba-Rubio, P. Marques-Vidal, N. Tobback, D. Andries, M. Preisig, C. Kuehner, P. Vollenweider, G. Waeber, G. Luca, M. Tafti, R. Heinzer, Bad sleep? Don't blame the moon! A population-based study. *Sleep Med.* **16**, 1321–1326 (2015).
 23. D. R. Samson, A. N. Crittenden, I. A. Mabulla, A. Z. P. Mabulla, C. L. Nunn, Does the moon influence sleep in small-scale societies? *Sleep Health* **4**, 509–514 (2018).
 24. C. P. Gómez, La luna y la feminidad entre los tobas del oeste formoseño (Gran Chaco, Argentina). *Campos.* **11**, 47–64 (2010).
 25. C. Helfrich-Förster, S. Monecke, I. Spiouzas, T. Hovestadt, O. Mitesser, T. A. Wehr, Women temporarily synchronize their menstrual cycles with the luminance and gravimetric cycles of the Moon. *Sci. Adv.* **7**, eabe1358 (2021).
 26. J. F. Duffy, S. W. Cain, A.-M. Chang, A. J. K. Phillips, M. Y. Munch, C. Gronfier, J. K. Wyatt, D.-J. Dijk, K. P. Wright Jr., C. A. Czeisler, Sex difference in the near-24-hour intrinsic period of the human circadian timing system. *Proc. Natl. Acad. Sci. U.S.A.* **108** (Suppl 3), 15602–15608 (2011).
 27. J. Li, M. V. Vitiello, N. S. Gooneratne, Sleep in normal aging. *Sleep Med. Clin.* **13**, 1–11 (2018).
 28. L. Tarokh, J. M. Saletin, M. A. Carskadon, Sleep in adolescence: Physiology, cognition and mental health. *Neurosci. Biobehav. Rev.* **70**, 182–188 (2016).
 29. R. C. Team, R: A Language and Environment for Statistical Computing (2019); <https://www.R-project.org/>.
 30. M. Delacore, O. Klein, Routliers: Robust outliers detection. *R package version 0.0.0.3* (2019); <https://CRAN.R-project.org/package=Routliers>.
 31. U. Lund et al., Circular Statistics (2017); <https://r-forge.r-project.org/projects/circular/>.
 32. D. Bates, M. Maechler, B. Bolker, S. Walker, Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
 33. R. Lenth et al., emmeans: Estimated Marginal Means, aka Least-Squares Means (2020); <https://cran.r-project.org/web/packages/emmeans/index.html>.
 34. E. Kleiman, EMAtools: Data Management Tools for Real-Time Monitoring/Ecological Momentary Assessment Data. *R package version 0.1.3* (2017); <https://CRAN.R-project.org/package=EMAtools>.
 35. A. Kuznetsova, P. B. Brockhoff, R. H. B. Christensen, lmerTest package: Tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26 (2017).

Acknowledgments: We are thankful to A. García, M. Pérez, K. Ortiz, M. Rotundo, E. R. Guiñazú, and N. West for field assistance and the Toba/Qom people for the tremendous support and collaboration. We thank B. Schwartz and C. Helfrich Foster and her team for comments on the manuscript. **Funding:** This study was supported by NSF RAPID award #1743364 to E.F.-D., C.V., and H.O.d.I.I. and by Leakey Foundation grant 1266 to H.O.d.I.I. **Author contributions:** L.C. designed the study, collected Toba/Qom data, analyzed data, and wrote the manuscript. I.S. analyzed data and wrote the manuscript. G.P.D. collected Toba/Qom and UW students' data and revised the manuscript. K.M. organized and processed Toba/Qom recordings and revised the manuscript. E.F.-D. and C.V. provided resources for the study and wrote the manuscript. H.O.d.I.I. designed the study, provided resources for the study, collected Toba/Qom and UW students' data, analyzed data, and wrote the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors or accessed at https://osf.io/nxtvk/?view_only=6baffd62ae8a485c9e64cd77f9a128c.

Submitted 28 July 2020

Accepted 17 November 2020

Published 27 January 2021

10.1126/sciadv.abe0465

Citation: L. Casiraghi, I. Spiouzas, G. P. Dunster, K. McGlothlen, E. Fernández-Duque, C. Valeggia, H. O. de la Iglesia, Moonstruck sleep: Synchronization of human sleep with the moon cycle under field conditions. *Sci. Adv.* **7**, eabe0465 (2021).

Supplementary Materials for

Moonstruck sleep: Synchronization of human sleep with the moon cycle under field conditions

Leandro Casiraghi, Ignacio Spiouzas, Gideon P. Dunster, Kaitlyn McGlothlen, Eduardo Fernández-Duque, Claudia Vallengia, Horacio O. de la Iglesia*

*Corresponding author. Email: horacioid@uw.edu

Published 27 January 2021, *Sci. Adv.* 7, eabe0465 (2021)
DOI: 10.1126/sciadv.abe0465

This PDF file includes:

Figs. S1 to S12
Tables S1 to S10
Supplementary Text

Fig. S1.

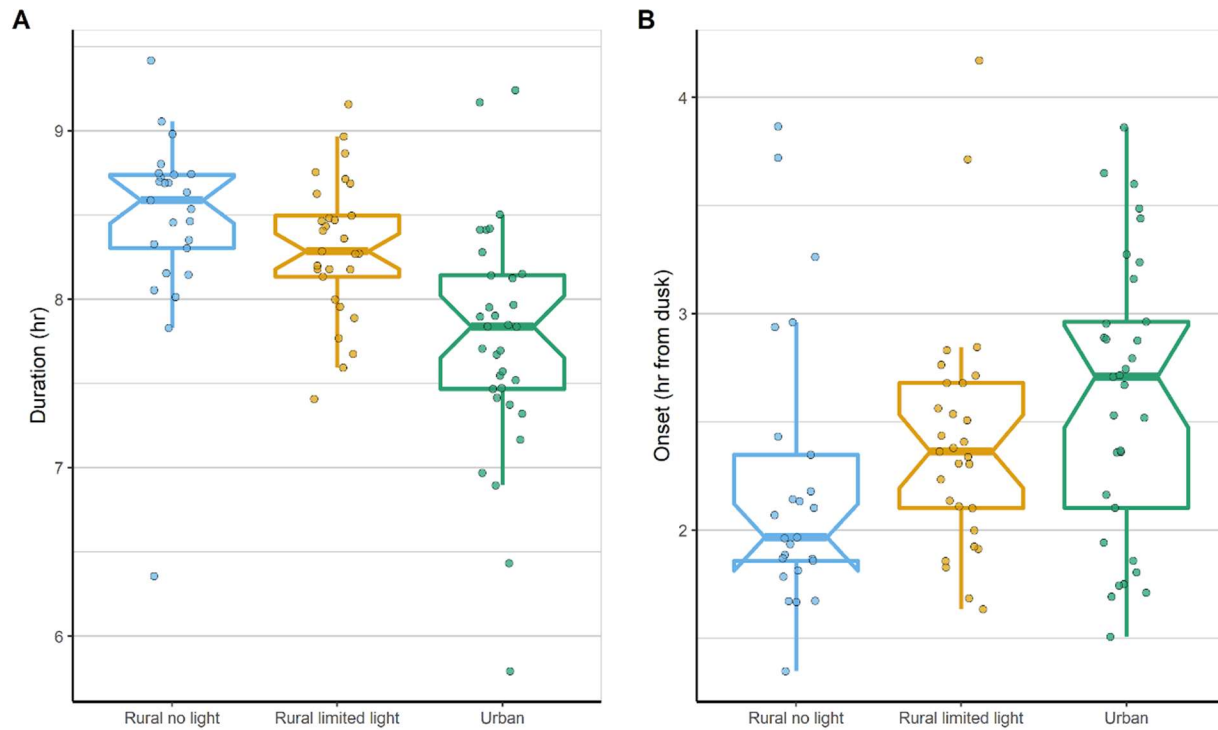


Figure S1. Duration of sleep and time of sleep onset in the three Toba-Qom communities. (A) Sleep duration in hours, and (B) start of sleep in hours from the time of astronomical dusk. Data summary is shown as boxplots with notches indicating the 95% CI of the median of the data. Dots represent individual participants' mean value for the variables across all the recording periods. LMEMs accounting for community, sex, and age as fixed effects, and subjects' identity as a random factor revealed associations between the level of access to electric light and both variables (see **Table S2**). Participants: Ru-NL, 25; Ru-LL, 29; Ur, 33.

Fig. S2.

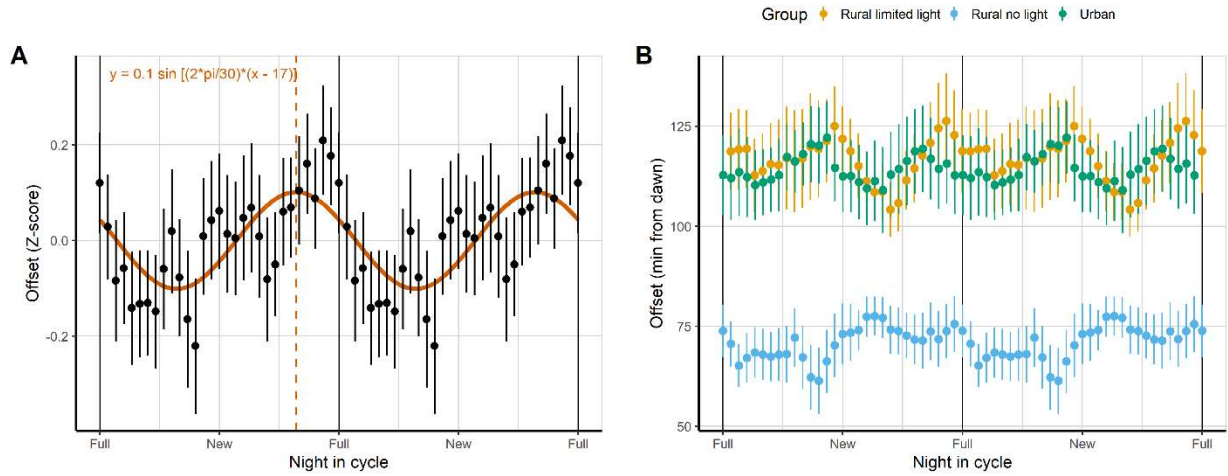


Figure S2. Waking-up times across the moon cycle. (A) Double-plot of the mean offset of sleep (expressed as z-scores) measured from the time of astronomical dusk across the moon cycle (N=69). The red solid line represents the best-fit to a sine curve with a 30-day period from a non-linear least squares fit (see Methods), and the vertical dashed line indicates the acrophase of sleep offset (i.e. the latest waking-up time) according to the fit. The best-fit equation is indicated for the fit. Fitted sine wave amplitude mean and 95%CI: 0.10[0.04/0.16]. (B) Double-plot of the mean values of the offset of sleep in the three communities (Number of participants: Ru-LL, 20; Ru-NL, 23; Ur, 26). Vertical error bars on data points represent standard errors of the mean. Individual data series were filtered through moving-average with a window of seven days before summarizing the data. All data in these figures correspond to participants with records for at least 80% of the moon cycle.

Fig. S3.

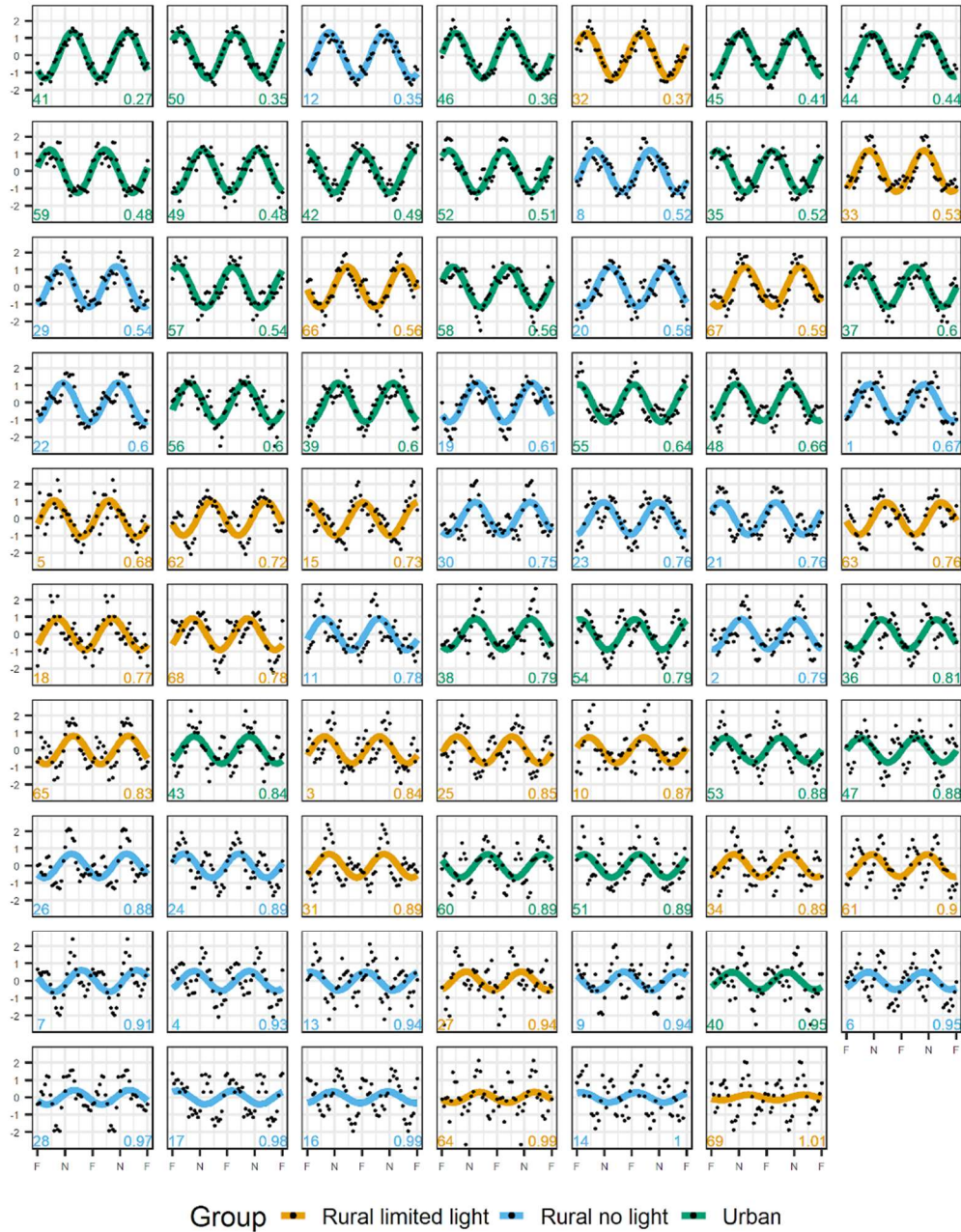


Figure S3. Individual patterns of sleep duration across the moon cycle. Double-plots of sleep duration expressed as z-scores of individual participants in the study across the moon cycle. Dots indicate the duration of sleep on each night in the cycle, and colored lines represent the best fit of a sine wave with a 30-days period through a non-linear least squares approach. The number on the bottom left of each plot identifies the participant and the one on the bottom right the standard error of the regression (S). The data correspond to participants with records for at least 80% of the moon cycle. Participants are ordered from best to worst fits as evaluated by S: minimum = 0.27, median = 0.76, maximum = 1.01. F = full moon, N = new moon.

Fig. S4.

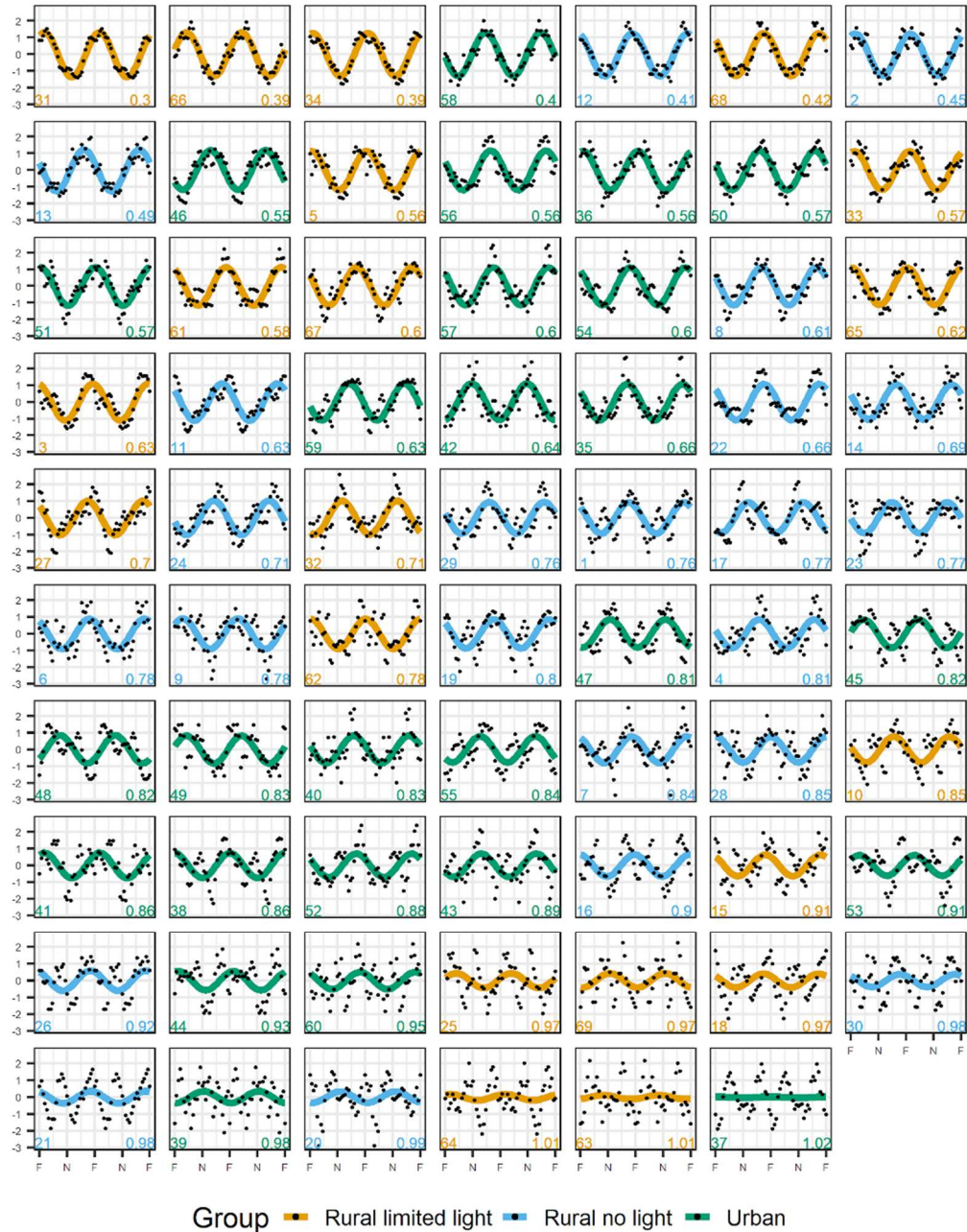


Figure S4. Individual patterns of sleep start times across the moon cycle. Double-plots of sleep onset expressed as z-scores of individual participants in the study across the moon cycle. Dots indicate the onset of sleep on each night in the cycle, and colored lines represent the best fit of a sine wave with a 30-days period through a non-linear least squares approach. The number on the bottom left of each plot identifies the participant and the one on the bottom right the standard error of the regression (S). The data correspond to participants with records for at least 80% of the moon cycle. Participants are ordered from best to worst fits as evaluated by S: minimum = 0.30, median = 0.78, maximum = 1.02. F = full moon, N = new moon.

Fig. S5.

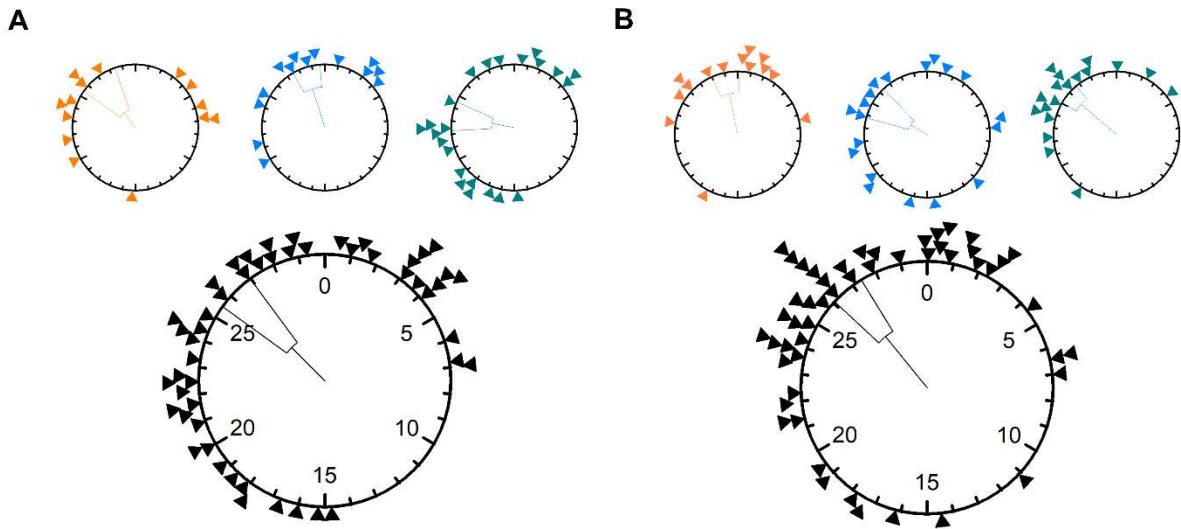


Figure S5. Average phases of shortest duration and latest start times of sleep in the Toba/Qom communities. Circular distribution of (A) the troughs of sleep duration and (B) the acrophases of sleep onset calculated from sine-wave fits, for the 51 subjects in the three higher quartiles of goodness of fit, measured through the standard error of the regression. The direction of the vectors indicates the mean calculated phase in days from the full moon, and the brackets indicate the standard error of the mean. Triangles represent the calculated individual phases. Mean phase [fiducial limits] and Rayleigh z-test p-values: Duration, 26.2 [25-27.5], $p = 0.0006$; Onset, 26.7, [25.6-27.8], $p = 3 \times 10^{-7}$. Communities are split in the top row of the panels (no relevant differences between groups; see Supplementary Text).

Fig. S6.

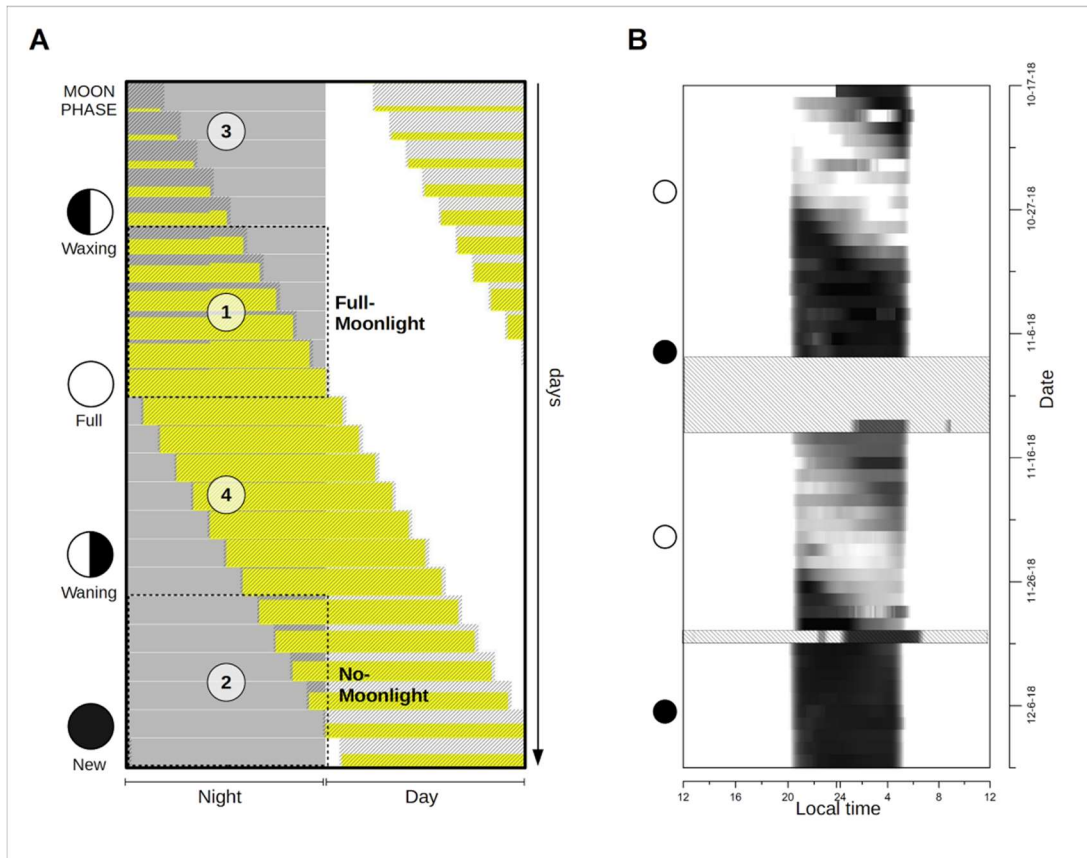


Figure S6. The hours when moonlight is available change predictably across the moon cycle. (A) Schematic representation of the progression of moonrise during a complete synodic moon cycle. Consecutive days are stacked vertically, with the shaded grey area representing the night hours. The textured areas represent the times when the moon is above the horizon, and the height of the yellow area represents the phase of the moon in terms of % of illuminated surface, from the new moon (no yellow) to the full moon (full yellow). Moonlight is available throughout the first six hours of the evening night in the interval indicated with number 1; we refer to it as the *Full Moonlight* phase (F-ML). During the interval indicated with number 2, no moonlight is available during said hours, and so we designate it as the *No Moonlight* phase (No-ML). The intervals indicated with numbers 3 and 4 are those in which the moon sets or rises during the first 6 hours of the evening, respectively. We refer to these generically as the *Waxing-Waning Moonlight* phases (W-ML). Note: for simplicity sake, the synodic lunar cycle was slightly shortened, and changes in the times of dusk and dawn were not simulated. **(B)** Actual recording of sky illuminance from a location far from any electric light source near the Vaca Perdida settlement, from 10/17/2018 to 12/10/2018. The grayscale gradient was set so that the highest luminance levels equal to that of daylight. The brightest sky luminance recorded during the full moon was around 17.5 magnitudes per square arcsecond, while the darkest recordings obtained during new moons were around 22 mag/square.arcsec, indicating a ~34-fold difference in night sky brightness between moon phases. Shaded boxes indicate missing or defective recording intervals. Data was recorded every 10 minutes with the Unihedron SQM-LU-DL device (Grimsby, ON, Canada).

Fig. S7.

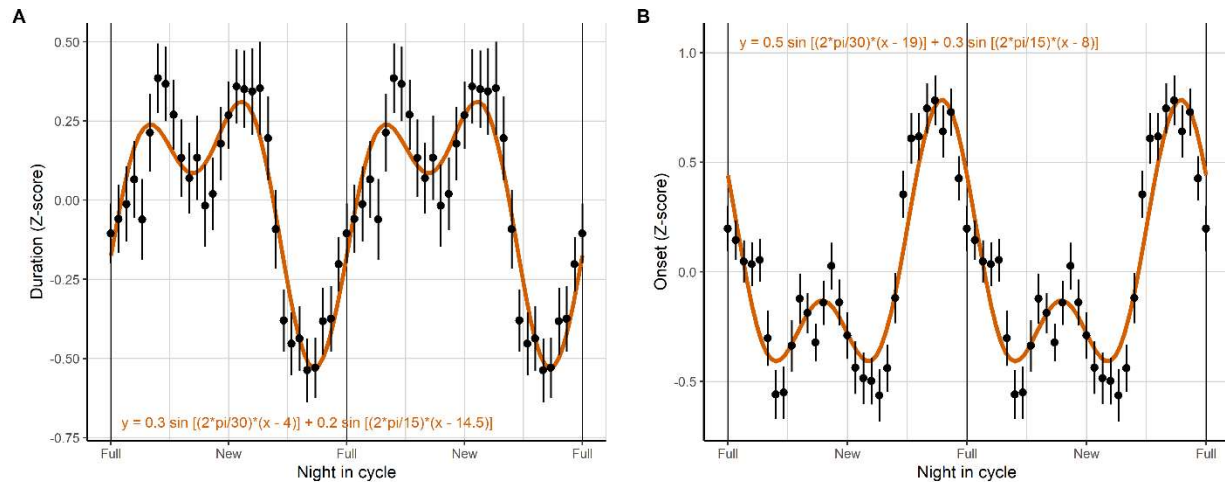


Figure S7. Evaluation of an additional 15-day long component in the lunar patterns of sleep duration and onset. Double-plots of (A) the average duration and (B) onset of sleep (measured from the time of astronomical dusk), expressed as z-scores (\pm SEM). Red solid lines represent the best-fits to equations involving a sine curve with a 30-day period and a second sine curve with a 15-day period, calculated using a non-linear least squares approach (see Methods). Individual data series from the 69 Toba/Qom participants with records for at least 80% of the moon cycle were filtered through moving-average with a window of seven days before summarizing the data. The equation and standard error of the regression (S) for the best fitting model are indicated for each variable. Fitted amplitudes mean and 95% CIs: Duration, A_{30} : 0.31[0.25/0.37]; A_{15} : 0.22[0.16/0.28]; Onset, A_{30} : 0.46[0.40/0.51]; A_{15} : 0.33[0.27/0.38]. Fitted phase parameters are summarized in **Table S10**.

Fig. S8.

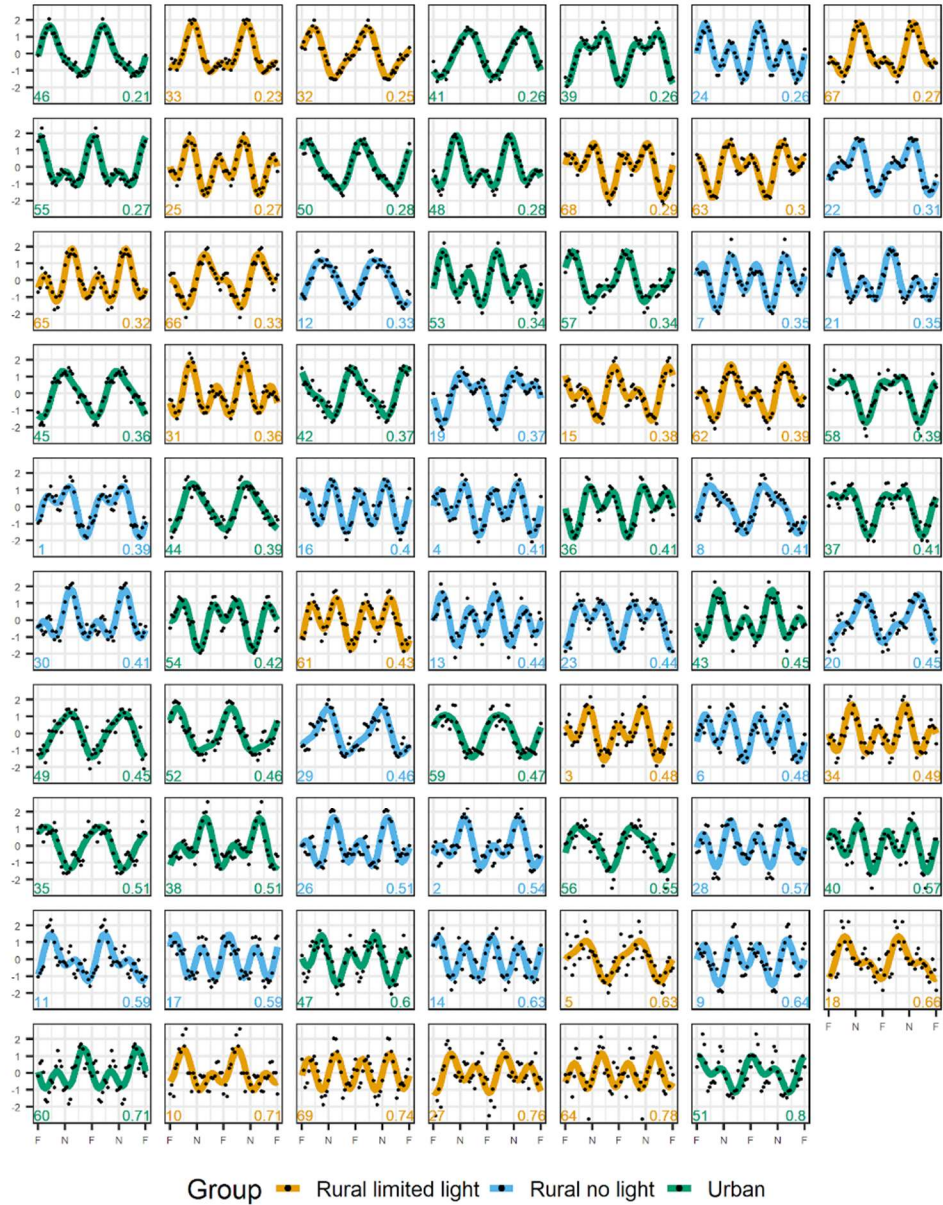


Figure S8. Individual patterns of sleep duration across the moon cycle, adding an additional 15-day long sinusoid component to fits. Double-plots of sleep duration expressed as z -scores of individual participants in the study across the moon cycle. Dots indicate the duration of sleep on each night in the cycle, and colored lines represent the best fit to an equation involving a sine curve with a 30-day period and a second sine curve with a 15-day period through a non-linear least squares approach. The number on the bottom left of each plot identifies the participant and the one on the bottom right the standard error of the regression (S). The data correspond to participants with records for at least 80% of the moon cycle. Participants are ordered from best to worst fits as evaluated by S : minimum = 0.21, median = 0.40, maximum = 0.80. F = full moon, N = new moon.

Fig. S9.

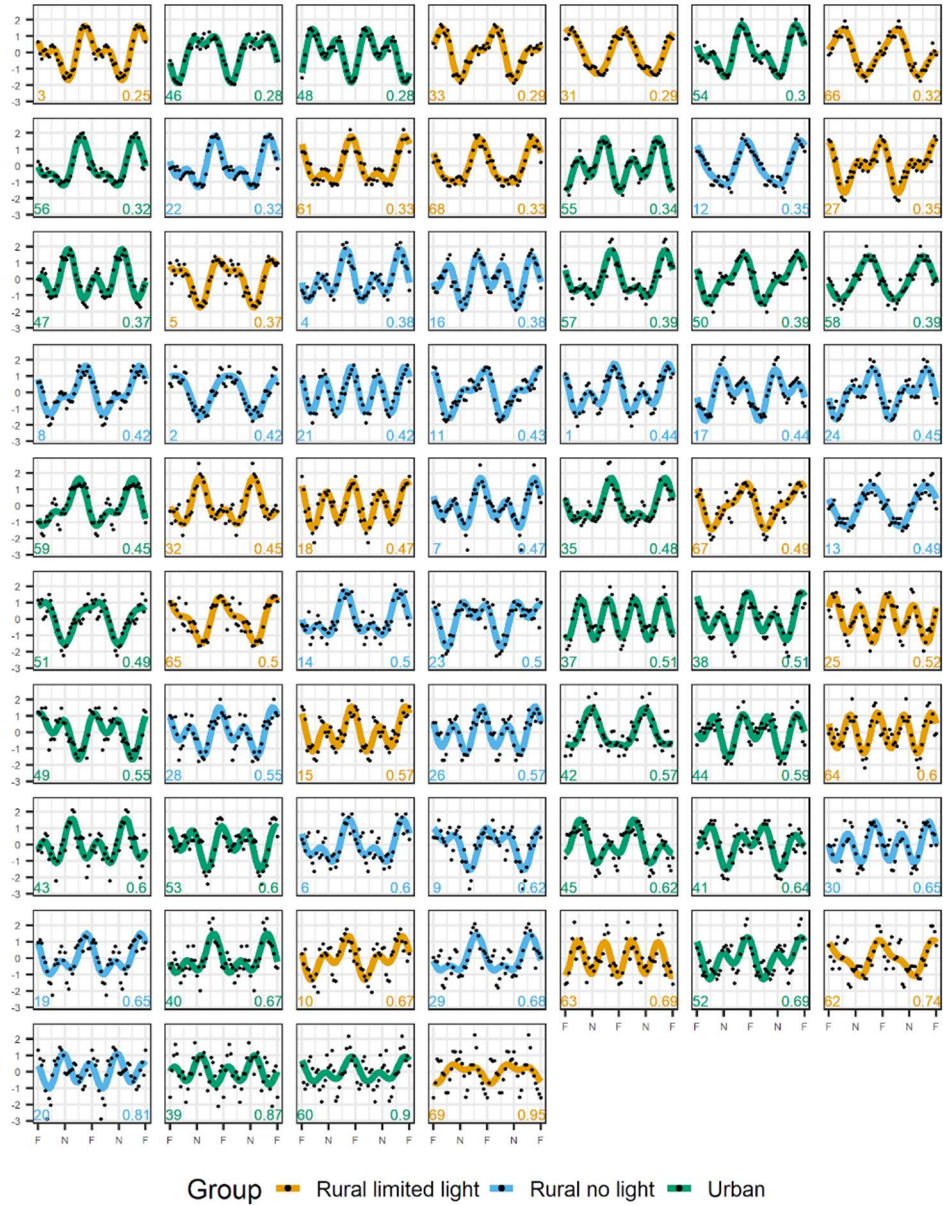


Figure S9. Individual patterns of sleep start times across the moon cycle, adding an additional 15-day long sinusoid component to fits. Double-plots of sleep onset expressed as z-scores of individual participants in the study across the moon cycle. Dots indicate the duration of sleep on each night in the cycle, and colored lines represent the best fit to an equation involving a sine curve with a 30-day period and a second sine curve with a 15-day period through a non-linear least squares approach. The number on the bottom left of each plot identifies the participant and the one on the bottom right the standard error of the regression (S). The data correspond to participants with records for at least 80% of the moon cycle. Participants are ordered from best to worst fits as evaluated by S: minimum = 0.25, median = 0.49, maximum = 0.95. F = full moon, N = new moon.

Table S1. *Composition of study communities*

Group	n	Females (%)	Age mean (range)	Year(s)
Rural, no light	25	15 (60%)	23.2 (12 – 51)	2016
Rural, limited light	33	17 (50%)	22.7 (12 – 57)	2016, 2018
Urban	40	23 (58%)	25.8 (12 – 75)	2017, 2018
UW students	464	290 (62%)	21.5 (18.2 – 37.8)	2015-2018

Note: n: number of participants

Table S2. *Fixed-effect terms included in the best-fitting model comparing sleep duration and onset of sleep between communities.*

Magnitude	Fixed effect	Estimate	95% CI		Std. error	df	p-value	Estimate	95% CI	
Duration (min)	(Intercept)	516.13	498.55	533.74	9.14	81.42	< 2e-16	-	-	-
	Group-- (Ru-LL)	22.14	8.18	36.08	7.25	79.81	0.00308	0.683	0.253	1.114
	Group-- (Ru-NL)	34.21	20.14	48.27	7.31	75.86	1.24E-05	1.074	0.632	1.515
	Sex (Male)	6.06	-5.69	17.79	6.10	78.78	0.32425	0.224	-0.210	0.657
	Age	-1.95	-2.52	-1.39	0.29	88.20	2.67E-09	-1.411	-1.821	-1.001
Onset (min from dusk)	(Intercept)	132.11	109.81	154.37	11.58	80.78	<2e-16	-	-	-
	Group -- (Ru-LL)--	-11.28	-29.01	6.45	9.22	80.23	0.2246	-0.273	-0.703	0.156
	Group -- (Ru-NL)--	-21.83	-39.87	-3.78	9.38	78.60	0.0226	-0.525	-0.959	-0.091
	Sex (Male)	15.00	0.04	29.96	7.78	79.72	0.0573	0.432	0.001	0.863
	Age	0.72	0.01	1.43	0.37	83.27	0.0538	0.429	0.007	0.851

Note: These models were fit from data from all participants with records: Ru-NL, 25; Ru-LL, 29; Ur, 33

Table S3. *Descriptive statistics of sleep variables according to the No Moonlight (No-ML) and the Full Moonlight (F-ML) phases.*

Group	n	Phase	Duration (mins)			Onset (mins from dusk)			Offset (mins from dawn)		
			Mean	SD	95%CI	Mean	SD	95%CI	Mean	SD	95%CI
Rural, no light	25	F-ML	488	38	472 – 503	153	48	133 – 172	85	46	66 – 104
		No-ML	513	35	499 – 527	129	34	115 – 142	80	41	63 – 97
Rural, limited light	25	F-ML	483	30	471 – 495	157	36	142 – 172	116	49	95 – 136
		No-ML	504	38	488 – 520	138	33	124 – 152	119	49	99 – 140
Urban	32	F-ML	461	47	444 – 478	164	46	147 – 181	112	57	91 – 132
		No-ML	472	46	455 – 489	154	45	138 – 170	114	52	95 – 133

Note: The table contains data from the 82 participants who presented records for at least four nights in each moonlight phase. n: number of participants.

Table S4. Fixed-effect terms included in the best-fitting model comparing sleep variables between the No Moonlight (No-ML) and the Full Moonlight (F-ML) phases.

Magnitude	Fixed effect	Fixed effects					Effect size (Cohen's d)			
		Estimate	95% CI		Std. error	df	p-value	Estimate	95% CI	
Duration (min)	(Intercept)	537.22	518.53	555.91	9.54	91.39	< 2e-16	-	-	-
	ML-Phase(No-ML)	25.09	13.40	36.77	5.96	2110.26	2.67E-05	0.183	0.098	0.269
	Group(Ru-LL)	-7.56	-25.08	9.95	8.94	112.21	0.3991	-0.160	-0.530	0.210
	Group(Urban)	-18.03	-34.62	-1.44	8.46	110.30	0.0353	-0.406	-0.779	-0.033
	Sex (Male)	1.43	-11.16	14.02	6.43	72.49	0.8243	0.052	-0.408	0.513
	Age	-2.17	-2.77	-1.57	0.31	82.12	4.74E-10	-1.560	-1.992	-1.127
	ML-Phase(No-ML):Group(Ru-LL)	-5.92	-23.09	11.24	8.76	2131.05	0.4991	-0.029	-0.114	0.056
	ML-Phase(No-ML):Group(Urban)	-14.59	-30.31	1.13	8.02	2119.01	0.0691	-0.079	-0.164	0.006
Onset (min from dusk)	(Intercept)	123.22	99.96	146.49	11.87	80.76	< 2e-16	-	-	-
	ML-Phase(No-ML)	-21.66	-30.32	-13.01	4.42	2107.55	1.01E-06	-0.214	-0.299	-0.128
	Group(Ru-LL)	7.79	-13.32	28.90	10.77	86.91	0.4716	0.155	-0.265	0.576
	Group(Urban)	10.68	-9.38	30.73	10.23	86.12	0.2998	0.225	-0.198	0.647
	Sex (Male)	16.28	-0.02	32.58	8.32	74.34	0.0541	0.454	-0.001	0.909
	Age	0.92	0.16	1.68	0.39	77.97	2.04E-02	0.536	0.092	0.980
	ML-Phase(No-ML):Group(Ru-LL)	0.08	-12.67	12.82	6.50	2115.44	0.9904	0.001	-0.085	0.086
	ML-Phase(No-ML):Group(Urban)	12.28	0.62	23.94	5.95	2110.88	0.0391	0.090	0.005	0.175
Offset (min from dawn)	(Intercept)	118.91	91.74	146.08	13.86	81.59	5.17E-13	-	-	-
	ML-Phase(No-ML)	-3.02	-11.85	5.82	4.51	2109.27	0.5039	-0.029	-0.114	0.056
	Group(Ru-LL)	28.58	4.03	53.13	12.53	86.30	0.0250	0.491	0.069	0.913
	Group(Urban)	36.71	13.37	60.05	11.91	85.67	0.0028	0.666	0.243	1.090
	Sex (Male)	16.36	-2.78	35.49	9.76	76.58	0.0979	0.383	-0.065	0.831
	Age	-1.81	-2.70	-0.92	0.45	79.45	1.45E-04	-0.896	-1.336	-0.456
	ML-Phase(No-ML):Group(Ru-LL)	5.21	-7.81	18.22	6.64	2115.20	0.4332	0.034	-0.051	0.119
	ML-Phase(No-ML):Group(Urban)	4.48	-7.43	16.39	6.08	2111.78	0.4611	0.032	-0.053	0.117

Note: The models were fit with data from 82 participants who presented records for at least four nights in each moonlight phase: Ru-NL, 25; Ru-LL, 25; Ur, 32.

Table S5. Type III analysis of variance table for the LMEM models (estimates on Table S4).

Magnitude	Fixed effect	Sum Sq	df num	df den	F-value	p-value
Duration (min)	ML-Phase	175518	1	2130.67	28.41	1.09x10⁻⁷
	Group	70885	2	71.88	5.74	4.89x10⁻³
	Sex	307	1	72.49	0.05	0.824
	Age	308521	1	82.12	49.93	4.74x10⁻¹⁰
	ML-Phase:Group	20926	2	2129.61	1.69	0.184
Onset (min from dusk)	ML-Phase	161469	1	2115.34	47.62	6.80x10⁻¹²
	Group	9985	2	74.14	1.47	0.236
	Sex	12989	1	74.34	3.83	0.054
	Age	18987	1	77.97	5.60	0.020
	ML-Phase:Group	19260	2	2114.98	2.84	0.059
Offset (min from dawn)	ML-Phase	24	1	2115.13	6.7x10 ⁻³	0.934
	Group	43621	2	75.43	6.17	0.003
	Sex	9922	1	76.58	2.81	0.097
	Age	56333	1	79.45	15.94	1.45x10⁻⁴
	ML-Phase:Group	2726	2	2114.87	0.39	0.680

Note: *df den* are calculated using the Satterthwaite's method of approximation.

Table S6. Tukey contrasts for the LMEM models (estimates on Table S4) using the estimated marginal means of each group.

		Contrast F-ML - No-ML			
Magnitude	Group	Estimate	95% CI		Cohen's d
Duration (min)	Ru-NL	-25.1	-36.8	-13.4	-0.183
	Rr-LL	-19.2	-31.7	-6.6	-0.129
	Urban	-10.5	-21.0	0	-0.09
Onset (min from dusk)	Ru-NL	21.7	13.0	30.3	0.214
	Rr-LL	21.7	12.2	30.9	0.196
	Urban	9.4	1.6	17.2	0.102
Offset (min from dawn)	Ru-NL	3.0	-5.8	11.9	0.029
	Rr-LL	-2.2	-11.7	7.4	-0.020
	Urban	-1.5	-9.44	6.5	-0.016

Table S7. *Descriptive statistics of sleep offset between nights in which there is moonlight available for the last six hours before dawn (MLBD) and those without any moonlight in those six hours (No-MLBD)*

Community	Participants	Phase	Mean (min after dawn)	SD	95%CI
Rural, no light	24	No-MLBD	77	29	65 – 89
		MLBD	65	34	51 – 79
Rural, limited light	22	No-MLBD	109	40	91 – 127
		MLBD	122	43	103 - 141
Urban	27	No-MLBD	108	53	87 – 129
		MLBD	112	45	94 – 130

Note: The table contains data from 73 participants who presented records for at least four nights in each moonlight phase.

Table S8. *Fixed-effect terms included in the best-fitting model comparing times of sleep offset between nights in which there is moonlight available for the last six hours before dawn (MLBD) and those without any moonlight in those six hours (No-MLBD)*

Fixed effect	Fixed effects						Effect size (Cohen's d)		
	Estimate	95% CI		Std. error	df	p-value	Estimate	95% CI	
(Intercept)	78.83	47.72	109.93	15.87	77.15	3.99E-06	-	-	-
ML-Phase(No-ML)	11.35	-0.46	23.15	6.02	1140.53	0.0598	0.112	0.132	0.362
Group(Ru-LL)	56.06	31.78	80.35	12.39	105.91	1.59E-05	0.879	-0.393	0.156
Group(Urban)	49.42	26.80	72.05	11.54	103.77	4.15E-05	0.841	-0.589	-0.025
Sex (Male)	14.96	-2.64	32.56	8.98	67.45	0.1004	0.406	-0.303	0.380
Age	-0.81	-1.88	0.25	0.54	67.41	0.1386	-0.365	-1.242	-0.703
ML-Phase(No-ML):Group(Ru-LL)	-25.18	-42.03	-8.34	8.60	1145.46	0.0035	-0.173	-0.159	0.077
ML-Phase(No-ML):Group(Urban)	-16.08	-31.82	-0.35	8.03	1144.77	0.0454	-0.118	-0.223	0.008

Note: The model was fit with data from 73 participants who presented records for at least four nights in each moonlight phase: Ru-NL, 24; Ru-LL, 22; Ur, 27.

Table S9. Parameters from fits of each community's absolute data to a single sine-wave with a 30-day period. Equation: $y = A_{30} * \sin[(2\pi/30) * (x-P_{30})] + M$

Variable	Community	Parameter	Estimate	95% CI
Duration (minutes)	Ru-NL	A_{30}	8.8	4.9-12.8
		P_{30}	5.9	3.7-8.2
		M	505	502-507
	Ru-LL	A_{30}	7.5	4.0-11.1
		P_{30}	5.5	3.1-7.9
		M	494	492-497
	Ur	A_{30}	9.4	4.6-14.2
		P_{30}	0.7	-1.7-3.2
		M	467	463-470
Onset (minutes from dusk)	Ru-NL	A_{30}	10.0	6.2-13.7
		P_{30}	18.7	16.9-20.5
		M	127	124-129
	Ru-LL	A_{30}	12.1	9.1-15.1
		P_{30}	22.4	21.2-22.6
		M	137	135-139
	Ur	A_{30}	6.4	2.6-10.3
		P_{30}	17.1	14.1-20.2
		M	155	152-157

Table S10. Parameters from fits of each community's absolute data to two sine waves with 30- and 15-day periods. Equation: $y = A_{30} * \sin[(2\pi/30) * (x-P_{30})] + A_{15} * [(2\pi/15) * (x-P_{15})] + M$

Variable	Community	Parameter	Estimate	95% CI
Duration (minutes)	Ru-NL	A_{30}	8.9	5.0-12.8
		A_{15}	14.2	10.2-18.2
		P_{30}	5.9	3.7-8.1
		P_{15}	0	(-0.8)-0.5
		M	504	501-507
	Ru-LL	A_{30}	7.7	4.2-11.2
		A_{15}	2.6*	(-0.9)-6.1*
		P_{30}	5.5	3.3-7.8
		P_{15}	11.2	7.9-14.6
		M	494	491-496
	Ur	A_{30}	9.4	4.6-14.2
		A_{15}	3.9*	(-0.9)-8.6*
		P_{30}	0.8	(-1.5)-3.1
		P_{15}	8.3	5.6-11.2
		M	467	463-470
Onset (minutes from dusk)	Ru-NL	A_{30}	9.9	6.2-13.6
		A_{15}	8.4	4.6-12.1
		P_{30}	18.6	16.9-20.4
		P_{15}	7.9	6.9-8.9
		M	127	124-129
	Ru-LL	A_{30}	12.0	9.0-15.0
		A_{15}	4.6	1.6-7.8
		P_{30}	22.4	21.2-23.6
		P_{15}	8.2	6.7-9.8
		M	136.7	134-139
	Ur	A_{30}	6.5	2.6-10.3
		A_{15}	3.9*	(-0.8)-7.0*
		P_{30}	17.2	14.3-19.9
		P_{15}	7.5	4.6-10.4
		M	155	152-157

Note: * indicates amplitude parameters which confidence intervals include the zero value, suggesting that the corresponding 15-day sine component is negligible.

Supplementary Text

Statistical model definitions and diagnostics

Linear-Mixed Effects Models used to analyze sleep variables between groups and/or moonlight phases. The *lmer* function belongs to the *lme4* R package (30).

1) Comparing sleep duration and onset between communities

Syntax example:

```
Model <- lmer(Variable ~ Group + Sex + Age + (1|ID), data = dataframe)
```

Fig. S10

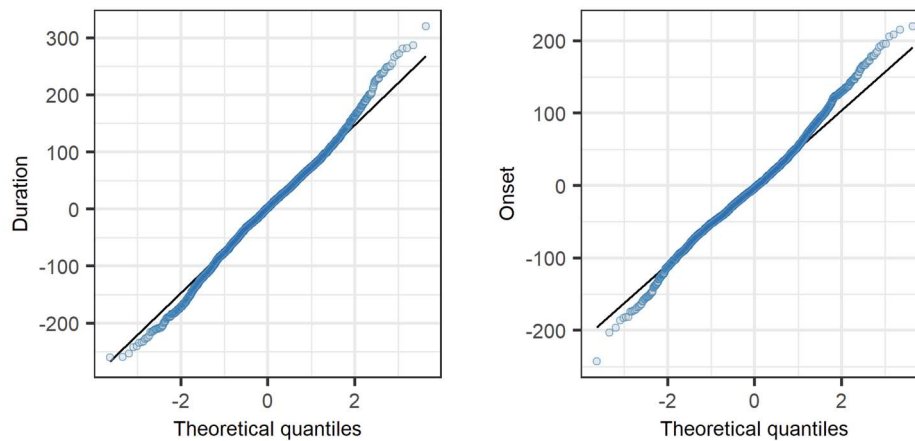


Figure S10. qq plots for the LMEMs presented in Table S2:

2) Comparing sleep variables between the Full Moonlight and No Moonlight phases

Syntax example:

```
Model <- lmer(Variable ~ Moonlight_phase * Group + Sex + Age + (1|ID), data = dataframe)
```

Fig. S11

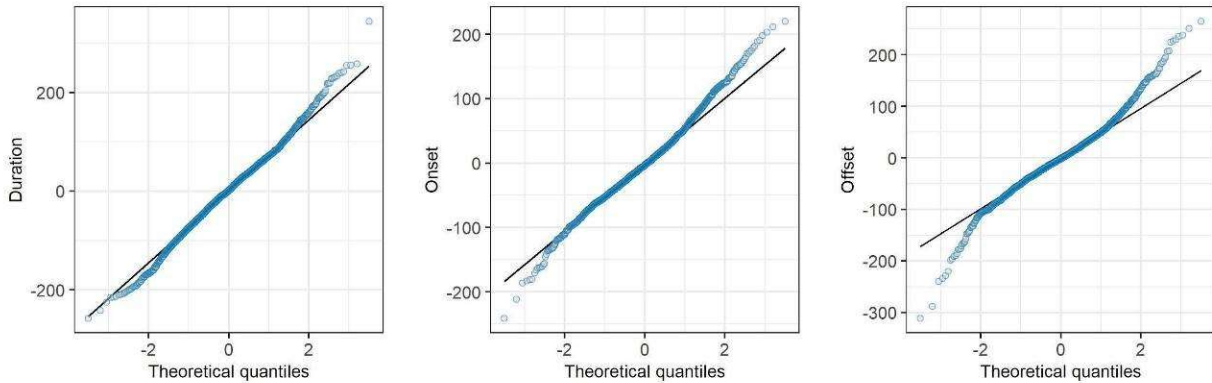


Figure S11. qq plots for the six LMEMs presented in full in Table S4.

3) Comparing sleep offset between the nights in which there is moonlight available for the last six hours before dawn (MLBD) and those without any moonlight in those six hours (No-MLBD)

Syntax example:

```
Model <- lmer(Offset ~ Moonlight_phase * Group + Sex + Age + (1|ID), data = dataframe)
```

Fig. S12

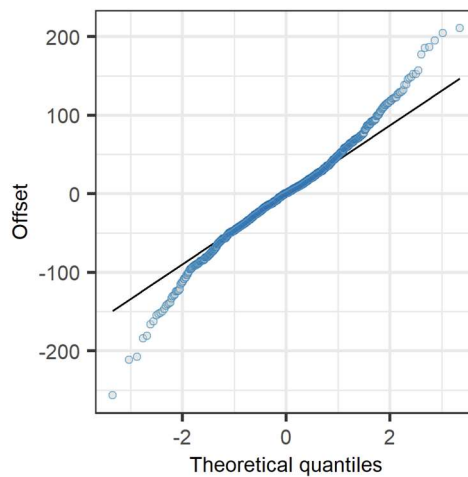


Figure S12. qq plot for the LMEM presented in Table S6.

Comparison of communities' phases from individually fitted data

1) Sleep duration through phases

Mean in days to (negative values) or from (positive values) the full moon [fiducial limits]:

Rural, no light community: -1.5 [-3.4 / 0.4]

Rural, limited light: -3.1 [-5.8 / -0.4]

Urban: -6.6 [-8.5 / -4.7]

Watson-Wheeler Test for Homogeneity of phases between groups (from *circular* package in R):

$W = 6.5348$, $df = 4$, $p = 0.1626$

2) Sleep onset peak phases

Mean in days to (negative values) or from (positive values) the full moon [fiducial limits]:

Rural, no light community: -4.9 [-7.2 / -2.7]

Rural, limited light: -1.0 [-2.8 / 0.4]

Urban: -4.1 [-5.6 / -2.7]

Watson-Wheeler Test for Homogeneity of phases between groups:

$W = 9.1582$, $df = 4$, $p = 0.0573$