Report

Current Biology

Circadian Entrainment to the Natural Light-Dark Cycle across Seasons and the Weekend

Highlights

- Living in the modern electrical lighting environment delays the human circadian clock
- The human circadian clock adapts to seasonal changes in the natural light-dark cycle
- A weekend camping trip prevented the typical weekend circadian and sleep delay

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In Brief

Late sleep timing is associated with health problems. Stothard et al. show that the human circadian clock is timed later in modern society, especially after the weekend, compared to natural light-dark cycles. Further, the clock responds to seasonal natural light-dark cycle changes and is rapidly shifted earlier by weekend camping.

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Report

Circadian Entrainment to the Natural Light-Dark Cycle across Seasons and the Weekend

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SUMMARY

Reduced exposure to daytime sunlight and increased exposure to electrical lighting at night leads to late circadian and sleep timing [1–3]. We have previously shown that exposure to a natural summer 14 hr 40 min:9 hr 20 min light-dark cycle entrains the human circadian clock to solar time, such that the internal biological night begins near sunset and ends near sunrise [1]. Here we show that the beginning of the biological night and sleep occur earlier after a week's exposure to a natural winter 9 hr 20 min:14 hr 40 min light-dark cycle as compared to the modern electrical lighting environment. Further, we find that the human circadian clock is sensitive to seasonal changes in the natural light-dark cycle, showing an expansion of the biological night in winter compared to summer, akin to that seen in non-humans [4–8]. We also show that circadian and sleep timing occur earlier after spending a weekend camping in a summer 14 hr 39 min:9 hr 21 min natural light-dark cycle compared to a typical weekend in the modern environment. Weekend exposure to natural light was sufficient to achieve ~69% of the shift in circadian timing we previously reported after a week's exposure to natural light [1]. These findings provide evidence that the human circadian clock adapts to seasonal changes in the natural light-dark cycle and is timed later in the modern environment in both winter and summer. Further, we demonstrate that earlier circadian timing can be rapidly achieved through natural light exposure during a weekend spent camping.

RESULTS AND DISCUSSION

Late circadian and sleep timing are associated with negative cognitive performance and health outcomes such as daytime sleepiness, reduced driving and school performance [9, 10], substance abuse [11], mood disorders [12, 13], diabetes [14], and obesity [15, 16]. Contributing factors to late sleep timing include the period and phase of the circadian clock [17, 18], exposure to light at night [1, 19], circadian rhythm sleep-wake disorders [20], stimulant intake [21, 22], and work/school week versus weekend social schedules [23, 24]. As noted, we have shown that later circadian and sleep timing occur after exposure to the modern electrical lighting environment compared to the natural summer light-dark cycle [1].Thereafter, others have reported later circadian and/or sleep timing in Brazilian rubber tappers [2] and in hunter-gatherers from the indigenous Toba/Qom in the Argentinean Chaco with access to electrical lighting compared to those from the same communities without access to electrical lighting [3]. Beyond the studies noted above, little is known about the impact of exposure to the combination of electrical and natural lighting in our modern world, henceforth referred to as modern electrical lighting, in comparison with exposure to only the natural light-dark cycle on the human circadian clock and sleep. Some unexplored questions include how the human circadian clock responds to seasonal changes in the natural light-dark cycle in the absence of electrical lighting, as well as how quickly the timing of the clock changes in response to the natural summer light-dark cycle. To begin to address these questions, we conducted two studies: the first aimed to quantify the impact of a week-long exposure to the natural winter light-dark cycle compared to exposure to modern electrical lighting on the timing of the human circadian clock; the second aimed to quantify the circadian response to a weekend of exposure to the natural summer light-dark cycle.

Study 1: Winter Week-Long Camping

Five physically active individuals (four males, one female) aged 30.4 ± 8.6 years (mean ± SD) participated in a 2-week-long protocol (Figure S1A) near the winter solstice during December in Colorado, USA, between latitudes ~40°N and ~41°N and longitudes ~105.0°W and ~105.5°W. The melatonin rhythm—the most precise marker of internal biological time—was first assessed in the laboratory after ~6 days of participants maintaining habitual, self-selected sleep times in their modern electrical lighting environment. Participants then went backcountry camping together for ~6 days in the Rocky Mountains of Colorado,

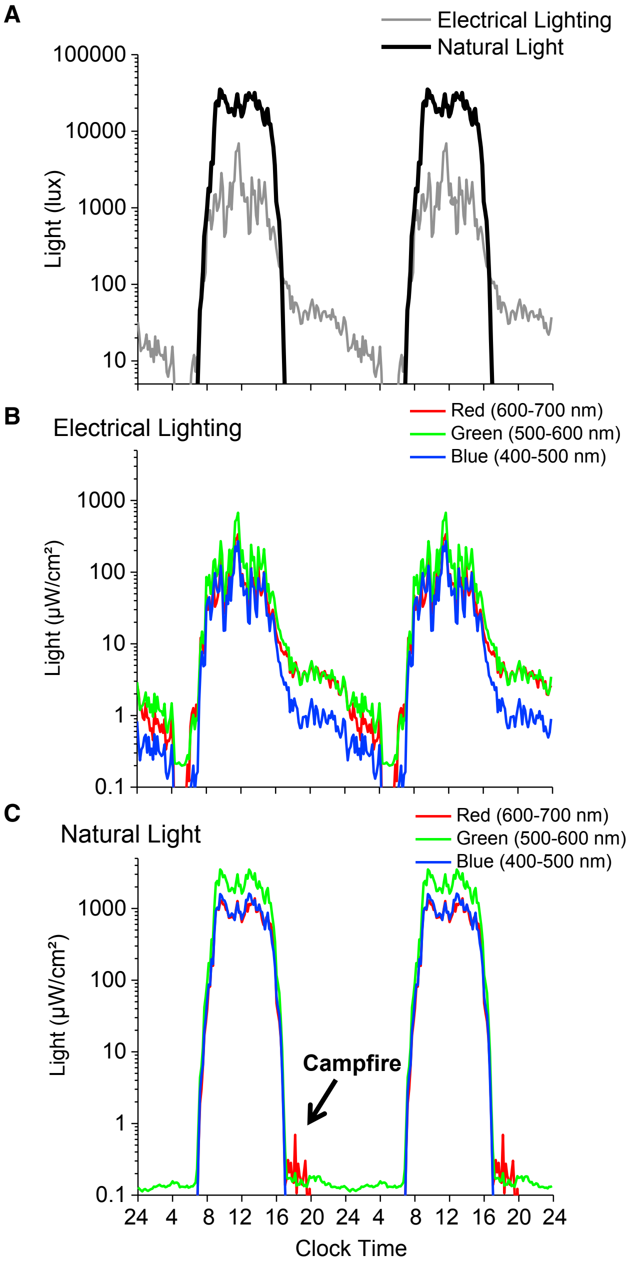

Figure 1. Winter Light Exposure

Average white light exposure and light of different wavelengths during the week of exposure to (A and B) electrical and natural lighting in the modern environment and exposure to (A and C) only natural light during the week spent camping. Exposure to longer-wavelength red light of campfires can be seen in (C). Data are represented as mean on a log scale and are double plotted so light levels can be seen across midnight (24 hr local time). See also Figure S1A and Table S1.

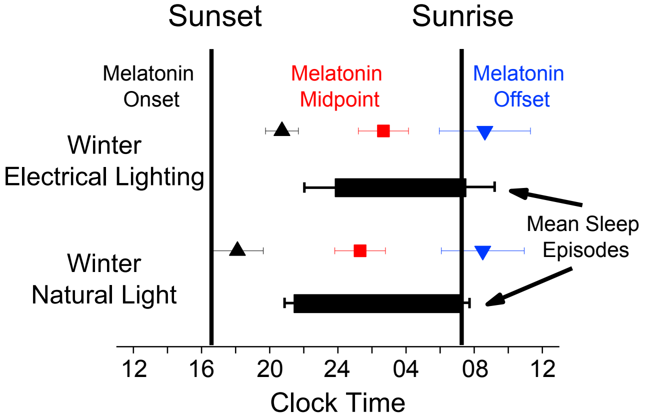

Figure 2. Winter Circadian and Sleep Timing

Average timing of melatonin onset (black upward triangles), midpoint (red squares), and offset (blue downward triangles) following 1 week exposure to electrical and natural lighting in the modern environment versus following 1 week exposure to only natural light while camping. Average sunrise and sunset times for the ~2-week study are denoted by vertical black lines. Average sleep start and end times are indicated by the black bar for each week. Clock time denotes local time. Data are represented as mean ± SD. See also Figures S1–S3.

slept in tents at self-selected times, and were exposed to only natural light (i.e., sunlight, moonlight, and campfires; no flashlights, no personal electronic devices, etc.) as in our prior research [1]. Immediately after camping, participants returned to the laboratory for a 24 hr melatonin rhythm reassessment. The onset and offset of the melatonin rhythm was used to define the beginning and end of the internal biological night, respectively [1, 25].

During waking hours, participants were exposed to illuminance levels greater than 13 times higher while winter camping (10,297 ± 2,700 lux) compared to the modern electrical lighting environment (752 ± 424 lux; $p < 0.001$, Figure 1A). Additionally, time spent exposed to illuminance levels greater than 100, 550, and 1,000 lux during the waking day was higher in the natural compared to electrical lighting environment (Table S1). Further, exposure to red, green, and blue light levels was significantly higher during the waking day in the natural compared to the modern electrical lighting environment (Figures 1B and 1C; Table S1).

Sleep start time occurred ~2.5 hr earlier while camping than in the modern electrical lighting environment ($p < 0.05$), whereas wake time was similar in both environments ($p = 0.76$) (Figure 2). As a result, average sleep duration was ~2.3 hr longer during winter camping (9.9 ± 0.4 hr) compared to the modern electrical lighting environment (7.6 ± 0.5 hr; $p < 0.01$). Sleep efficiency, as estimated by wrist actigraphy (Supplemental Information), showed a non-significant trend to be lower during camping (89.4% ± 3.2%) compared to the modern electrical lighting environment (91.9% ± 1.7%; $p = 0.064$). Subjects had on average longer-duration awakenings when camping (2.3 ± 0.3 min camping versus 1.5 ± 0.2 min modern electrical lighting environment versus $p < 0.005$). Sleep duration increased across days while camping (data not shown), and thus the longer sleep duration did not likely reflect recovery from sleep debt that accumulated in the modern electrical lighting environment, as a decrease across days while camping would be expected. A likely contributing factor to the longer sleep duration during winter camping, in contrast to prior findings during summer camping [1], is that participants spent more time in the warmth of the tent and sleeping bag due to the cold ambient temperatures (Figure S2).

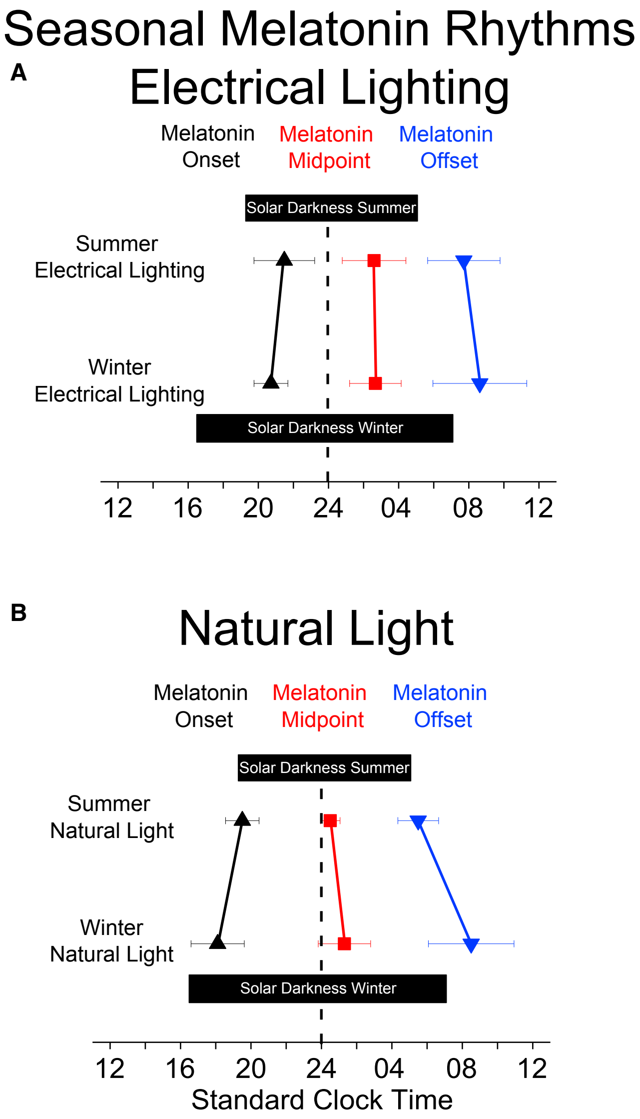

Figure 3. Melatonin Circadian Phase during Summer and Winter Relative to Solar Darkness

Average timing of melatonin onset (black upward triangles), midpoint (red squares), and offset (blue downward triangles) following ∼1 week exposure to electrical and natural lighting in the modern environment or only natural light after camping during summer versus winter. The summer data shown are from our previous study [1]. Clock time denotes standard time. Timing of solar darkness (scotophase) is represented by black bars. Data are represented as mean ± SD.

Participants also showed increased daytime activity levels during the week of natural light exposure while camping (Figure S3), which could have contributed to the longer sleep duration [26]. Changes in ambient temperature and activity levels are unlikely to have had a large impact on circadian timing in our study [27–29] (Figures S2 and S3).

Figure 2 shows that, on average, melatonin onset occurred prior to sleep onset, melatonin midpoint occurred in the first half of the sleep episode, and melatonin offset occurred after the end of the sleep episode and sunrise, regardless of condition. After exposure to the winter natural light-dark cycle, average melatonin onset occurred ∼2.6 hr earlier compared to the modern electrical lighting environment ($p < 0.01667$, one-tailed Bonferroni correction; Figure 2), similar to [1], with a large effect size for condition ($\eta^2_G = 0.57$). No significant changes in melatonin midpoint ($p = 0.085$, one-tailed Bonferroni correction) or offset ($p = 0.57$, one-tailed Bonferroni correction) were observed. The duration between melatonin onset and sleep start time ($p = 0.83$), as well as between melatonin offset and wake time ($p = 0.97$), were similar across conditions (Figure 2).

Seasonal Responses

The circadian system of many species is responsive to seasonal changes in the natural light-dark cycle. For example, hamsters and sheep show a longer duration of high melatonin levels in winter than in summer, which in turn influences seasonal changes in reproductive status, coat color, and/or weight gain [4–6]. Such changes appear to be mediated by photoperiodic changes in the suprachiasmatic nuclei [30, 31] that control the circadian melatonin rhythm and by responses in peripheral tissues [5]. Therefore, we compared the circadian melatonin rhythm following exposure to the natural winter light-dark cycle in study 1 to our previously published data following exposure to the natural summer light-dark cycle [1] (Figure 3). Melatonin rhythms were also compared following exposure to the modern electrical lighting environment during winter study 1 and summer [1]. Melatonin onset ($p = 0.35$), midpoint ($p = 0.93$), offset ($p = 0.46$), and duration ($p = 0.15$) were similar after exposure to the modern electrical lighting environment in both seasons (Figure 3). Exposure to a natural winter light-dark cycle resulted in a non-significant trend for melatonin onset to be timed earlier ($p = 0.059$) and for melatonin offset to be significantly later ($p < 0.05$) compared to exposure to a natural summer light-dark cycle. Melatonin midpoint ($p = 0.12$) was relatively similar across seasons. There was thus a longer duration of the internal biological night after exposure to the natural winter versus natural summer light-dark cycle (14.4 ± 2.8 hr versus 10.0 ± 1.8 hr, $p < 0.025$, one-tailed Bonferroni correction), with a large effect size for season ($\eta^2_G = 0.53$). Our findings are consistent with those from classic studies by Wehr et al. that scheduled participants to 16 hr:8 hr and to 10 hr:14 hr combined electrical and natural light-dark cycles [25, 32]; however, participants in studies by Wehr et al. slept in the lab and were permitted to leave for work during the daytime. Specifically, Wehr et al. found that after 1 month of a 14 hr compared to an 8 hr sleep opportunity (6 hr difference in length of darkness), melatonin duration was expanded by ∼2.2 hr. Our findings of >4 hr expansion in melatonin duration after 6 days of an approximately 5.33 hr difference in solar darkness suggests a substantial seasonal circadian response to the natural light-dark cycle. Illnerova and colleagues reported no change in melatonin duration between seasons in the modern electrical lighting environment but reported that melatonin onset was delayed in the winter by 1.5 hr when assessed under electrical lighting plus sunlight conditions in the laboratory [33], inconsistent with our findings. Exposure to dissimilar sunlight and electrical lighting conditions across seasons when assessing the melatonin rhythm is a limitation of [33] and of other studies in which the

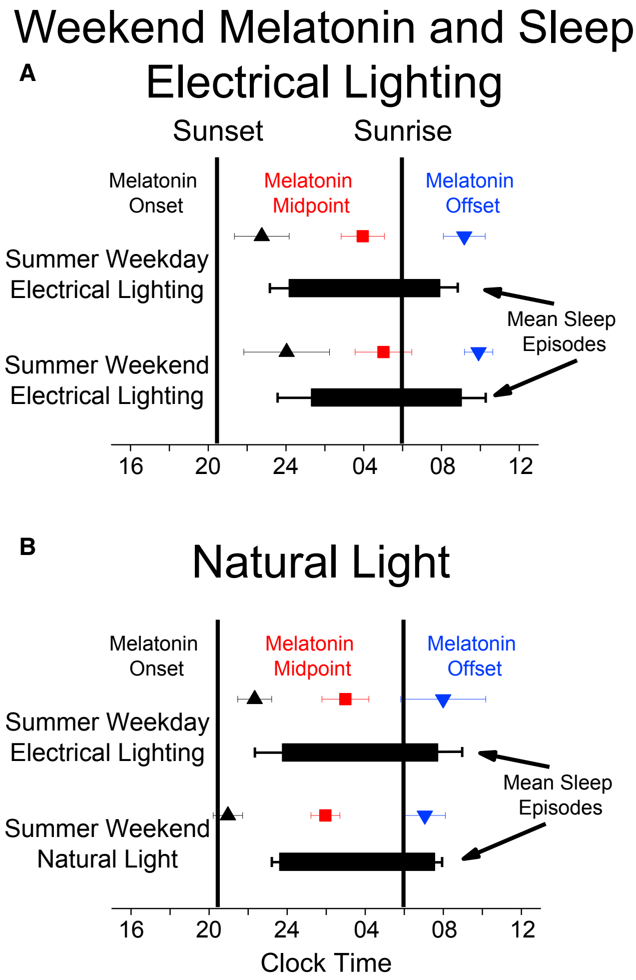

Figure 4. Summer Circadian and Sleep Timing: Weekend

Average timing of melatonin onset (black upward triangles), midpoint (red squares), and offset (blue downward triangles) after 2 weekdays exposure to electrical and natural lighting in the modern environment and following 2 weekend days exposure to electrical and natural light in the modern environment or 2 weekend days exposure to natural light while camping. Average sunrise and sunset times for the study are denoted by vertical black lines. Average sleep start and end times are indicated by the black bar for each weekday and weekend part of the study. Clock time denotes local time. Data are represented as mean ± SD. See also Figures S1–S4 and Table S2.

melatonin peak [34] or melatonin offset [35] times were reported to be earlier in summer versus winter.

Study 2: Summer Weekend Camping

Fourteen physically active individuals (seven female) aged 28.4 ± 8.8 years (mean ± SD) completed a 7-day protocol (Figures S1B and S1C) during July in Colorado, USA, at latitude ∼40°N and longitude between 105°W and 106°W. The melatonin rhythm was first assessed in the laboratory after 2 days of maintaining habitual self-selected sleep times in the modern electrical lighting environment. Afterward, participants spent the weekend either in the modern environment (weekend electrical lighting group, $n = 5$) or in the natural environment backcountry camping in the Rocky Mountains of Colorado, USA, and slept in tents (weekend natural light group, $n = 9$; self-selected). Unlike in our prior study [1] and in study 1 above, participants in the weekend natural light group were permitted to use flashlights or headlamps.

Participants in the weekend camping group were exposed to illuminance levels that were more than four times higher during waking hours while weekend camping (9,181 ± 2,229 lux) than while in the modern electrical lighting environment before camping (2,070 ± 1,120 lux; $p < 0.0001$; Figure S4). This >4-fold increase in light exposure during weekend summer camping is similar to that previously reported [1] but smaller than the >13-fold increase seen during winter camping in study 1. The latter appears to be largely driven by less light exposure in the modern electrical lighting environment during winter versus summer (study 1 versus study 2; $p < 0.05$), consistent with [36, 37], and not by a difference in light exposure during the natural winter and weekend summer light-dark cycle (study 1 versus study 2; $p = 0.36$). Additionally, time spent exposed to illuminance levels above 50, 100, 550, and 1,000 lux and average exposures to red, green, and blue wavelengths of light during the waking day were significantly higher during natural light exposure in the weekend camping group than while in the modern electrical lighting environment before camping and compared to the weekend modern electrical lighting group (Figure S4; Table S2).

Figure 4 shows that sleep start and end times were similar between weekdays and weekends in the weekend camping group ($p = 0.76$ and $p = 0.63$, respectively), but sleep start and end times were both delayed by ∼1.1 hr on the weekend compared to weekdays in the modern electrical lighting group ($p < 0.05$). This resulted in sleep start time being delayed by ∼1.8 hr and sleep end time being delayed by ∼1.5 hr during the weekend in the electrical lighting versus camping group ($p < 0.05$). Total 24 hr sleep duration and nighttime sleep efficiency were similar within groups and between conditions on both weekdays and weekends (Figure S3). Activity levels were higher during weekend camping versus weekdays and compared to those who spent the weekend in the modern environment; activity levels were similar during weekdays and the weekend for those living in the modern electrical lighting environment (Figure S3).

Figure 4 shows that, on average, melatonin onset occurred prior to sleep onset, melatonin midpoint occurred in the first half of the sleep episode, and melatonin offset occurred after sunrise, regardless of condition or group. After exposure to the natural light-dark cycle while weekend camping, melatonin onset and midpoint were ∼1.4 hr and ∼1.0 hr earlier within the same participants compared to the weekday ($p < 0.01$; with large and medium effect sizes for condition [$\eta^2_G = 0.45$ and 0.20, respectively]), despite no change in sleep timing. Further, after exposure to the natural light-dark cycle, the change in the timing of the melatonin offset was not significant ($p = 0.11$), although average melatonin offset occurred during sleep rather than after (Figure 4), supporting previous findings [1]. We also observed significant differences between groups for the change in circadian timing after the weekend (melatonin onset moved 1.4 hr earlier in weekend natural light versus 0.98 hr later in the weekend modern electrical lighting environment, $p < 0.01$; midpoint 1.0 hr earlier versus 1.0 hr later, $p < 0.01$; offset 0.94 hr earlier versus 0.77 hr later, $p < 0.05$, respectively; with large effect sizes for group [$\eta^2_G = 0.60$, 0.78, and 0.45, respectively]). Later circadian timing in the modern electrical lighting environment on Monday morning may be associated with staying up later on the weekend (e.g., due to social factors). Additionally, a later bedtime may increase the opportunity for exposure to light at night, when light delays the timing of the circadian clock. Access to electrical lighting and electronic devices is also permissive for work and social activities to be extended beyond sunset and late into the night. Further, a later wake time on the weekend may decrease the opportunity for exposure to morning sunlight, when light typically advances the timing of the circadian clock earlier. In the natural world, there is no bright light exposure after sunset that would delay the circadian clock later. However, throughout evolution, humans have constructed environments that provide shielding from the natural environment, and one could hypothesize that sleeping in late could decrease the opportunity for exposure to morning sunlight and thus delay the timing of the circadian clock.

In summary, our findings demonstrate that the human melatonin rhythm adapts to short summer and long winter nights when living in a natural light-dark cycle—something that has been assumed but never demonstrated with respect to the "natural light-dark cycle." We further show that living in the modern electrical lighting environment reduces seasonal circadian responsiveness by delaying the beginning of the biological night in both winter and summer [1]. It has been argued that humans live in a constant summer photoperiod (i.e., duration of light exposure) in the modern electrical environment [38], and this appears to be true for the duration of biological night but not for circadian timing. Our finding of later circadian timing in the modern environment across seasonal extremes at the latitude studied indicates that modern lighting environmental conditions do not entirely replicate living in the natural summer photoperiod. Relatedly, we observed that the timing of the middle of the biological night, but not the middle of the sleep episode, occurs close to the timing of the middle of solar darkness when living in natural winter and summer light-dark cycles, but less so when living in the modern environment (Figure 4). Our findings also show that a weekend of camping prevents the typical weekend circadian and sleep delay [23], which is an important contributor to the phenomenon of social jet lag. Specifically, the weekend phase delay in the modern electrical lighting environment contributes to social jet lag on Monday morning because there is a mismatch between biological (circadian delay) and social (awakening early for work/school) timing, the definition of social jet lag [39]. This suggests that weekend exposure to the natural light-dark cycle may help with social jet lag [16], and also with initiating treatment for winter depression [40] and circadian rhythm sleep-wake disorders (e.g., delayed sleep-wake phase) that show late sleep and/or circadian timing; additional research is needed in such populations. The current studies were conducted on a relatively small number of healthy, physically active individuals; therefore, additional studies are needed with a greater number of participants at different latitudes and of different cultures to increase our understanding of how geographical location, activity, prior light history, and other variables may impact human circadian physiology in response to the natural light-dark cycle. Because we did not randomize subjects to group in study 2, or to condition order in either study, randomized, crossover studies are needed for replication and to assess how long it takes for the effects of the natural light environment on the timing of the circadian clock to be reversed by the modern electrical lighting environment. Further, additional research is also needed to determine how quickly the human circadian clock adapts to natural winter light-dark cycles and to seasonal changes further away from the equator, as well as the potential consequences of seasonal circadian responses for humans. Lastly, studies are needed to test potential health benefits of increased exposure to natural light through effects on the circadian timekeeping system.

EXPERIMENTAL PROCEDURES

Participants provided written informed consent. Activity, sleep, and light exposure data were continuously gathered at the wrist (Actiwatch Spectrum, Philips) by accelerometer and photodiode providing information about sleep timing, sleep efficiency, and white and colored light exposure. Salivary melatonin levels were assessed hourly under controlled laboratory conditions to determine 24 hr circadian timing following each condition. Melatonin onset and offset were defined as the linear interpolated point in time at which melatonin levels reached 25% of the fitted peak-to-trough amplitude of individual data, as determined by a three-harmonics least-squares regression analysis (Supplemental Experimental Procedures). Data are presented as mean ± SD.

Ethics Committee Approval

The University of Colorado Bolder Institutional Review Board approved study procedures.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, four figures, and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.12.041.

AUTHOR CONTRIBUTIONS

Conceptualization, E.R.S., A.W.M., and K.P.W.; Methodology, E.R.S., A.W.M., C.M.D., and K.P.W.; Investigation, E.R.S., A.W.M., C.M.D., B.R.B., T.M.M., H.K.R., J.R.G., E.D.C., J.A., M.K.L., and K.P.W.; Writing – Original Draft, E.R.S., A.W.M., and K.P.W.; Writing – Review & Editing, C.M.D., B.R.B., T.M.M., H.K.R., J.R.G., E.D.C., J.A., and M.K.L.; Funding Acquisition, K.P.W.; Resources, M.K.L. and K.P.W.; Supervision, K.P.W.

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