

to a greater number of signals and stresses.

#### SUPPLEMENTAL INFORMATION

Supplemental Information includes Experimental Procedures, one figure and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.02.058>.

#### ACKNOWLEDGEMENTS

We thank Nan Hao for insightful discussions. The Howard Hughes Medical Institute supported this work.

#### REFERENCES

- Behar, M., and Hoffmann, A. (2010). Understanding the temporal codes of intracellular signals. *Curr. Opin. Genet. Dev.* 20, 684–693.
- Purvis, J.E., and Lahav, G. (2013). Encoding and decoding cellular information through signaling dynamics. *Cell* 152, 945–956.
- Hao, N., and O’Shea, E.K. (2012). Signal-dependent dynamics of transcription factor translocation controls gene expression. *Nat. Struct. Mol. Biol.* 19, 31–39.
- Hansen, A.S., and O’Shea, E.K. (2013). Promoter decoding of transcription factor dynamics involves a trade-off between noise and control of gene expression. *Mol. Syst. Biol.* 9, 704.
- Hansen, A.S., and O’Shea, E.K. (2015). *cis* determinants of promoter threshold and activation timescale. *Cell Rep.* 12, 1226–1233.
- Hansen, A.S., Hao, N., and O’Shea, E.K. (2015). High-throughput microfluidics to control and measure signaling dynamics in single yeast cells. *Nat. Protoc.* 10, 1181–1197.
- Dalal, C.K., Cai, L., Lin, Y.H., Rahbar, K., and Elowitz, M.B. (2014). Pulsatile dynamics in the yeast proteome. *Curr. Biol.* 24, 2189–2194.
- Batchelor, E., Loewer, A., Mock, C., and Lahav, G. (2011). Stimulus-dependent dynamics of p53 in single cells. *Mol. Syst. Biol.* 7, 488.
- Purvis, J.E., Karhohs, K.W., Mock, C., Batchelor, E., Loewer, A., and Lahav, G. (2012). p53 dynamics control cell fate. *Science* 336, 1440–1444.
- Imayoshi, I., Isomura, A., Harima, Y., Kawaguchi, K., Kori, H., Miyachi, H., Fujiwara, T., Ishidate, F., and Kageyama, R. (2013). Oscillatory control of factors determining multipotency and fate in mouse neural progenitors. *Science* 342, 1203–1208.

<sup>1</sup>Department of Molecular Cell Biology, HHMI, Li Ka Shing Center, University of California, Berkeley, CA 94720, USA. <sup>2</sup>Department of Chemistry and Chemical Biology, Harvard University, 12 Oxford Street, Cambridge, MA 02138, USA. <sup>3</sup>Howard Hughes Medical Institute, Harvard University, Northwest Laboratory, 52 Oxford Street, Cambridge, MA 02138, USA. <sup>4</sup>Faculty of Arts and Sciences Center for Systems Biology, Harvard University, Northwest Laboratory, 52 Oxford Street, Cambridge, MA 02138, USA. <sup>5</sup>Department of Molecular and Cellular Biology, Harvard University, Northwest Laboratory, 52 Oxford Street, Cambridge, MA 02138, USA.

\*E-mail: [erin\\_oshea@harvard.edu](mailto:erin_oshea@harvard.edu)



## Correspondence

### Ancestral sleep

Horacio O. de la Iglesia<sup>1</sup>,  
Claudia Moreno<sup>2,3</sup>, Arne Lowden<sup>3</sup>,  
Fernando Louzada<sup>4</sup>,  
Elaine Marqueze<sup>2,5</sup>,  
Rosa Levandovski<sup>6</sup>, Luisa K. Pilz<sup>7,12</sup>,  
Claudia Valeggia<sup>8</sup>,  
Eduardo Fernandez-Duque<sup>8</sup>,  
Diego A. Golombek<sup>9</sup>,  
Charles A. Czeisler<sup>10</sup>,  
Debra J. Skene<sup>11</sup>, Jeanne F. Duffy<sup>10</sup>,  
and Till Roenneberg<sup>12,\*</sup>

While we do not yet understand all the functions of sleep, its critical role for normal physiology and behaviour is evident. Its amount and temporal pattern depend on species and condition. Humans sleep about a third of the day with the longest, consolidated episode during the night. The change in lifestyle from hunter-gatherers via agricultural communities to densely populated industrialized centres has certainly affected sleep, and a major concern in the medical community is the impact of insufficient sleep on health [1,2]. One of the causal mechanisms leading to insufficient sleep is altered exposure to the natural light–dark cycle. This includes the wide availability of electric light, attenuated exposure to daylight within buildings, and evening use of light-emitting devices, all of which decrease the strength of natural light–dark signals that entrain circadian systems [3].

While a change in sleep timing from pre-industrial to industrial, and from rural to urban lifestyles is generally accepted, the sleep research community has not reached consensus on whether sleep duration has changed as people moved from pre-industrial to industrial societies with indoor work in enclosed buildings and 24/7 access to electricity [3–5]. A recent study by Yetish *et al.* [6] recorded activity–rest patterns in 94 individuals from three hunter-gatherer communities living without electricity (in Tanzania, Namibia and Bolivia; near to or within 20° south of the equator). While we commend them on carrying out this difficult study, we disagree with their interpretation that “...sleep in industrial societies has not been

reduced below a level that is normal for most of our species’ evolutionary history”, and that the recorded sleep patterns in their study “... are central to the physiology of humans living in the tropical latitudes...”.

In approaching the question of how human sleep may have evolved, pre-electricity communities are of special interest, but are becoming increasingly harder to find. The effort of Yetish *et al.* to identify and study such groups is therefore important. However, to use such diverse groups (spread over two continents) for the interpretation of sleep behaviour in the context of evolution, one needs comparisons to groups of similar ethnic and sociocultural background with access to artificial light in more industrialized environments. In two recently published studies [7,8] and one ongoing one [9], the rest–activity and light exposure patterns of genetically and culturally homogeneous communities that live both in their traditional settings as well as in more modern ones were investigated. The average sleep duration of the Toba/Qom from Argentina [7], who still rely to some extent on hunting-gathering and live exposed to similar photoperiods and temperatures as the communities studied by Yetish *et al.* was longer (7.0–8.5 h) than in the latter report (5.7–7.1 h), and was significantly shortened by access to electricity (by up to one hour). Moreno *et al.* also showed that sleep (assessed by sleep diaries) is shorter with concomitant delayed melatonin onsets when Amazon rubber tappers have access to electricity [8]. These differences underline the large variability among populations and individuals (also evident from Figure 3 in Yetish *et al.* [6]).

Evidence for changes in sleep duration in modern societies is mixed [4,5]. The Munich ChronoType study, which has accumulated about 250,000 world-wide entries (using the Munich ChronoType Questionnaire, MCTQ), revealed that sleep on workdays shortened by 3.7 min/year over the past decade [2] while only that on work-free days remained the same. Overall, people sleep more than three hours less per week than ten years ago.

Yetish *et al.* reported that the standard deviation (SD) in sleep

duration was mainly due to sleep onset (SD 1.3–2.52 h) compared to sleep end (SD 0.68–0.88 h), and that there was a greater SD around sleep onset than sleep offset in all San and Tsimane individuals. They show data from three representative San individuals in [Table S4](#) to support this point. However, [Table S2](#) shows mean onset and offset clock times averaged for each recording period, and in only one of the three recording periods are the sleep onset time SDs of the San larger than their sleep offset time SDs. This makes it somewhat difficult to interpret. However, the greater synchronization of sleep offset times may be due to the individuals being awakened by the increasing light levels (this group is described as sleeping outdoors on the ground) and/or ambient sounds, similar to alarm clocks or small children in western societies [9]. We know that individuals in industrialized societies typically accumulate sleep debt under these conditions [10], and thus we cannot rule out that the individuals in the three groups studied by Yetish *et al.* may also experience insufficient sleep. Furthermore, the authors claim that the uniformity in daily sleep patterns among the three studied communities suggest that these sleep patterns “are central to the physiology of humans living in the tropical latitudes...” However, this statement has no statistical support, *i.e.*, sleep duration or any other aspects of sleep were not compared between the three communities. The fact that one can survive for a long time with restricted sleep does not mean sleep deficiency is “normal” or without consequences for health or performance. While the diseases associated with insufficient sleep in industrialized societies may not be present in the groups studied by Yetish *et al.*, there is extensive evidence that the sleep durations observed in these three pre-industrial societies results in serious health consequences for many individuals in modern industrialized societies, where the diet, daily activity, and overall lifestyle are dramatically different. We believe the authors’ conclusion that sleep duration has remained unchanged throughout human history is a strong over-interpretation.

On the contrary, sleep habits must have drastically changed through the

course of human history as the first humans migrated out of Africa into various photoperiods and climates in Europe and Asia, then into the inhospitable ice bridge of the Bering strait and later down to the South American latitudes where one of the communities studied by the authors lives. Thus, the notion that people in industrialized societies — with widely different genetic pools, concentrated mainly in the northern hemisphere, and facing radically different environmental factors and stimuli — should have similar sleep patterns or similar sleep needs as hunter gatherer communities in tropical Africa and South America is unrealistic given our knowledge of the effects of the environment on sleep patterns.

The authors also describe light exposure profiles for the three groups of hunter-gatherers, with brightest light in the morning and shade at midday, which they attribute to behavioural thermoregulation. However, neither the Toba/Qom [7], nor the Amazon rubber tappers [8], nor the Quilombolas [9] show this profile under natural daylight conditions, so it may be specific to the local environment and lifestyle of the groups studied, rather than applying to hunter-gatherers in general. It is a well-known rule that light exposure in the morning advances circadian clocks while light in the evening delays them [3]. Early awakenings are, however, not only typical for people who expose themselves predominantly to morning light, but also for people exposed to strong light throughout the day [1]. The insights by Yetish *et al.* would have benefitted from more circadian analyses.

Sleep need is determined by many factors, including biological and environmental factors, and these interact with social factors to influence sleep duration. Given the drastically different environments, lifestyles, social structures, and sleeping accommodations between and among ancient and modern humans, there is no reason to expect that sleep duration should have stayed the same throughout human history. Thus, assuming normative values for a complex trait like sleep duration will help us understand neither the evolution nor the function of sleep. We should rather strive for understanding

the variability of sleep duration, how it relates to sleep need, and the inter-individual and population- and condition-specific differences in sleep, and why it may change over time.

## REFERENCES

1. Wright, K.P., Jr., McHill, A.W., Birks, B.R., Griffin, B.R., Rusterholz, T., and Chinoy, E.D. (2013). Entrainment of the human circadian clock to the natural light–dark cycle. *Curr. Biol.* 23, 1554–1558.
2. Roenneberg, T., Allebrandt, K.V., Mewes, M., and Vetter, C. (2012). Social jetlag and obesity. *Curr. Biol.* 22, 939–943.
3. Czeisler, C.A. (2013). Perspective: casting light on sleep deficiency. *Nature* 497, S13.
4. Matricciani, L., Olds, T., and Petkov, J. (2012). In search of lost sleep: secular trends in the sleep time of school-aged children and adolescents. *Sleep Med. Rev.* 16, 203–211.
5. Bin, Y.S., Marshall, N.S., and Glozier, N. (2012). Secular trends in adult sleep duration: a systematic review. *Sleep Med. Rev.* 16, 223–230.
6. Yetish, G., Kaplan, H., Gurven, M., Wood, B., Pontzer, H., Manger, P.R., Wilson, C., McGregor, R., and Siegel, J.M. (2015). Natural sleep and its seasonal variations in three pre-industrial societies. *Curr. Biol.* 25, 2862–2868.
7. de la Iglesia, H.O., Fernandez-Duque, E., Golombek, D.A., Lanza, N., Duffy, J.F., Czeisler, C.A., and Valeggia, C.R. (2015). Access to electric light is associated with shorter sleep duration in a traditionally hunter-gatherer community. *J. Biol. Rhythms* 30, 342–350.
8. Moreno, C.R., Vasconcelos, S., Marquete, E.C., Lowden, A., Middleton, B., Fischer, F.M., Louzada, F.M., and Skene, D.J. (2015). Sleep patterns in Amazon rubber tappers with and without electric light at home. *Sci. Rep.* 5, 14074.
9. Roenneberg, T. (2013). The human sleep project. *Nature* 498, 427–428.
10. Van Dongen, H.P., Maitlin, G., Mullington, J.M., and Dinges, D.F. (2003). The cumulative cost of additional wakefulness: dose-response effects on neurobehavioral functions and sleep physiology from chronic sleep restriction and total sleep deprivation. *Sleep* 26, 117–126.

<sup>1</sup>Department of Biology, University of Washington, Seattle, WA 98195-1800, USA.

<sup>2</sup>School of Public Health, University of São Paulo, 01246-904, Brazil. <sup>3</sup>Stress Research Institute, Stockholm University, 106 91, Sweden. <sup>4</sup>Department of Physiology, Federal University of Paraná, 80610-280, Brazil.

<sup>5</sup>Catholic University of Santos, 11.015-002, Brazil. <sup>6</sup>Programa de Saúde Coletiva (UFRGS), Porto Alegre, RS, 90460-150, Brazil. <sup>7</sup>Departamento de Psiquiatria e Medicina Legal (UFRGS), Porto Alegre, RS, 90035-903, Brazil. <sup>8</sup>Department of Anthropology, Yale University, New Haven, CT 06511, USA. <sup>9</sup>Departamento de Ciencia y Tecnología, Universidad Nacional de Quilmes, 1876, Argentina. <sup>10</sup>Brigham and Women’s Hospital and Harvard Medical School, Boston, MA 02115-1104, USA.

<sup>11</sup>Faculty of Health & Medical Sciences, University of Surrey, GU2 7XH, UK. <sup>12</sup>Ludwig-Maximilian-University, Munich, 80336, Germany.

\*E-mail: roenneberg@lmu.de