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Response to de la Iglesia *et al*.

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We wish to respond to the commentary of de la Iglesia *et al*. [1]. Studies comparing sleep in different communities have different goals. One frequent goal has been to determine how sleep is affected by manipulating specific 'modern' conditions. Many studies have investigated the effect of artificial light and electronic entertainment. Such studies have clearly shown that light, particularly blue light, delays sleep onset [2]. Studying the effect of artificial light on sleep was not a goal of our study.

Our goal was to study the nature and timing of sleep of pre-industrial humans [3]. Since humans migrated out of Africa, the environment to which they are exposed has changed radically. In particular, during the last century not only artificial light, but also sleeping surfaces, central air conditioning and heating, soundproofing, predation risk, insect exposure and innumerable other aspects of the sleep and waking environment have been transformed. Some of these alterations may have increased sleep, whereas others may have decreased sleep. These changes are far too rapid for us to have evolved adaptations to them. The data we collected and presented in considerable detail can readily be compared to data gathered with the same instruments and processed with the same algorithm in modern societies (see Supplemental Information in [3]). Environmental changes may contribute to sleep pathologies including insomnia, which afflict up to 20% of the post-industrial population [4,5]. One cannot fully understand these pathologies without knowing the evolutionary history of sleep, much as a good clinician seeks to determine the development of a sleep disorder in a patient.

The cited study by de la Iglesia *et al*. [6] in the Toba/Qom is difficult to compare with our study. We restricted our sample to subjects aged 20–55 years (average was 37). This is an age range with relatively stable sleep parameters, facilitating comparison with other studies. In the Toba/ Qom study [6], by comparison, the average ages of two of the four groups listed were 17 and 27, with some subjects as young as 14. It is well known that sleep duration is much greater in teenagers than in adults, so one would expect much higher average sleep durations in that study than in ours, even if the adult population means were identical. Further, their Toba/Qom subjects were described in the following way: "Most adults are unemployed and subsist on governmental subsidies and/ or very short-term temporary jobs." There is evidence that unemployment in the United States is associated with increased sleep [7]. They do not present health or BMI (body-mass index) data on their subjects or environmental temperature data. But a paper published in the same year by this group describes the Toba/Qom as "a population in transition," with a 45% obesity rate [8], comparable to that of the most severely affected populations in the United States (http://www.cdc.gov/), along with very high levels of hypertension. The prevalence of metabolic syndrome (greatly elevated risk for, and incidence of, heart disease, diabetes, and stroke) in the Toba/Qom is 38% [8]. We feel that our study populations are much more informative for extrapolating to those of ancestral humans because of the heavy reliance on foraged and hand-cultivated food sources in all three of our population groups, and the minimal influence of government subsidies. Table S1 in Supplemental Information published with this article online displays the average sleep duration by population and season of the studies referenced in our paper and in the de la Iglesia *et al*. commentary [1], all using the same methodology.

The study of rubber tappers mentioned in the critique adds to a vast literature on sleep among different employment groups and ethnicities, but does not speak to the validity of our observations. It also does not present actigraphic data on sleep duration, rather using sleep diary data to estimate sleep period. Because of the very different living conditions, one would not expect the light exposure or behavior patterns of the rubber tappers or the Toba/Qom to resemble those of our three pre-industrial groups, who show quite similar patterns of light exposure to each other.

The referenced work of the Munich ChronoType in modern societies is similarly interesting. It reveals weekday–weekend differences in sleep period. But the method of measuring sleep period was questionnaires, not actigraphy or polysomnography. The populations polled are quite different from ours and it is not clear what its bearing is on the systematic measures we made of sleep timing and duration in pre-industrial populations. The days of the week are largely irrelevant to the behavior of the groups we studied.

Health investigation of the three populations we studied have shown that the adults, although they suffer from infectious diseases endemic to the tropical regions in which they live, as do visitors to the tropics, are in many respects healthier than those in our post-industrial society. They have higher levels of cardiovascular fitness than typical in our society and much lower rates of hypertension and atherosclerosis [9]. None of our 94 randomly selected subjects was obese. The obesity rate in the overall Tsimane population is less than 3% as has also been described in the Hadza and Ju/'hoansi (Table S2 in [3]).

The 'diversity' of our groups is not a problem, but rather a very important strength of our study, allowing us to determine that these major aspects of sleep are not idiosyncratic to each group. The parameters of sleep in each group are described in the paper and Supplemental Information in [3]. One cannot prove the null hypothesis, i.e. that the groups are identical, but certainly the duration, seasonal differences and the link between the sleep period and the coldest part of the night are apparent.

The strong relation of the sleep period to the 24 hour environmental temperature cycle may be the most important finding of our study. This needs to be emphasized, especially given how, even now, some readers assume the similarity among our three

populations is due to light exposure, despite our data suggesting that temperature is a more proximate regulator of sleep than light in this context. The natural cycle of ambient temperatures has been attenuated or eliminated in most post-industrial countries. We also find a very large difference (nearly 1 hour) between winter and summer sleep durations, with longer sleep durations in winter. Another important finding was that the incidence of insomnia in these populations is far lower than that of more technologically advanced societies. Also, napping and mid-night awakening were not part of the normal daily pattern. The similarity in sleep timing and synchrony with ambient temperature across three independent groups is a striking finding, especially considering that the most salient commonalities that they all share is a reliance on subsistence food sources and an exposed sleeping environment.

Sleep onset occurred, on average, 3.3 hours after sunset. We show in Figure 4 and in Table S2 [3] a strong linkage of average waking time to the nadir of environmental temperature. Most awakenings occur prior to sunrise, and virtually all groups awakened near the temperature nadir. We digitally recorded ambient sounds for 24 h/day for 5 day periods in the Ju/'hoansi (San) village and questioned subjects as to what awakened them. There was no evidence that noise was responsible.

We reported that the duration of individual nights of sleep are highly correlated with sleep onset time. We stated that "The SD (standard deviation) of sleep onset times exceeded the SD of sleep offset times in all San individuals (N = 27, p = 7.4E-5, binomial test) and in all Tsimane individuals (N = 45, p = 2.0E-08), with a similar trend in the more limited dataset from the Hadza. Therefore, sleep duration was much more strongly correlated with sleep onset time than with sleep offset time in both summer and winter. Sleep onset and offset times were very weakly correlated with each other (Table S1)." The critique suggests that despite these extremely low p values and consistent effects, our conclusion is incorrect because although the data in Table S4, with daily sleep values for three representative subjects illustrate the effect, our Table S2 does not. Table S2 shows data averaged across subjects in each group. One would not expect the SD of subject averages of sleep onset and offset times to reflect the effects seen from night to night within each subject. Very extensive data presented in Table S1 [3] give the correlations between duration, onset and offset within each subject and the relevant statistics, showing the remarkably strong correlation between sleep onset time and sleep duration.

Our goal was not to determine an optimal amount of sleep or what is 'sufficient' sleep. Rather it was to record the pattern in pre-industrial humans before such groups vanish. Nowhere in our paper do we suggest that the sleep amounts or patterns of pre-industrial humans are to be emulated; rather, we intentionally avoid describing sleep in our study populations as either sufficient or insufficient because there is no evolutionarily informed empirical criteria upon which to define a cutoff point between sufficient and insufficient sleep. Recommendations for sleep durations should only be made on the basis of prospective studies that might indicate that lowering or raising sleep time has health benefits. However, our findings do have some policy relevance. In June of 2015, while our study was under review, the American Academy of Sleep Medicine and Sleep Research Society made a 'one size fits all' sleep duration recommendation [10]. This recommendation, to "see your health care provider if you sleep less than 7 hours," would send nearly half of all hunter-gatherers to their 'health care provider' in the summer and perhaps one-quarter of them in the winter (and a similar percentage of modern post-industrial populations). It is important to appreciate that average sleep durations in technologically advanced societies are not shorter than those in pre-industrial peoples, despite frequent claims.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.02.057.

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