Journal of Human Evolution 113 (2017) 91–102

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

The evolution of human sleep: Technological and cultural innovation associated with sleep-wake regulation among Hadza hunter-gatherers

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ARTICLE INFO

Article history:
Received 25 July 2016
Accepted 3 August 2017

Keywords:
Actigraphy
Thermodynamics
Forager
Homo
Technology
Fire

ABSTRACT

Sleep is necessary for the survival of all mammalian life. In humans, recent investigations have generated critical data on the relationship between sleep and ecology in small-scale societies. Here, we report the technological and social strategies used to alter sleep environments and influence sleep duration and quality among a population of hunter-gatherers, the Hadza of Tanzania. Specifically, we investigated the effects that grass huts, sound levels, and fire had on sleep. We quantitatively compared thermal stress in outdoor environments to that found inside grass hut domiciles to test whether the huts function as thermoregulated microhabitats during the rainy season. Using physiological equivalent temperature (PET), we found that the grass huts provide sleep sites with less overall variation in thermal stress relative to outside baseline environments. We also investigated ambient acoustic measures of nighttime environments and found that sound significantly covaried with sleep-wake activity, with greater sound levels associating with less sleep. Finally, after controlling for ecological variables previously shown to influence sleep in this population, fire was shown to neither facilitate nor discourage sleep expression. Insofar as data among contemporary sub-tropical foragers can inform our understanding of past lifeways, we interpret our findings as suggesting that after the transition to full time terrestriality, it is likely that early *Homo* would have had novel opportunities to manipulate its environments in ways that could have significantly improved sleep quality. We further conclude that control over sleep environment would have been essential for migration to higher latitudes away from equatorial Africa.

1. Introduction

Sleep is a fundamental requirement for mammalian life (Horne, 1988; Kushida, 2004). All mammals studied, to date, experience some form of sleep and, if deprived, they suffer impairment of physiological function and cognitive performance (Rechtschaffen, 1998) – which, if prolonged, can ultimately result in death (Rechtschaffen and Bergmann, 2002). Sleep expression in primates is characterized by several distinct features relative to other mammals, including a more consolidated sleep pattern, general reductions in sleep times among diurnal primates, increased sleep intensity (i.e., depth of sleep staging) and the maintenance of social contact during sleep (Nunn et al., 2010). Comparatively, human sleep is unique in that it is shorter, deeper, and exhibits a higher proportion of REM (rapid eye movement) than expected when compared to other primates (Samson and Nunn, 2015). Moreover, it has been hypothesized that human sleep in post-industrialized countries is vastly different from the sleep of our hominin ancestors (Worthman and Melby, 2002; Worthman, 2008). Therefore, in order to determine the variability in human sleep patterns and attempt to make inferences about the past, it is necessary to study sleep in small-scale mobile and semi-nomadic populations whose ecological environment may more closely resemble that of our hominin ancestors.

A critical factor that influences sleep is the sleep site, which can function to reduce predation risk and thermodynamic stress, and facilitate social bonds (Kappeler, 1998; Lesku et al., 2006; Lima and Rattenborg, 2007; Capellini et al., 2008). Factors that acutely

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http://dx.doi.org/10.1016/j.jhevol.2017.08.005
0047-2484/

stimulate or inhibit sleep are known as “masking factors.” In other words, they are behavioral facilitators and inhibitors that either encourage or discourage sleep expression (Webb, 1988; Moore, 1990). Arguably, the most significant behavioral facilitator of sleep in human and non-human primates is the sleep site — that is, all aspects of the sleeping environment, which include photoperiod, thermal stress, noise, sociality, and familiarity of surroundings (Haskell et al., 1981; Libert et al., 1991; Epstein et al., 1997). Interestingly, non-human great apes in the wild not only sleep arboreally, but construct sleeping platforms on which to sleep (Fruth and Hohmann, 1996). Ape sleeping platforms have been found to improve sleep site safety (van Casteren et al., 2012; Samson and Hunt, 2014), repel insects (Samson et al., 2013), reduce thermal stress (Stewart, 2011), improve comfort (Stewart et al., 2007), and augment post-sleep cognitive ability (Martin-Ordas and Call, 2011; Shumaker et al., 2014).

Here, we quantitatively investigate the sleep sites among the Hadza of Tanzania, adding to previous qualitative descriptions of sleep sites among small-scale populations (Worthman and Melby, 2002; Hewlett and Roulette, 2014) and to recent cross-cultural analyses of sleep among foragers (Yetish et al., 2015; Samson et al., 2017a). To this end, we focus on the construction of sleeping sites and domiciles, sound levels, and the use of fire. The functional role of a shelter is often assumed to relate to the size, layout, and construction materials of a domicile. Shelters in small-scale societies vary across geography and subsistence strategy (Eibl-Eibesfeldt, 1989). For example, when they were still foraging, the !Kung of the Kalahari (southern Africa) slept in small, stick-framed, grass covered huts with few to no physical barriers to the environment (Worthman and Melby, 2002). The Lese horticulturalists (Democratic Republic of the Congo) and Swat Pathan mixed agriculturalists (Afghanistan/Pakistan border) sleep in shelters made of mud and branches that have constructed partitions that can extend to the ceiling (Barth, 1981), and the Gebusi highland horticulturalists (New Guinea) sleep in 20–30 m long communal long house structures with large internal partitions that provide visual but not acoustic separation from the other 20–100 other residents (Knauft, 1985).

Moreover, a wide range of sleeping platforms are observed across cultures, ranging from vertically raised bedsteads to thin floor mats (Beldegreen, 1991). Piles of vegetation constructed from branches, lianas, leaves, and grasses, which are sometimes interwoven or lashed together, have been observed among pastoralists and farmers (e.g., East African Maasai, Central African Tonga and Azande) and forest-dwelling hunter-gatherers (e.g., Central African Efe, South American Caingang, Jivaro in Ecuador, Thai Mrabri) (Métraux, 1946; Schlipp, 1956; Turnbull, 1962; Talbot, 1963; Reynolds, 1968; Hewes, 1994). Sleeping platforms are also constructed with animal hides, with or without a foliage base, such as those constructed by the Alaskan Alutiiq, who prepare the ground by first laying grass down and then layering mountain-goat and bear skins on top (Schlipp, 1956; Turnbull, 1962). Despite the cross-cultural variation seen in sleeping substrate, to our knowledge this is the first study to directly test how such variation in sleeping substrates influences sleep duration and quality.

The acoustic properties of sleeping sites (e.g., human voices, animal movement or calls, and weather-generated noises) can be influenced by the way individuals distribute themselves in their environment. For example, extreme ambient noise levels have been associated with low socioeconomic status among individuals living in post-industrialized economies (Tsai et al., 2009). These noisy environments may contribute to lower sleep duration and quality and may, in turn, generate negative health outcomes (Gangwisch, 2014), such as reported associations between living near traffic-heavy areas and an increased likelihood of dementia (Chen et al., 2017). Acoustic levels are particularly pertinent in small-scale populations that lack environmental barriers, such as insulated buildings that blunt noise, common in the post-industrialized west. Given that the majority of sub-tropical hunter-gatherer societies are not densely populated, with a camp on average consisting of approximately 30 individuals (Marlowe, 2006), sound may influence sleep-wake activity in novel ways compared to industrialized societies.

Fire, which acts as a source of light, heat, smoke, white noise, visual stimulation and/or psychological comfort, is another consideration when choosing a sleep site, as it can influence sleep in several significant ways (Worthman, 2008). Fire has been implicated as a predator deterrent (Wrangham and Carmody, 2010), a way to regulate thermal stress (Coolidge and Wynn, 2006), and a fumigant to repel biting insects (Moore et al., 2007). Additionally, in the cultural west, exposure to controlled fire has been empirically shown to reduce blood pressure and increase prosociality (Lynn, 2014). Several of these factors have led researchers to speculate that the controlled use of fire was important throughout early human evolution (Dunbar and Gowlett, 2014). Taken together, the characteristics of fire could positively influence sleep duration and quality. Alternatively, fire needs constant tending, is a source of light which could potentially suppress melatonin (i.e., sleep-wake regulating hormone) (Burton, 2011), and could increase nighttime activity by facilitating social engagement (Dunbar and Gowlett, 2014). Whether a facilitator or impediment to sleep, either outcome could lend credence to the hypothesis that the controlled use of fire was critical to early human evolution (Coolidge and Wynn, 2006; Wrangham, 2006; Wrangham and Carmody, 2010; Samson and Nunn, 2015).

Studying sleep among hunter-gatherers and other mixed-subsistence small-scale populations is important because forager populations continue to be used as referential standards for inferring evolutionary origins of behavior (Lee, 1992; Crittenden and Schnorr, 2017). Attempts to describe the adaptive sleep-wake pattern among humans have varied, including controlled experiments manipulating photoperiod (Wehr, 1992, 1999), investigations into the effects of artificial light on circadian patterns (de la Iglesia et al., 2015; Samson et al., 2017c), analysis of historical accounts of segmented sleep (Ekirch, 2006, 2016), and comparative analyses on non-human and human primates (Samson and Nunn, 2015). Importantly, activity patterns of non-industrial societies are assumed to be more closely linked to adaptive daily and seasonal rhythms, as such populations lack environmental barriers, such as environmentally controlled buildings with insulation that blunts noise (Yetish et al., 2015), that are likely to influence sleep. Therefore, while the Hadza are by no means analogs to the Paleolithic past, they do offer unique insight into the investigation of sleep-wake activity that might influence our understanding of past lifeways. They are semi-nomadic, live in close contact with their environment (e.g., soil, water, plants, animals), consume a diet that is largely composed of wild foods, and reside in temporary domiciles that do not have artificial light or climate control. Exploring sleep-wake patterns and sleep site construction among the Hadza offers relevant data on the evolution of human sleep, as they live in an environment that is most similar to the one in which our ancestors evolved.

The primary aims of the present study were to (1) characterize human-created environments that influence sleep, (2) assess sleep related social strategies, and (3) investigate how both factors function to influence sleep among the Hadza. We hypothesized that sleep duration and quality were influenced by the use of shelter, sleep substrate, sound, and use of fire. We used our data to test the following predictions: (a) if shelter functions to reduce thermal stress, then domicile constructions will regulate nighttime indices