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Sleep under evolutionarily relevant conditions

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Studies of sleep in animals and humans have generally been done under controlled conditions, with fixed thermoneutral temperature, 12-12 lighting, "*ad libitum*" food availability and in the absence of threat or stress. Such studies were well justified as an initial approach to studying the phylogeny of sleep, utilizing laboratory polygraphs or in the case of zoos, visual observation. However, although such studies allowed comparison of sleep across species in similar, though unnatural conditions, they are unable to fully explore the adaptive function of sleep under the dynamic real world conditions that have shaped evolution.

Rapid advances in electronics have now enabled more naturalistic studies of the functions and species differences in sleep. Rattenborg has been a pioneer in the application of this approach. This includes the small devices pictured in the current illustrations [1-3].

Of great interest is the sleep in birds under naturalistic conditions that have been shown by Rattenborg, including asymmetry between the two cortical hemispheres, correlated with eye state. He has also explored changes in sleep duration during migration, as is illustrated here, and during mating behavior [4,5].

We have recently used Actiwatch monitoring of the timing of sleep in wild African elephants [6]. We found that, in the wild, elephants have half the average sleep duration seen in captivity and we were able to describe the variability and timing of their sleep in relation to natural light and temperature for the first time. Such studies challenge the simplistic idea that sleep duration is fixed and that sleep in the wild is greater in duration than sleep under laboratory conditions. Indeed although animals in the wild are usually healthier that those confined to laboratories and zoos, animals in the wild often have less sleep that those in zoos. Sloths in the lab average 15 h/day of sleep, but they sleep 9 h/day in the wild [7]. Frigate birds in cages sleep 9.3 h, but when flying over the ocean for 10 day periods they sleep 0.7 h/day [3], without rebound. Fur seals have 80 min of REM sleep/day on land, but in water, where they spend >70% of their life, they average 3 min of REM a day. They have no REM "rebound" when they return to land [8]. A recent study in the oryx, studied under the extreme seasonal temperature variations in which they evolved showed major changes in sleep duration and timing as a function of season [9].

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Conflict of interest

The ICMJE Uniform Disclosure Form for Potential Conflicts of Interest associated with this article can be viewed by clicking on the following link: https://doi.org/10.1016/j.sleep.2020.01.003.

The study of sleep in animals with asymmetric electroencephalogram (EEG), allows the neurochemical substrates of EEG asymmetry to be determined. In our studies of unihemispheric sleep in the fur seal we showed the participation of acetylcholine, rather than norepinephrine and serotonin in the marked EEG asymmetry seen in fur seals having unihemispheric sleep [10-12]. Our recent study using digital recording devices showed that unihemispheric high voltage EEG expression is linked to a nearly complete loss of REM sleep when fur seals are in the water, where they spend 10 months a year, with no rebound when returning to land [8].

The use of digital devices that record activity, travel direction and that allow unrestrained long-term monitoring of sleep in animals and humans, along with “big data” approach of large populations (for example, hundreds of thousands of humans wearing Fitbits) under natural conditions are producing great advances in our understanding of sleep. The development of these techniques opens to door to seeing sleep's evolutionary function in ways that contrast with sleep measurement and deprivation in animals placed in conditions differing greatly from those which drove evolution. In the case of humans we recently reported consistently lower sleep durations in hunter-gatherers than in industrial populations [13]. Inevitable advances in sleep monitoring and in data processing will make this approach increasingly important in understanding sleep and its pathologies.

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