Adaptive Solutions to the Problem of Vulnerability During Sleep

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Abstract
Sleep is a behavioral state whose quantity and quality represent a trade-off between the costs and benefits this state provides versus the costs and benefits of wakefulness. Like many species, we humans are particularly vulnerable during sleep because of our reduced ability to monitor the external environment for nighttime predators and other environmental dangers. A number of variations in sleep characteristics may have evolved over the course of human history to reduce this vulnerability, at both the individual and group level. The goals of this interdisciplinary review paper are (1) to explore a number of biological/instinctual features of sleep that may have adaptive utility in terms of enhancing the detection of external threats, and (2) to consider relatively recent cultural developments that improve vigilance and reduce vulnerability during sleep and the nighttime. This paper will also discuss possible benefits of the proposed adaptations beyond vigilance, as well as the potential costs associated with each of these proposed adaptations. Finally, testable hypotheses will be presented to evaluate the validity of these proposed adaptations.

Keywords Sleep · Predation · Evolution · Vigilance · Chronotype

Introduction
Sleep is a behavioral state of reduced activity with multiple apparent biological functions (Barone & Krieger, 2015). In practical terms, sleep requires an adaptive trade-off between fulfillment of its intrinsic biological functions, whatever they may be, and the fulfillment of other biological goals necessary for survival, goals that can only be accomplished during the waking state, such as finding food, water, and mates (Samson, 2021; Siegel, 2009). However, the sleeping organism is confronted with the additional challenge of enhanced vulnerability to species-specific external threats, such as predators, conspecific enemies, and the forces of nature. While asleep, we are less responsive to our external environment, slow in responding once awakened, and unable to move at all during one specific phase of sleep (REM sleep), in the case of species that experience this particular stage of sleep (Tassi & Muzet, 2000).

Even without considering specific biological functions of sleep, all organisms face the challenge of expending energy to secure resources, while not wasting energy during periods when resources are scarce and they are especially vulnerable to predators and other natural threats (Roth et al., 2010; Siegel, 2009). In this sense, sleep can be viewed as a state of “adaptive inactivity,” with organisms sleeping for amounts and in ways that best match and promote survival in their specific ecological niche (Siegel, 2009). Add to this foundation the increasing body of evidence supporting various functions of sleep, such as the clearing of toxins from the brain (Haugland et al., 2020; Xie et al., 2013), memory processing (e.g., Rasch & Born, 2013; Stickgold, 2013), synaptic modulation (Tononi & Cirelli, 2020), energy homeostasis (Scharf et al., 2008; Schmidt, 2014), regulation of the immune system (Besedovsky et al., 2019), and emotional adaptation (Goldstein & Walker, 2014; Walker & van Der Helm, 2009), to name some of the proposed functions that have received considerable attention in recent years.

This paper will explore the possibility that many of the features of sleep evolved at least in part to solve the vulnerability problem inherent to sleep. Any feature that can mitigate vulnerability inherent to this behavioral state could, in principle, increase the chances of reproductive success and the survival of that species. A major purpose of this paper is to consider potential adaptations that may have enhanced vigilance and reduced vulnerability during sleep in our
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adaptation for its present role, but was subsequently co-

adaptations (e.g., Lima et al., 2005; Nunn et al., 2016; Samson et al.,

2017b; Snyder, 1966; Worthman, 2008).

Importantly, this paper will acknowledge the distinction between more or less instinctual sleep-relevant traits that may have evolved specifically for the purpose of reducing vulnerability during sleep (i.e., adaptations) and those that may have been co-opted later in evolutionary history to perform such a function (i.e., exaptations). In addition, this paper will consider separately some recent cultural developments that may have utility in terms of reducing vulnerability during sleep, even if they are too recent in evolutionary time to have acquired adaptive significance in a strict biological sense.

**Adaptations vs. Exaptations**

George Williams argued many decades ago that we should not call any observed effect an evolutionary adaptation, unless that effect “is clearly produced by design and not by chance” (p. 3). Moreover, “when recognized, adaptation should be attributed to no higher a level of organization than is demanded by the evidence. Natural selection is the only acceptable explanation for the genesis and maintenance of adaptation” (Williams, 1966, p. 3). Subsequent authors, such as Stephen Jay Gould, made additional distinctions between features that originated to serve a specific function and features that were co-opted later to serve a different function, i.e., exaptations.

Before proceeding, let us clarify the difference between an adaptation and an exaptation. An adaptation has been defined as “an inherited and reliably developing characteristic that came into existence as a feature of a species through natural selection because it helped directly or indirectly to facilitate reproduction during the period of its evolution” (Buss et al., 1998, p. 535). In contrast, an exaptation is “a feature, now useful to an organism, that did not arise as an adaptation for its present role, but was subsequently co-opted for its current function” (Gould, 1991, p. 43). Using Gould’s definition “a mechanism must possess a biological function that contributes to fitness in order to qualify as an exaptation” (Buss et al., 1998, p. 539). A specific example cited by Buss et al. and used by many other evolutionary psychologists and biologists is helpful in understanding this distinction: Feathers in birds may have evolved originally for thermal regulation, but later were “co-opted” for the purpose of flight.

An additional—and potentially useful—concept presented by Gould that builds on exaptations is the concept of spandrels. A spandrel is an architectural term that refers to the spaces left over between structural elements of a building. An example used by Buss et al. (1998) in this context is the spaces between the pillars of a bridge, which “can subsequently be used by homeless persons for sleeping, even though such spaces were not designed for providing such shelter” (p. 539). In contrast to co-opted adaptations, spandrels are “features that did not arise as adaptations through natural selection but rather as side effects of adaptive processes and that have been co-opted for a biological function (co-opted spandrels)” (p. 539).

Adaptations, exaptations, and spandrels have several standards in common, which can be categorized as either conceptual or empirical. Conceptual criteria include: “complexity, efficiency, reliability, specificity, capability of solving adaptive problem, and evolvability”. Empirical criteria include: “capable of generating specific and falsifiable empirical predictions”, and finally, “must account for known data better than alternative hypotheses” (Buss et al., 1998). Readers may conclude that at least some of the primarily biological traits discussed in this paper are more appropriately thought of as spandrels rather than as adaptations or exaptations, a thread of discussion I will consider later.

With respect to sleep, any adaptations that can mitigate vulnerability inherent to this behavioral state could, in principle, increase the chances of reproductive success and the survival of that species. Exaptations would also mitigate vulnerability during sleep and increase the chances of survival of that species, even if the trait in question did not evolve originally for that purpose. This paper will not attempt to determine whether any of the biologically based sleep-related traits are best viewed as adaptations, exaptations, or spandrels. Instead, I will propose as a general working hypothesis that a number of these sleep-related traits, behavioral and physiological, could have benefited in our evolutionary past individuals and groups that possessed those traits, leading to a higher probability of survival and the opportunity to pass their genes along to succeeding generations.

The focus of this paper is vulnerability during human sleep, but it will include animal data, where relevant. Many of the ideas presented here are not new, but are typically treated in isolation. The goal of this interdisciplinary review is to consolidate these ideas and to offer some additional thoughts about minimization of vulnerability during this critical biological state. In addition, we will consider other benefits conferred by these sleep-related traits and variations, as well as the costs attached to them. After considering all of the proposed adaptations, along with their ancillary benefits and costs, I will offer testable hypotheses, a requirement for any “adaptationist” research program that seeks to
move beyond mere conjecture and speculation (Mayr, 1983; Williams & Nesse, 1991). These testable hypotheses could be investigated individually or collectively as part of a larger research program on the evolution of sleep, with a focus on the vulnerability problem. My hope is that the ideas in this paper will stimulate further thinking and perhaps help launch relevant lines of inquiry concerning the evolution of sleep, especially human sleep.

The Challenge of the Night

For our species, the nighttime is a period of particular vulnerability. We are largely a diurnal species that depends heavily on vision, which is much poorer at night than it is during the day. At night we are less able to see approaching threats and other potential dangers. Some of those threats include animal predators, human enemies, and forces of nature, such as storms, fires, and floods. Even though we can hear approaching threats, smell them, and occasionally—depending on nighttime conditions, such as the presence of moonlight—see them, we are still at a significant disadvantage at night compared to daylight hours. This disadvantage is compounded by the vulnerability inherent to the behavioral state of sleep, which diminishes (but does not eliminate) our sensory responsiveness to external events, as well as our motor responsiveness and reactivity, should an actual threat emerge. The range of threats that have concerned human beings throughout our history do not stop at natural threats, but extend to perceived supernatural ones as well (Ekirch, 2005; Koslofsky, 2011; Millar, 2018; Worthman & Melby, 2002). How these threats may have been—and continue to be—addressed will be examined in detail. But before doing so, it would be useful to review the basics of sleep.

Sleep Basics

Sleep is considered to be the product of two interacting biological processes, process S and process C (Borbély et al., 2016). Process S reflects an accumulation of sleep debt, resulting in the urge to sleep; it determines sleep duration. Process C concerns the contribution of circadian rhythms, which influence sleep timing. The interaction of these two processes is hypothesized to account for the particulars of sleep in any individual. A number of genes have been identified that regulate sleep as well (Zhang & Fu, 2020). Evidence suggests that Process C is shaped by specific genetic variants, a list that includes PER2, CKIβ, CRY1, and CRY2. Process S seems to be regulated by the genetic variants DEC2, ABCC9, DRD2, ADA, and FAB7. Both processes appear to involve the gene PER3. A number of other genes have been identified that regulate sleep, reviewed in Webb and Fu (2021). Besides these genes, a variety of brain structures, circuits, and neurochemical substances have been identified that regulate sleep as well (Brown et al., 2012).

Sleep in most mammals consists of several relatively discrete stages, distinguished primarily by differences in electrical brain wave patterns (measured using electroencephalography or EEG, which reflects electrical activity of neurons in the cerebral cortex), muscle activity (measured using electromyography or EMG), eye movements (using electro-oculography or EOG), and behavior. Human sleep is generally divided into two main categories of sleep: non-REM and REM (rapid-eye movement) sleep. Non-REM sleep consists of several stages: N1, N2, and N3 (Carlson & Birkett, 2017; Carskadon & Dement, 2017). In the original sleep scoring system developed by Rechtschaffen and Kales (1968), sleep was divided into stages 1, 2, 3, and 4, and REM. In the new system, stages 3 and 4 are folded into N3; the others remain the same (Iber et al., 2007). When someone falls asleep, they first enter stage N1. This stage consists of irregular waves, including some theta waves, whose frequency is approximately 3.5–7.5 Hz (i.e., cycles per second) (Carlson & Birkett, 2017) and typically lasts about 1–7 min. A sleeper then moves into stage N2. The EEG record of stage N2 is marked by electrical waves that are slower, more regular, and of greater amplitude than the waves observed in N1. EEG recordings from this stage of sleep are marked by two special kinds of waveforms, known as sleep spindles and K-complexes. Sleep spindles are short bursts of brain waves in the frequency range of 12–14 Hz. K-complexes are sudden sharp waveforms that appear to be largely confined to this stage of sleep. The N2 stage lasts about 10–25 min. Next is stage N3, also sometimes referred to as slow-wave sleep (SWS) in humans. This stage consists of regular, high-voltage (at least 75 µV) slow waves (about 2 cps) known as delta waves, which make up at least 20% of the EEG record. The N3 stage lasts about 20–40 min during the first sleep cycle of the night in a healthy young adult. After stage N3, sleepers retreat back into stage N2. After some period of time REM sleep appears, about 70–110 min after sleep onset. The first REM stage of the night lasts about 10 min.

REM sleep in humans is characterized by both phasic and tonic components (Simor et al., 2020). Phasic components consist of rapid, saccadic eye movements, which are phase-locked to electrical waves known PGO spikes (PGO stands for pons-geniculo-occipital, i.e., the brain structures of pons-lateral geniculate (of the thalamus)-occipital cortex). Other phasic features include the contraction of middle ear muscles, twitching of skeletal muscles, sawtooth EEG waves, and irregular heart rate and respiratory activity. Tonic components include muscle atonia, an EEG profile consisting of desynchronized, low-amplitude, fast-wave activity, genital arousal,
and vivid dreaming (Carlson & Birkett, 2017; Carskadon & Dement, 2017; Simor et al., 2020).

People typically experience four to five sleep NREM-REM sleep cycles per night. The amount of N3 is generally greater during the first half of the night, whereas N2 and REM are greater during the second half of the night. REM stages get progressively longer across the night. Stage N1 occupies about 2–5% of sleep, N2 about 45–55%, N3 about 10–20%, and REM about 20–25% in healthy young adults (Carskadon & Dement, 2017). It is important to emphasize that sharp boundaries do not exist between sleep stages; blended states can occur with elements of different sleep stages occurring simultaneously (Antelmi et al., 2016; Mahowald & Schenck, 1992).

In humans deep slow-wave sleep, i.e., N3, is accompanied by a reduction of brain activity, higher auditory arousal thresholds, and slower responsiveness upon awakening (“sleep inertia”) compared to other stages of sleep (Rechtschaffen et al., 1966; Tassi & Muzet, 2000). However, auditory arousal thresholds have been found to be highest in REM sleep in sleepwalkers and following sleep deprivation in both sleepwalkers and controls (Pilon et al., 2012). Also, arousal thresholds in response to auditory stimulation are highest during the phasic components of REM sleep compared to all other periods of sleep (Simor et al., 2020). However, people are more likely to be awakened by meaningful stimuli than non-meaningful presented during REM sleep compared to stage 2 sleep (Langford et al., 1972). Because of the greater probability of experiencing vivid dreaming during REM, it is fair to say that REM is a brain state that is focused on internally generated sensory events.

These disadvantages with respect to vulnerability, i.e., motor paralysis and relatively high arousal thresholds, are mitigated somewhat by the fact that the mammalian brain is highly active during REM and is thus in a state of arousal upon awakening. Indeed, studies of sleep inertia often find that awakening people from REM yields levels of alertness comparable to wakefulness (Tassi & Muzet, 2000). Moreover, tonic REM periods may provide a “transient alerting mechanism” to counteract the sensory disconnection inherent in phasic REM periods (Simor et al., 2020). Of relevance for this paper, spontaneous awakenings are more likely to occur while people are in REM sleep than in other sleep stages (Campbell, 1985; Ficca et al., 1999; Langford et al., 1972) though not under all conditions. For example, Barbato et al. (1994) found no significant differences between spontaneous awakenings from REM vs. non-REM sleep on baseline nights, but found more than twice as many awakenings from REM under an imposed sleep schedule of 14-h nights. Despite this variability in findings, the brain is clearly processing external sensory information during REM, certainly during its tonic phases. This notion is reinforced by the demonstrated ability to generate evoked potentials during REM (Bastuji & Garcia-Larrea, 1999). Importantly, the brain is processing external signals during all stages of sleep, as evidenced by cortical evoked potentials in response to sensory stimuli (Bastuji & Garcia-Larrea, 1999).

During the REM stage sensory information is internally generated, but external sensory information may be incorporated into dream mentation as well, without awakening the dreamer. Neural activity in the locus coeruleus, a brainstem structure involved in monitoring, detecting, and responding to environmental changes, especially noxious or threatening ones (Dayan & Yu, 2006; Grant & Redmond, 1984; Rasmussen et al., 1986; Sara & Bourret, 2012) is virtually eliminated during REM sleep (Aston-Jones & Bloom, 1981; Foote et al., 1981; Rasmussen et al., 1986; Takahashi et al., 2010). On the other hand, immobility during REM makes it less likely that the sleeper will generate any movements or sounds that might attract the notice of potential predators. Moreover, if awakening from REM does occur, the cerebral cortex is in a state of high activation and is ready to spring into action, as already noted.

However, as Symons (1993) has pointed out, when it comes to dreaming not all senses are equal. During dreaming, vision is focused exclusively on internally generated sensory experiences. Although the other senses, such as hearing and touch, also involve internally generated stimuli during dreaming, they do so to a lesser degree. In addition, the other senses continue to respond to external stimuli, albeit at a different threshold of activation. So even though locus coeruleus activity is reduced during sleep—and shuts down completely during the REM state—our brains can still respond to external stimuli and potential threats. Sounds, smells, and tactile stimuli can still arouse us from sleep, especially if they convey essential, survival-related information for ourselves or for those around us. Importantly, the amygdala, a brain structure critical for processing emotion and detecting external threats (LeDoux, 2015), is highly active during the REM state (Braun et al., 1997; Maquet et al., 1996; Noftinger et al., 1997) even if the locus coeruleus is not.

**Proposed Adaptations**

Given these challenges to vigilance at night, particularly while we sleep, one or more adaptations would, in principle, be of potential benefit. For purposes of expediency, I am going to use the word adaptation for the time being as a general term that can include both adaptations and exaptations. However, I do not want readers to think that I am assuming what I (or anyone else) have yet to prove.

Continuing this line of discussion, one can imagine a number of possible adaptations that might reduce nighttime vulnerability, especially when taking into account the specific
characteristics of human sleep. Snyder (1966) suggested many decades ago that REM sleep itself might perform such a vigilance function, in that periods of cerebral alertness are typically followed by brief awakenings. Freemond (1970) proposed a reciprocal environmental surveillance model in which both REM and non-REM sleep take turns monitoring the environment. He made the assumption that individual renewal functions take place during both non-REM and REM sleep. When one state is engaged in renewal functions the other state takes on the responsibility of monitoring the environment. Freemond’s model is based on two observations: (1) that meaningful stimuli are more likely than non-meaningful stimuli to awaken the sleeper (Langford et al., 1974; Oswald et al., 1960) and (2) that during REM and non-REM sleep the neocortex and limbic structures oscillate in a reciprocal fashion between low-voltage fast-frequency electrical activity and high-voltage, low-frequency electrical activity (Freemond et al., 1970; Jouvet, 1967). As already noted, even within REM sleep, reciprocal roles in monitoring the environment may take place between its tonic and phasic components. In any case, a number of other adaptations could, in principle, enhance nighttime vigilance and potentially increase chances of survival, both for the individual and for the group to which that individual belongs. Again, the orientation of this paper is to view sleep as a group phenomenon as much as an individual one. By viewing sleep in this fashion, one will be able to see that many proposed adaptations, though problematic for the individual sleeper, may in fact benefit the larger group, and thus plausibly enhance its survival. The majority of these adaptations may do so by enhancing group vigilance, at least in principle. The group benefits of variations in individual sleep patterns, including sleep disorders, have been explored previously to some degree (Samson et al., 2017b; Snyder, 1966). This paper will extend that discussion and provide some additional insights, including the potential costs of these proposed adaptations. I will consider these candidate adaptations in three different groups of human societies: those who lived in our ancestral environment, contemporary humans living in environments that approximate the human ancestral environment, and humans living in modern, industrialized societies. I will also bring in data from animal studies, especially those involving non-human primates, where relevant.

The candidate adaptations that may have reduced vulnerability during sleep in our evolutionary past include:

1. REM sleep.
2. A reduced ability to initiate sleep.
3. Frequent awakenings.
4. Reduced sleep duration.
5. “Lighter” sleeping, which would enhance sensory responsiveness to external events and motor responsiveness, if the sleeper is awakened.
6. Continuous sensory monitoring of the external environment during sleep.
7. Redistribution of sleep across the 24-h cycle so that some of it occurs during the daylight hours, when humans are less vulnerable—at both individual and group levels.
8. Increased fear and anxiety responses at night and during sleep, which would promote vigilance and readiness to act upon awakening.
9. Having some brain areas remain awake while others sleep.
10. Sleeping in groups, at close proximity.
11. Having a variety of chronotypes within one’s group.
12. Choosing sleeping locations that promote safety and enhance vigilance.

To this list we can add developments from our recent historical past that could serve to promote nighttime vigilance and contribute to personal and group safety in our species. Such developments could be passed down culturally from generation to generation. Although they are not adaptations in a strict biological sense, they offer solutions to the problem of vulnerability during sleep, and could have enhanced the survival of individuals and groups that employed them. We might view these as emerging adaptations. These developments are:

1. Controlled fire, which would partially compensate for reduced nighttime vision and ward off predators.
2. The intentional deployment of human sentinels during the night while most others are sleeping.
3. The use of domesticated animals, especially dogs, as nighttime guards.

Each of the proposed instinctual adaptations and cultural developments incur potential costs as well as benefits, an important factor I will address. Also, as acknowledged earlier, each of the proposed adaptations could have evolved originally for some purpose other than enhancement of vigilance. Nevertheless, I will make the argument that, at the very least, each of these sleep-related features can in principle serve to reduce vulnerability during sleep and the nighttime, even if that particular feature did not evolve specifically for that purpose.

**Vigilance**

This section begins by discussing potential adaptations that are primarily instinctual and involuntary. Importantly, the adaptations proposed here overlap considerably and are not mutually exclusive. As a result, some themes and lines of discussion will recur across the various adaptations presented. These potential adaptations are oriented primarily toward enhancing vigilance, but they could have reduced
vulnerability in other ways as well. Finally, although the term “vigilance” is oriented primarily toward the detection of external threats, it can also encompass the detection of positive opportunities as well, such as potential food and mates.

**Instinctual Adaptations**

**Potential Adaptation No. 1: REM Sleep**

REM sleep evolved well before the emergence of hominids. REM is found in a wide range of species, including birds and mammals that are much older, evolutionarily speaking, than we are. The precise biological function or functions of REM sleep have yet to be determined, despite many hypotheses that have been offered over the years. Among the candidate functions of REM are roles in brain development, memory processing, emotional adaptation, and neural plasticity (Li et al., 2017; Miller & Gehrman, 2019; Peever & Fuller, 2017). But REM sleep could also have been one of the first adaptations in the animal kingdom to reduce vulnerability during sleep. For the purposes of this paper, the key question is whether REM sleep, or at least some components of REM sleep, could have served a vigilance function, as some others have previously suggested (Freemon, 1970; Snyder, 1966). But REM has another crucial characteristic that can, at least on its surface, make us more vulnerable: muscle atonia. During the REM state we are essentially paralyzed (Peever & Fuller, 2017), even if in our dreams we are running full speed, trying to escape a predator, or standing our ground and fighting an assailant. Except for occasional twitching of the extremities, that means a quiet, immobile organism. However, such a characteristic may be quite useful. An animal that’s immobile might be mistaken for a dead one, and more easily escape detection. Moreover, movement is a stimulus for attack on the part of many species (e.g., Thompson et al., 1981). So REM immobility could serve to reduce the chances of being attacked by a carnivorous predator. In this vein, Tsoukalas (2012) has proposed a theory that REM sleep has its origins in tonic immobility in animals. Importantly, REM atonia reduces the chances of acting out one’s REM-related dreams and thus attracting the attention of nocturnal predators or disturbing the sleep of those around us.

But in humans there are limitations as to how much tonic immobility may reduce predator attack and therefore enhance one’s chances for survival. Coss et al. (2009) found that humans who remained stationary as opposed to running away from pumas had a higher probability of being attacked and experiencing severe injury. However, the humans who were attacked were upright, not in a prone position on the ground, which is more suggestive of a dead animal. Immobility issues aside, during REM our brains are in an alert, aroused state (Peever & Fuller, 2017). So even if we were to be awakened during this stage of sleep by a dangerous animal, human assailant, or natural threat, we could take protective action more quickly, such as running, fighting, or engaging in some other evasive maneuver, especially actions that demand a significant degree of cognitive processing.

In the ancestral environment, the brief awakenings that followed the end of REM sleep episodes would have allowed humans periodic opportunities to survey the external environment for threats, thus reducing vulnerability during sleep. But REM awakenings could also have served positive functions as well. The reliable occurrence of sexual arousal during REM sleep (Fisher et al., 1965, 1983), which carries into wakefulness, would arguably have increased the probability that sexual intercourse would have taken place, along with increased chances for conception. That’s consistent with the concept of an adaptation.

**Costs of REM Sleep**

Besides the inherent vulnerability of REM atonia, this state of sleep is also characterized by high levels of activity and increased blood flow to many brain regions, with energy usage comparable to that seen in waking states (Maquet et al., 1996). Thus, REM is costly compared to other stages of sleep. On the negative side, a bias toward REM sleep is also associated with clinical depression in contemporary humans. A faster onset to the first REM period, i.e., reduced REM latency, is correlated with depression (Palagini et al., 2013). On the other hand, antidepressant drugs inhibit REM sleep and delay REM sleep onset (Vogel et al., 1990). As one might predict, selective REM deprivation mitigates depression (Vogel, 1975). However, REM deprivation has been found to produce variable and inconsistent results on cognitive function, including learning and memory (Boyce et al., 2017; Vogel, 1975), although some recent data in mice using optogenetic techniques confirms a role for REM sleep in memory consolidation (Boyce et al., 2016).

In summary, REM sleep is a complex behavioral state with a number of possible functions. It is difficult to know what its original function may have been, but several features of REM are consistent with a reduction of vulnerability during sleep. These features could have enhanced the chances of survival, at both individual and group levels, in our evolutionary past. Moreover, one additional feature, increased sexual arousal, could have played a positive, direct role in enhancing the chances of reproductive success. Future research could help determine which features of REM were original adaptations, which ones were exaptations, and which ones best fit the definition of spandrels.
Potential Adaptation No. 2: An Inability to Fall Asleep

Many humans experience difficulty getting to sleep. This difficulty could be the result of a circadian sleep–wake rhythm shifted toward a later bedtime (Abbott et al., 2017; Lack et al., 2017), but it could also be the result of a reduced ability to fall asleep, independent of any circadian rhythm disorder (Bjorvatn et al., 2021). An inability to fall asleep at a “conventional” time is characteristic of delayed sleep–wake phase disorder (Abbott et al., 2017), but individuals with anxiety disorders may also experience problems with sleep onset (Hertenstein et al., 2019).

Survivors of trauma have difficulty falling asleep. Trauma-induced insomnia is in part related to fear of losing the ability to remain vigilant, as would occur during sleep (Werner et al., 2021). In any case, trauma-induced insomnia may be considered adaptive, in that the survivor is on the alert for the re-appearance of whatever caused the individual trauma in the first place. If difficulty falling asleep is not a modern problem but a feature with ancestral roots, the relevant question here is whether it could have served a vigilance function. Problems falling asleep would translate potentially into extended vigilance during the hours of darkness, both for the individual and for one’s group. Difficulty falling asleep in the ancestral environment would have prolonged the period of environmental surveillance, with potential benefits for both the individual and the group to which they belonged.

Costs of Reduced Ability to Fall Asleep

Reduced ability to fall asleep could translate into a net reduction of sleep duration. One cannot assume that those who cannot get to sleep will automatically compensate by sleeping later. Even in non-industrial societies with no cultural requirements for early morning awakening, it may be difficult for some to maintain sleep once morning light appears or an internal circadian rhythm alarm goes off.

The negative consequences of sleep deprivation among contemporary humans are well-documented. These include impairments in mood, learning, memory, cognition, emotional regulation, and motor functions, among others (e.g., Blagrove et al., 1995; Harrison & Horne, 1999; Newbury et al., 2021; Pilcher & Huffcutt, 1996; Schochat et al., 2014; Simon et al., 2021). Sleep durations of less than 6 h per night are linked to a number of medical conditions, including obesity (Jean-Louis et al., 2014; Nielsen et al., 2011; Vgontzas et al., 2014), diabetes (Katano et al., 2011), and cardiovascular disease (Eguchi et al., 2008). On the other hand, a subgroup of people with clinical depression experiences a transient improvement in mood after sleep deprivation (Ioannou et al., 2021). On the whole, however, reduced sleep generally has detrimental effects across a wide range of measures. So, although reduced ability to fall asleep could potentially increase vigilance at the beginning of the sleep cycle, it may also result in significant short- and long-term costs. Those long-term costs would presumably have applied as well to at least some percentage of ancestral humans.

In summary, difficulty initiating sleep could be adaptive in that it prolongs a state of vigilance compared to the state of sleep. Difficulty initiating sleep could serve, in principle, to reduce vulnerability, even if it’s a by-product of something else.

Potential Adaptation No. 3: Frequent Awakenings

In terms of vigilance, ancestral humans, would likely have benefitted from frequent awakenings, whether or not they occurred reliably at the conclusion of REM sleep periods. Among contemporary humans, nocturnal awakenings are quite common. For example, in a large-scale telephone study of 22,740 people conducted across five European countries, 31.2% of those interviewed, ages 15–101, reported awakening at least three nights per week (Ohayon, 2009b). Similar results were found in a survey of 8937 Americans, with 35.5% reporting awakening three or more nights per week (Ohayon, 2009a).

Nocturnal awakenings are caused by a variety of factors. These include the need to urinate, thirst, hunger, noise, children, pain, bed partners, and dreams (Ohayon, 2009a). They are also associated with severe clinical depression (Kupfer et al., 1973). But some awakenings have no discernible cause.

The prevalence of awakenings varies by age group and is a function of the criteria used to define them. For example, a study of frequent nocturnal awakenings in schoolchildren by Li et al. (2014) defined “frequent awakenings” as two or more awakenings per night for at least two nights per week. Using this criterion, these investigators found that approximately 10% of the 20,505 children between five and 12 years of age they randomly sampled displayed frequent awakenings. Using a stricter criterion of three or more awakenings per week, Ohayon found that 50% of adults 65 and older experienced frequent awakenings, and 34.6% reported nightly awakenings (Ohayon, 2009a).

Importantly, frequent awakenings can occur as a result of medical issues and/or psychological stress (Ohayon, 2010). Whether frequent awakenings, in the absence of medical/psychological causes, are a “design feature” that evolved to promote vigilance remains an open question. But by design or default, frequent awakenings, even very brief ones, can provide additional windows of opportunity across the night to monitor the external environment for both threats and opportunities. Again, such monitoring could serve to benefit both the individual and the group.
With respect to opportunities, it is significant to note that frequent awakenings and reduced sleep efficiency are characteristic of one particular eating disorder, anorexia nervosa (Allison et al., 2016; Christensen & Short, 2021; Nobili et al., 1999). From an adaptive perspective, it makes sense that an organism in a state of caloric and nutritional deprivation would be better served by staying awake and monitoring their environment for potential food sources.

Although nocturnal awakenings are quite common, many people are additionally afflicted with an inability to resume sleep, once awakened. An inability to resume sleep can be quite disturbing and even reach the level of clinical significance, earning the diagnostic label of insomnia (Lichstein et al., 2017). In Ohayon’s (2009b) large-scale European telephone study, 16.1% of respondents in the general population complained of an inability to resume sleep after awakening. Difficulty resuming sleep was defined as “a complaint of nocturnal awakenings accompanied by a complaint of difficulty resuming sleep OR an inability to resume sleep” with these complaints “occurring at least three nights per week for at least one month” (p. 935). About 59% reported the ability to resume sleep, but about 41% “were unable to get back to sleep and stayed awake most of the time” (p. 936). In Ohayon’s American sample, of those who reported awakening three or more times per week, 43% reported “great difficulty resuming sleep once awakened” (p. 50). Among those with diagnosed insomnia, the inability to resume sleep is more common than the ability to initiate sleep (Bjorvatn et al., 2021; Buysse, 2013).

Some groups are more prone to insomnia than others. For example, women experience a higher rate of insomnia complaints than men (Lichstein et al., 2017). Insomnia is especially common in the elderly (Patel et al., 2018). Yetton et al. (2018) found increased sleep fragmentation (i.e., sleep interrupted by awakenings), reduced SWS duration, and reduced duration of morning REM in middle-aged and elderly individuals. Disturbances in sleep maintenance frequently co-occur in those with anxiety disorders, clinical depression, and medical problems that involve physical pain (Ohayon, 2009a, 2010; Vargas & Perlis, 2020). Also, one of the causes of insomnia is understood to be hypervigilance and arousal during waking/daytime that extends into the night (Lichstein, 2017; Schneider et al., 2019). Finally, there are documented cases characterized by the subjective perception of being awake and unable to sleep despite objective EEG evidence to the contrary. The latter condition is known as paradoxical insomnia, formerly called sleep state misperception (Rizaei et al., 2018). Instances of insomnia in these populations could reflect the inheritance of functional biological tendencies, or simply be the result of enhanced perception of social, environmental, and disease threats.

One of the causes of insomnia is daytime hyperarousal that carries over into the night. Even if evolution did not select for traits like anxiety and depression with accompanying insomnia, it did not select against them. Regardless of their origins, and in spite of their costs, any condition that results in insomnia increases the chances of vigilance, along with the positive opportunities that wakefulness provides, such as finding food, socializing, or engaging in sex.

Returning to the higher rates of insomnia in women, one evolutionary interpretation is that this tendency is consistent with greater chances for detecting and surviving external threats, given the smaller size and reduced muscle mass of women compared to men. It may also be adaptive in terms of protecting one’s children, especially infants and small children. A third possible biological function of a tendency toward insomnia relates to monitoring infant awakening for the purposes of optimizing breastfeeding (Mosko et al., 1997a, b).

But labeling certain sleep phenomena as insomnia, and therefore a sleep disorder worthy of treatment, is based in no small part on cultural expectations. In Western, industrialized nations we assume that that “normal” sleep is continuous and uninterrupted. But that’s not the case in indigenous hunter-gatherer societies. Rather, the norm is for sleep to be frequently interrupted, because of noise, conversation, singing, dancing, and/or music, or by someone inviting you to participate in an interesting waking activity deemed more important than sleeping (Galinier et al., 2010; Worthman & Melby, 2002). In many non-industrial societies the boundaries between sleep and waking are much more fluid, and sleep is not treated as a private activity, one that should not be interrupted (Yetish & McGregor, 2019; Yetish et al., 2015).

Despite the aforementioned discussion, it is possible that a certain amount of periodic awakening throughout sleep is built into our brains, independent of cultural and medical considerations. Historical and anthropological evidence is abundant for the existence of a lengthy period of awakening after several hours of sleep, followed by another segment of sleep that typically lasts several hours. Ekirch (2005) noted such a pattern when examining diaries of people in North America and Europe during the early modern era, roughly 1500 to 1750. Diarists kept referring to “first sleep” and “second sleep” along with descriptions of how they spent their time during the lengthy period of awakening between these sleep periods. Such segmented sleep has been documented in the nineteenth and twentieth centuries by ethnographers in groups not exposed to modern electric lighting (Ekirch, 2016). Groups exhibiting segmented sleep include the Surinamese Maroons on the northeast coast of South America, the Asante and Fante on the west African coast, the Tiv of central Nigeria, the Sinhalese of Ceylon (now Sri Lanka), and the Woolwa of Central America. It is also been found
example, during migration season, the nighttime migrating
animals that are able to secure safe sleeping locations within
their particular ecological niche sleep longer (Nunn et al.,
2018). Comparative analysis across mammalian species
shows that sleep duration inversely correlates with preda-
tion risk (Capellini et al., 2008). Sleep duration also varies
among species, with a higher ratio of REM sleep to total sleep duration than any
other primate whose sleep architecture has been investigated thus far. Nunn and Samson (2018)
found that humans were predicted to have sleep durations of
9.55 h. The fact that average human sleep durations are much
less than 9.55 h suggests that human sleep evolved to be more
“intense”. In fact, humans have a shorter sleep duration and a higher ratio of REM sleep to total sleep duration than any
other primate whose sleep architecture has been investigated thus far. Nunn and Samson suggest that humans have been

Costs of Frequent Awakenings

Frequent awakenings may contribute to reduced overall sleep
quantity and quality. As noted previously, the consequences
of sleep deprivation are well-documented and numerous.
Although frequent awakenings, whether or not the person
awakened is able to quickly get back to sleep, can potentially
enhance night time vigilance, they can also contribute to
next day impairments. Such impairments would also have
applied to ancestral humans, potentially affecting their abil-
ity to function in the context of a wide range of day time
activities, including hunting, fishing, foraging, searching for
water sources, building protective dwellings, etc.

In summary, frequent awakenings could serve to enhance
vigilance and promote environmental surveillance. Whether
a tendency toward frequent awakenings is a heritable trait,
is unknown, but in principle it provides another potential
mechanism for reducing vulnerability.

Potential Adaptation No. 4: Reduced Sleep Duration
and/or Periodic Total Absence of Sleep

A reduction in sleep duration, independent of problems
going to sleep or staying asleep, translates into a greater
number of hours of wakefulness. An increase in waking
time could have served to enhance vigilance in the ancestral
environment, especially during the night, the most vulner-
able period of time for humans.

A generalization across the animal kingdom is that ani-
mals that are more at risk from predators sleep less while
animals that are able to secure safe sleeping locations within
their particular ecological niche sleep longer (Nunn et al.,
2016). Comparative analysis across mammalian species
shows that sleep duration inversely correlates with predation
risk (Capellini et al., 2008). Sleep duration also varies
depending on seasonal needs and reproductive needs. For
example, during migration season, the nighttime migrating
bird Swainson’s thrush shows a substantial reduction of
nighttime sleep (66.6%), with a shift toward multiple, brief
daytime naps on a scale of seconds (Fuchs et al., 2006).
Similar sleep reductions are found in white-crowned spar-
rows during the migration season (Rattenborg et al., 2004).
For the first month following birth, killer whales and bottle-

nose dolphins and their mothers do not sleep at all (Lyamin
et al., 2005). For humans living in polar environments, sleep
is significantly reduced or shifted during times of the year
characterized by long days and short nights, as has been
found among the Inuit people (Galinier et al., 2010).

A certain percentage of the human population consistently
obtains less than 6 h of sleep per night (Jean-Louis et al.,
2014). This population can be subdivided into three groups.
The first group consists of those with insomnia. They would
like to get more than 6 h of sleep per night, but are unable
to do so. The second group needs more sleep, biologically
speaking, but chooses to forego it in favor of staying awake.
This second group is chronically sleep deprived. The third
group, however, may have a reduced biological need/drive
for sleep as a genetic trait (Aeschbach et al., 2003; Landolt,
2008; Webb & Fu, 2021). Indeed, genes have been identified
that are linked with short sleep durations and resistance to
the effects of sleep deprivation (e.g., Pellegrino et al., 2014).
Also, a reduced need for sleep appears to characterize peo-
ple during the manic state of bipolar disorder (Gruber et al.,
2011; Serretti & Olgiati, 2005), with anecdotal reports of
some unmedicated individuals going for days without sleep
(Gillin, 2002). [For a more in-depth discussion, the role of
genes in regulating sleep duration has been reviewed recently
by Webb and Fu (2021)].

It is possible, perhaps even probable, that short sleep
duration emerged in our evolutionary past for reasons other
than enhanced vigilance for threat detection. In the ancestral
environment, more time awake meant more time for hunting,
fishing, socializing, sex, and other productive activities, with
benefits to both the individual and the group. Consistent
with this line of discussion, Kasaeian et al. (2019) found, in
a modern sample, that shorter sleep durations correlated with
having more children.

Samson and Nunn (2015) and Nunn and Samson (2018)
have argued that human sleep, relative to the sleep of other
primates, evolved to be shorter, deeper, and to contain more
REM sleep as a proportion of total sleep time. In their phy-
logenetic modeling of primate sleep durations, which takes
into account 30 primate species, Nunn and Samson (2018)
found that humans were predicted to have sleep durations of
9.55 h. The fact that average human sleep durations are much
less than 9.55 h suggests that human sleep evolved to be more
“intense”. In fact, humans have a shorter sleep duration and
a higher ratio of REM sleep to total sleep duration than any
other primate whose sleep architecture has been investigated
thus far. Nunn and Samson suggest that humans have been
able to fulfill the biological needs that sleep delivers in a highly efficient manner, while maximizing waking time. A shorter sleep time would have reduced predation risk, as well as yielded more waking time to support opportunities for a variety of cognitive, social, and creative functions that characterize our species (Samson, 2021).

Interestingly, reduced sleep duration at night seems to be the norm in many non-industrial cultures. Yetish et al. (2015) studied sleep in three non-industrial cultures: the Hadza of northern Tanzania, the San of the Kalahari, and the Tsimane of Bolivia. Actigraphic studies showed an average sleep duration ranging from 5.7 to 7.1 h per night in these three geographically and genetically diverse groups, despite spending longer times in bed than people in industrialized societies. Similarly, in their study of the Malagasy of Madagascar, Samson et al. (2017a) found an average sleep duration of 6.5 h per night. In their investigation of the Himba of Namibia, semi-nomadic pastoralist society, Prall et al. (2018) found a mean sleep duration of 5.47 h, supplemented by an average of 50 min of nap time among that portion of the population who takes naps at least occasionally, which was 76% of those studied.

However, longer sleep durations have been found in other studies among indigenous societies living without electricity. de la Iglesia et al. (2015) observed sleep durations of closer to 8 h among the Toba/Qom of the Argentinian Chaco, who live a traditional lifestyle with no electricity. In contrast, other Tabo/Qom who live in environments with electricity were found to sleep less, although both groups showed shorter sleep durations during the summer than in the winter. Smit et al. (2019) also found sleep durations close to 8 h among indigenous Melanesians living on Tanna Island, Vanuatu, whose latitude (19°53’ S.) is close to that of the Hadza, San, and Tsimane. Siegmund et al. (1998) recorded sleep durations among adult Trobiand Islanders of Papua New Guinea ranging from 7 to 10 h, with a mean duration of 8.4 h.

Importantly, people in the “short-sleeping” cultures do not complain about being tired and not getting enough sleep (at least such complaints are not noted in published reports), even in those populations that do not typically nap. Also, to my knowledge, none of the short-sleeping cultures depend on caffeinated beverages or any other kind of stimulant to function on a daily basis. Follow up research is certainly warranted to determine what factors separate these “short-sleeping” cultures from “longer-sleeping” cultures, whose sleep durations are more in line with those found in modern, industrial societies, at least among the segment claiming to get sufficient sleep on a regular basis.

In the context of discussing reduced sleep duration as an evolutionary adaptation, an additional dimension worth mentioning concerns age-related changes in sleep duration. As noted above, insomnia complaints are common among the elderly in modern, industrialized societies.

Reduced sleep duration, with or without complaint, means a longer period of nighttime waking vigilance. But another way of looking at this issue is that the biological need for sleep is reduced in this age group, at least compared to teens and young adults, whose sleep durations tend to be relatively long (Fischer et al., 2017). Young people tend to be more physically, socially, and sexually active compared to elderly populations. This is the time of life that coincides with high levels of sexual interest and fertility (Rothman et al., 2013). If sleep duration is at least partially linked to reproductive function, then one might expect a reduced need for sleep as fertility wanes across the lifespan. On the other hand, a longer sleep duration means less time for sexual activity, which normally occurs in the waking state.

The data discussed in this section invariably point to the inherent ecological trade-off between the biological costs and benefits of sleeping versus staying awake. Arguably, any discussion of “normal” sleep duration in the context of healthy sleep recommendations would need to take the aforementioned anthropological data into account, since hunter-gatherer societies more closely approximate life in the ancestral environment compared to the lifestyles of people in modern, industrial societies. But such discussions would also need to consider important components of modern lifestyles that may increase the biological need to sleep longer, such as increased social stress, a topic beyond the scope of this paper (but see Slavich, 2020). Ultimately, what matters most is how people feel the next day and whether the amount and type of sleep they’re getting leads to impairment in functioning (Ohayon, 2009b, 2010; Shekleton et al., 2014).

**Costs of Reduced Sleep Duration**

Sleep length and sleep needs are quite variable. If a person feels good and functions well the next day, a shorter sleep length is not inherently problematic. In any event, the increased potential for nighttime vigilance and the benefits that go along with it are offset by the costs attached to insufficiently short sleep durations in those whose sleep durations do not match their sleep needs. Ancestral humans whose sleep length was too short to match their biological needs would presumably have suffered negative outcomes at least somewhat similar to those experienced by our sleep-deprived contemporaries.

In summary, a biological tendency toward reduced sleep duration increases the potential for monitoring the environment for potential threats, especially during a time when humans are most vulnerable to them. Of course, reduced sleep duration increases opportunities for positive survival-related behaviors that depend on wakefulness, such as finding food, water, and mates.
Potential Adaptation No. 5: “Light” Sleep

What constitutes “light sleep” depends in part on the species under discussion, but also precisely on how one defines it, with respect to sleep parameters. One example of “light sleep” is the behavioral state of drowsiness, a hybrid state of sleep and wakefulness found in some species of mammals as well as birds (Lima et al., 2005). Drowsiness is characterized by immobility, relative unresponsiveness, and eyes that are “at least partially opened” (Lima et al., 2005, p. 732). In addition to drowsiness, some bird species, such as diving ducks and mallards, can engage in “peeking”, i.e., short durations of eye opening against a backdrop of eye closure and sleeping (Gauthier-Clerc et al., 2002; Lendrem, 1983). Lima et al. (2005) opine that “there are almost certainly specific neural structures devoted to monitoring the predatory environment during sleep” (p. 732), citing the work of Lang et al. (2000) and Ohman and Mineka (2001). We humans can also experience drowsiness and hybrid states of sleep and wakefulness.

Before delving too deeply into a discussion of this potential adaptation as it applies to humans, a brief review of human sleep architecture is in order. Some of this discussion was covered earlier, but a review with elaboration is warranted in this context. In the human sleep literature, “deep sleep” typically refers to slow-wave sleep, also known as stages 3 and 4 of sleep, or stage N3 in the newer sleep nomenclature (Iber et al., 2007). By comparison, “light sleep”, or at least “lighter sleep”, would include stages 1 and 2 (N1 and N2) and perhaps REM sleep as well. A “light sleeper,” then, would be someone who experiences a lower percentage of slow-wave sleep (N3) than those who are not “light sleepers.” But the term “light sleeper” is also used in a behavioral sense to refer to someone who is easily aroused from sleep by external stimuli. A “light” sleeper presumably would be more vigilant than a “deep” sleeper, as the auditory thresholds during stage 2 and the tonic phases of REM are lower than the threshold for auditory stimuli during slow-wave sleep (Rechtschaffen et al., 1966). Moreover, awakening from slow-wave sleep is more likely to elicit grogginess and slowness in responding compared to awakening from other stages of sleep (Dinges et al., 1985; Tassi & Muzet, 2000), although discrepancies exist in this literature (Hilditch & McHill, 2019). But even without an external disturbance, people are more likely to awaken spontaneously from REM than from other stages of sleep (Campbell, 1985; Ficca et al., 1999). They are also more likely to be awakened during REM sleep by meaningful stimuli compared to non-meaningful stimuli (e.g., the sound of one’s name) compared to stage 2 sleep (Langford et al., 1974). So those whose sleep architecture is characterized by a higher percentage of REM sleep might be considered “light sleepers” on the basis of this criterion alone. For our purposes, it might be best to set aside the nuances of sleep stages and consider a light sleeper as one who fulfills any of the following criteria: more easily awakened by external stimuli, more alert once awakened, and/or more frequently awakened. At the end of the day (and into the night) a “light sleeper” is arguably more likely to be vigilant and attuned to their external environment than a “deep sleeper.” It is also the case that human sleep is skewed toward lighter sleep, given that only about 10–20% of a typical night of sleep is N3 sleep.

The concept of sleeping “lighter” as a biological strategy to enhance vigilance is supported by at least one anthropological example. Prior to the 1970s, the San were a nomadic people who moved around in order to seek out water sources. The first night after arriving at a new location, the older San adults, who remember their nomadic ways, report that they slept “lighter” compared to subsequent nights. Upon inspecting the surrounding areas the next day for evidence of potential threats, and finding none, they report sleeping more deeply on the nights that followed, presumably because of feelings of improved security (Yetish & McGregor, 2019). In the modern world, people tend to sleep poorly the first night in a sleep research laboratory, so much so that the first night’s data are typically not used. Not surprisingly, this phenomenon is referred to as the “first night effect” (Agnew et al., 1966; Lee et al., 2016; Tamaki et al., 2005a) and can occur even in people who are not predisposed towards suffering from an anxiety disorder (Tamaki et al., 2005b). Even in non-laboratory settings, abundant anecdotal evidence suggests that people sleep lightly (i.e., poorly) in a new sleep location. More in-depth analysis of the first-night effect suggests, however, that a number of sleep parameters are altered. These include lower sleep efficiency (i.e., less time sleeping compared to time in bed), increased wakefulness, longer sleep latency, longer REM latency, and decreased REM sleep (Toussaint et al., 1995). These changes are generally consistent with increased opportunities for vigilance, but are not entirely consistent with the definitions of “light sleep” presented earlier in this section. One might expect to see reduced slow-wave sleep, but that’s not what’s found. At the very least, the first-night effect is arguably an evolutionary adaptation that enhances vigilance and scanning for potential threats, even if it is appropriate to consider it more aligned with adaptations 2–5 above. The decreased amount of REM sleep and decreased REM latency of the first night effect suggest a more nuanced view of REM sleep as an adaptation promoting vigilance, as argued for in Adaptation No. 1.

Regarding the concept of “light sleep,” it is important to recognize that the boundaries between sleep and waking in humans can be quite fuzzy (Mahowald & Schenck, 1992). For example, in the parasomnia condition known as sleep paralysis with hypnagogic (at sleep onset) or hypnopompic (upon awakening) hallucinations, an individual might experience elements of REM sleep alongside waking. In disorders
of arousal, such as sleepwalking, an individual can experience elements of non-REM sleep, including low frequency high-voltage, synchronized EEG waves characteristic of N3 sleep, alongside waking activity, including complex motor activity, such as driving an automobile (Leschziner, 2019). Disorders like these may have consequences that ultimately reduce vulnerability, such as scaring off intruders or awakening other sleepers nearby. At the cultural level, anthropological work in non-industrial societies also supports the idea of reduced boundaries and increased fluidity between sleep and waking states (Yetish & McGregor, 2019), a factor addressed in more detail below.

In any case, “light” sleeping in the ancestral environment, at least under some circumstances, such as moving one’s camp to a new location, could have enhanced monitoring of the external environment for potential threats.

Costs of “Light” Sleep

Excessive amounts of “light” sleep translate into less N3 (slow-wave sleep) in humans. As discussed earlier, slow-wave sleep appears to be important for immune function, memory consolidation, and the removal of toxins. Thus, too much “light” sleep at the expense of deep (i.e., N3/slow-wave) sleep could potentially impair these functions in the individual and, by extension, one’s group.

In summary, a biological tendency towards “light” sleep could increase the chances of monitoring the environment for potential threats and, if detected, responding more quickly to those threats.

Potential Adaptation No. 6: Continued Sensory Monitoring of the External Environment During Sleep

Perhaps the best real-life illustration of the brain’s ability to monitor the external environment for meaningful information during sleep is the well-known ability of mothers of newborn infants to awaken in response to their infant’s crying, while others in the household continue to sleep. It is possible that women, more than men, are biologically predisposed toward both lighter sleep and greater sensitivity to the external environment, for evolutionary reasons related to care-taking of infants at night. Another possible biological reason for such a predisposition in women is personal protection, given their generally smaller size and reduced muscle mass compared to men, as already noted. Interestingly, mothers who co-sleep with their infants in the same bed experience more frequent arousals from sleep, as do their infants, without affecting total sleep amount (Mosko et al., 1997a, b).

In the laboratory, a significant amount of data has been collected that documents the ability of the sleeping brain to monitor the external environment for sensory change, regardless of gender. As discussed earlier, externally delivered sensory stimuli have been shown to evoke electrical potentials in the cerebral cortex in all sleep stages (Bastuji & Garcia-Larrea, 1999). The sleeping brain can respond to external auditory stimuli (Blume et al., 2018; Perrin et al., 1999; Portas et al., 2000). This enhanced responsiveness to relevant external events may be hemisphere specific, as discussed in more detail below in the section entitled “Potential Adaptation No. 9: Localized sleep in the brain.” Perhaps even more impressively, the sleeping brain can learn new information in response to external sensory stimulation (Rasch et al., 2007). In recent years, multi-modal imaging studies have underscored the ability of the sleeping brain to respond to the external environment and have further blurred the distinctions between sleep and wakefulness (Song & Tagliazucchi, 2020).

Costs of Continued Sensory Monitoring During Sleep

The relationship between monitoring of the external environment during sleep and its impact on sleep-related processes, such as immune function, memory consolidation, and plasticity are poorly studied and largely unknown. We also know little about the extent to which increased sensory monitoring may occur independent of reductions in sleep stages, especially N3 sleep. In principle, excessive sensory monitoring during sleep, even in the absence of awakening, could lead potentially to reductions in time spent in particular sleep stages, especially N3 sleep, with consequent impairments in mood, cognitive function, motor function, immune function, memory consolidation, plasticity, etc. So any benefits that increased sensory monitoring may bring to the individual and the group in terms of enhanced vigilance may come at a cost to both, in terms of processes that depend on sleep continuity and time spent in specific stages of sleep. Such costs would presumably have applied to ancestral humans.

In summary, the ability to monitor the environmental for sensory changes relevant to survival would have benefited ancestral humans, whether such monitoring occurred in the context of the aforementioned “light” sleep or independent of sleep stage.
Potential Adaptation No. 7: Redistribution of Sleep Across the 24-H Sleep/Wake Cycle

The concept of redistribution of sleep was introduced earlier in the case of the Swainson’s thrush. In our species, napping is common and many cultures employ a socially sanctioned daytime period of sleep (e.g., the “siesta”), especially during the mid-afternoon in climates characterized by high temperatures (Webb & Dinges, 1989; Worthman & Brown, 2007; Worthman & Melby, 2002). The motivation for initiating the siesta is probably rooted in avoiding activity during the hottest time of the day, but a case has been made that siestas may have originated in response to environments where infectious diseases were extant (Barone, 2000). Regardless of their origin, an ancillary benefit of siestas is less sleep time during the nighttime hours when vision is poor and nocturnal predators are afoot. Siestas are prevalent in a variety of cultures and locations, including Mediterranean countries, Latin America, and China (Fang et al., 2013; Naska et al., 2007; Webb & Dinges, 1989; Worthman & Brown, 2007), but can be found throughout the world, especially in non-industrial cultures (Barone, 2000).

In addition to siesta cultures with socially sanctioned midday periods of sleep, some cultures embrace unscheduled napping on an as-needed basis, including sleeping in public places and in social situations. Such an acceptance is not limited to non-industrial societies. For example, the Japanese have the practice of inemuri, which is sleeping in public during the day, such as at work, school, and on trains (Steger, 2003). Social acceptance of inemuri depends on context, including social rank. A person engaging in inemuri is assumed to be tired from staying up too late, especially because of work. The hours that would have been spent sleeping are instead spent awake and engaged in working/studying. However, this strategy of sleeping less at night and taking unscheduled naps during the day is rooted in enhanced work productivity and sleep efficiency, not out of any quest for enhanced nighttime vigilance. Although greater nighttime vigilance would be an ancillary benefit of this strategy, its need and value are reduced in a relatively safe country like Japan.

Another example of sleep redistribution is the alternation between periods of sleep and wakefulness across the nighttime (Worthman & Melby, 2002; Yetish & McGregor, 2019; Yetish et al., 2015). Roger Ekirch’s historical work on sleep during the early pre-modern era shows the prevalence of two periods of sleep interrupted by a bout of wakefulness around midnight recorded in diaries of Europeans and North Americans prior to the advent of electricity, i.e., segmented sleep (Ekirch, 2005). References to segmented sleep span cultures and historical periods (Ekirch, 2016), with the oldest known reference to “first sleep” found in Homer’s Odyssey, dated almost 3000 years ago (Ekirch, 2018). Segmented sleep has been documented by nineteenth and twentieth century ethnographers in a variety of groups not exposed to modern electric lighting, as well as more recently in a rural community in Madagascar that lacks electricity infrastructure (Samson et al., 2017c).

The hypothesis that the development of electric lighting accounts for the historical shift away from segmented sleep and toward consolidated sleep during the night has some empirical support. Wehr (1992) was able to induce segmented sleep in a modern sample by imposing a 10-h photoperiod with a laboratory “bedtime” of 1800 in an environment of total nighttime darkness. Participants gradually developed a biphasic sleep pattern consisting of two bouts of sleep, several hours in duration, separated by a period of awakening in the middle of the night that lasted from 1 to 3 h.

On the other hand, de la Iglesia et al. (2015) found no evidence for segmented sleep in their study of two indigenous hunter-gatherer communities (the Toba/Qom) in Argentina, one of which had access to electricity while the other did not. As expected, the community with electric lights showed later bedtimes and a shorter overall duration of sleep compared to a similar community with no access to electric lights. But the no-electricity community failed to show evidence of a biphasic sleep pattern. Similarly, a study of the indigenous Melanesians who live without electric lights on Tanna Island, Vanuatu found only scant evidence for segmented sleep (Smit et al., 2019). Adding to the list of non-industrial cultures that fail to show segmented sleep are the Hadza of northern Tanzania, the San of the Kalahari, and the Tsimane of Bolivia (Yetish et al., 2015). But a critical variable may be nighttime duration: at the subtropical and tropical latitudes where the aforementioned groups reside, the duration of darkness may not be long enough to generate segmented sleep patterns. In the case of the Toba/Qom of Argentina, for example, nighttime reaches a maximum length of 12.3 h during the winter months.

Segmented sleep may also depend on cultural conditions that emphasize greater uniformity in bedtimes, rising times, and other sleep parameters. In this context, it is important to reiterate that throughout much of the non-industrialized world, much greater fluidity and fuzzier boundaries exist between sleep and waking than what is found in the industrialized societies and assumed to be “normal” for our species (Worthman & Melby, 2002; Yetish & McGregor, 2019).

An additional variable that may be relevant in segmented sleep is sleep duration. In their investigation of three geographically disparate non-industrial communities that failed to show segmented sleep, Yetish et al. (2015) found average sleep durations of 5.7 to 7.1 h. On the other hand, the study by Samson et al. (2017a) of the Malagasy of Madagascar that uncovered evidence for segmented sleep found an average sleep duration of 6.5 h in that community. Sleep
duration, variability in bedtimes, nighttime length, and availability of electricity may all be contributing factors in determining whether segmented sleep is likely to occur in any given population. More work is needed to sort out these variables, but it is evident that human sleep is quite plastic and flexible (Yeth & McGregor, 2019).

One last example of redistribution can be found in cultures that exist at polar latitudes. For example, during the late spring and summer the Inuit will shift their sleeping until the morning hours, allowing them to continue hunting and engaging in other activities throughout their extended, very long days (Galinier et al., 2010). Of course, shift workers in modern societies do the same for occupational reasons that are independent of day/night cycles.

Ancestral humans could have benefitted from redistribution of sleep from night to day. Seasonal redistribution of sleep might have increased opportunities for securing some kinds of food sources. A shift from night sleep to sleeping during the day would also have increased vigilance during the hours when humans are most vulnerable.

Costs of Sleep Redistribution

Although redistributing sleep from night to day enhances vigilance during the vulnerable nighttime hours, it can also lead to missed opportunities for the individual, such as socializing, hunting, foraging, etc. Groups may also suffer if too many of its members are sleeping throughout the day, especially when it comes to activities that require group cooperation in large numbers, such as hunting and building.

A modern manifestation of sleep redistribution can be seen in night shift work. Although it arguably benefits human societies as a whole, night shift work is associated with significant costs for the individuals who undertake it. Over long periods it has been linked to a number of negative health conditions, such as type 2 diabetes, obesity, clinical depression, and breast cancer (Moreno et al., 2019; Ramin et al., 2015; Torquati et al., 2019; Wegrazyyn et al., 2017).

It is unknown whether ancestral humans would have engaged in anything approximating contemporary night shift work on a protracted basis. If any of them did, they might have suffered some of the same consequences as modern humans. However, one major difference between us and them is that their night shift work would not have involved the kinds or degrees of artificial lighting that characterize modern work settings. Thus, they would have been spared any negative effects that might be specific to modern artificial light sources. Other differences specific to modern humans, such as exposure to recently created environmental toxins, sedentary lifestyles, and diets laden with fat, sugar, and salt, must also be considered.

In summary, a biological tendency toward sleep redistribution in our evolutionary past could have shifted some portion of sleep to daylight hours, thus increasing wakefulness at night and reducing vulnerability to threats. A biological tendency toward sleepiness in the midafternoon could also have served conservation functions with respect to both energy and water usage during the time of maximal temperature.

Potential Adaptation No. 8: Increased Fear and Anxiety Responses at Night and During Sleep

Darkness provokes fear and anxiety responses in our species (Gordon et al., 2007; Levos & Zacchilli, 2015; Simon & Bögels, 2009). Fear of the dark is one of the most common phobias among children 8–12 years of age, accounting for 27% of all specific phobias in this age group (Simon & Bögels, 2009). A survey of 122 undergraduate students found that fear of the dark was rated one of the top five fears by over 50% of those studied (Levos & Zacchilli, 2015). Such fears may be explained, at least in part, by the increased threats that the nighttime brings, one of which is nocturnal predators. Humans, along with our primate relatives, have been hunted by large carnivores presumably since our origin as a species (Coss & Moore, 2002; Ehrenreich, 1997; Hart & Sussman, 2009). Among our primate relatives, baboons, for example, are targets of predation both day and night. Relevant to this discussion, one of their natural predators, leopards, has been found to be more successful hunting these primates at night than during the day (Cowlishaw, 1994). But the category of potential nocturnal predators extends, of course, to members of our own species. And that’s just natural predators. Malevolent spirits and other supernatural threats have also been associated with darkness and the nighttime across historical periods and cultures (Ekirch, 2005; Koslofsky, 2011; Worthman & Melby, 2002). Darkness and the nighttime were greatly feared by Europeans during the early modern era (Ekirch, 2005; Koslofsky, 2011; Millar, 2018) and continue to be a source of concern across a multitude of non-industrial cultures in the present era (Worthman & Melby, 2002). These fears were likely to have been—and still are—reinforced by negative dream experiences, including nightmares, night terrors, and hypnagogic (at sleep onset)/hypnopompic (upon awakening) hallucinations, which often accompany sleep paralysis (Arnulf, 2017; Bearden, 1994; Cheyne & Girard, 2007; Fisher et al., 1974; Gieselmann et al., 2019; Keith, 1975). The latter experience is also sometimes referred to as the incubus/succubus phenomenon. It arises out of sleep and involves an inability to move and a sense of pressure on one’s chest. The experience often includes a feeling of a presence in one’s room, frequently interpreted as having evil intent. The famous painting The Nightmare by the Swiss artist Henry Fuseli depicts this experience. As a testament to its emotional resonance, over 55,000 people viewed this painting when it was
first exhibited in London in 1782 (McNamara, 2008). As Broughton (1968) notes: “The German word Nachtmar and the French word, cauchemar, both contain the Teutonic root, mar, which means ‘devil’. Cauchemar also derives from caucher, an ancient French verb meaning ‘to press’, thus literally referring to a ‘pressing devil’” (p. 491). Many people in many different cultures throughout the world attribute this experience to a demon or evil spirit sitting on one’s chest. The incubus experience may be the origin of the word nightmare, which in common use today has a different meaning. In contemporary usage, a nightmare refers to an unpleasant dream experience, typically associated with REM sleep, that “usually involves threats to survival, security, or physical integrity” (Gieselmann et al., 2019, p. 1).

It is possible—perhaps even likely—that a predisposition toward fear of the dark and anxiety about the terrors it may hold is built into human neural circuitry. As a result, these negative emotions might be superimposed on the sleeping brain, with downstream effects on dreams. Both nightmares and sleep terrors may reflect the influence of evolutionary ancient forces at work. Boyden et al. (2018), for example, have suggested that night terrors in children may have evolved for the purpose of bringing small children closer to sleeping parents and guardians, decreasing the chances that they would be carried off by a nocturnal predator. Nightmares, too, may be adaptive. McNamara and Szent-Imrey (2007) and McNamara (2008) have presented the argument that someone experiencing a nightmare could have advanced their own status within their social group by claiming privileged access to the spirit world, access that could ultimately benefit their group. Nightmares would not only have made the person who experienced them more likely to remain awake in a state of vigilance, but also heighten the overall level of vigilance within their group upon reporting their nightmare to others.

In any case, ancestral humans who experienced fear and anxiety at night would have had difficulty getting to sleep and staying asleep. As a result, their prolonged periods of wakefulness could have served to enhance nighttime vigilance. Anxious, fearful humans are attentive humans. They would presumably have been primed to detect any nocturnal threats that may have emerged, benefiting themselves and their social groups.

Costs of Increased Fear and Anxiety at Night and During Sleep

Although increased fear and anxiety at night may result in a net increase in vigilance during the most vulnerable time of the day for our species, it comes with several potential costs. It may impair sleep quality and quantity, leading to the negative consequences that accompany sleep deprivation, in terms of next day functioning. Negative dream experiences may also result in powerful feelings and memories that carry over into the next day, further distracting and impairing the individual. In addition, such experiences may contribute to sleep avoidance, with further reductions in sleep quantity and a reduction in the benefits that sleep delivers, as already discussed. Ancestral humans experiencing anxiety and fear at night, including negative dream experiences such as nightmares and night terrors, would presumably have suffered the same psychological consequences as contemporary humans beset by these phenomena, perhaps even rising to the level of what we today label as nightmare disorder (Arnulf, 2017; Bearden, 1994; Gieselmann et al., 2019).

In summary, a biological tendency to be fearful at night, specifically in response to darkness, could have had adaptive benefits in our evolutionary past, enhancing vigilance and environmental surveillance for potential threats. Such a tendency could have, in principle, reduced vulnerability associated with sleep and the night.

Potential Adaptation No. 9: Localized Sleep in the Brain

The prototype of this category is unihemispheric sleep. While one hemisphere is enjoying the benefits of sleep, the other hemisphere is awake and monitoring the environment. Unihemispheric sleep has been observed in a variety of species, including cetaceans (dolphins, porpoises, and whales), eared seals, manatees, walruses, some species of birds (e.g., gulls, mallards, Japanese quail, European blackbirds, and domestic chicks) (Mascetti, 2016; Rattenborg et al., 2000) and possibly crocodiles as well (Kelly et al., 2015). Often, but not always, the eye contralateral to the awake hemisphere remains open, presumably to monitor the external environment and/or to guide movement, while the ipsilateral hemisphere is asleep. Some animals that employ unihemispheric sleep can switch to bihemispheric sleep, as conditions dictate. In mallard ducks, for example, those that sleep on the perimeters of a line do so with one eye open directed away from the center of the sleeping group. In this fashion the awake contralateral hemisphere can monitor the external environment in the direction where threats are likely to approach. In contrast, those in the middle sleep with both eyes closed, reflecting bihemispheric sleep (Lima et al., 2005; Rattenborg et al., 1999a, b). Migrating birds (Rattenborg et al., 2016) and fur seals (Kendall-Bar et al., 2019) can also switch from bihemispheric to unihemispheric sleep. In the previously cited example of birds, those sleeping in the middle of the line may be employing bihemispheric sleep. While unihemispheric sleep, strictly speaking, does not occur in humans, blended states of sleep and wakefulness occur in some non-REM sleep disorders (Baldini et al., 2019; Mahowald & Schenck, 1992). Moreover, there is at least one circumstance under which hemispheric asymmetries in sleep have been observed to occur: The first night
of recording in a sleep laboratory. Tamaki et al. (2016) found reduced sleep depth in one hemisphere compared to the other under these circumstances. Moreover, the hemisphere experiencing reduced sleep depth, typically the left hemisphere, showed enhanced evoked brain responses to deviant auditory stimuli. Enhanced responsiveness to these deviant auditory stimuli occurred during slow-wave sleep.

Abundant evidence exists across species that some brain areas can be asleep while others, at the same time, are awake (Nobili et al., 2011; Song & Tagliazucchi, 2020; Vyazovskiy et al., 2011). Corroborating evidence can be found in our species across a number of sleep disorders, in which elements of REM sleep, non-REM sleep, and waking can be found simultaneously, as previously discussed (Antelmi et al., 2015; Mahowald & Schenck, 1992). In principle, localized sleep alongside localized wakefulness could result in an individual better able to respond to external threats.

Ancestral humans who experienced localized brain areas of wakefulness in parallel with localized areas of sleep may have been positioned to better monitor the external environment and interact with it, thus enhancing net vigilance for themselves and for their social groups.

Costs of Localized Sleep

Localized sleep can result in blended states of sleep and waking, as discussed earlier. Blended states can be problematic for the individual sleeper and for the group. People experiencing blended states may be subject to night time wandering, putting themselves at risk (Baldini et al., 2019). Night time wandering may enhance the chances of attracting the attention of nocturnal predators, increasing the risk of hypothermia, or rendering the individual susceptible to accident. Also, people experiencing blended states may act out their dreams, sometimes resulting in violence against others, even when those others pose no actual threat (e.g., Schenck et al., 1989). Localized sleep and blended states of sleep and wakefulness may be the result of opposing evolutionary forces, both positive and negative. For our species, localized sleep appears to incur greater potential net costs compared to net benefits. It is difficult to know whether localized sleep would have provided a net benefit or a net liability for ancestral humans.

In summary, a biological tendency toward localized sleep could have translated into mixed states of sleep and wakefulness in our evolutionary past, with respect to both brain activity and behavior. Mixed states allow for experiencing the benefits that sleep delivers while simultaneously delivering some portion of the benefits conferred by wakefulness. Whether such mixed states provided selective advantages in our evolutionary past or are simply variations that were not selected against remains to be determined.

Potential Adaptations Nos. 10 & 11: Group Sleeping and Chronotype Variation

Because these two variables are so closely related, it seems appropriate to discuss group sleeping and chronotype variation together. For the purposes of this paper, group sleeping will be defined as two or more people sleeping in the same room, hut, or similar dwelling, or sleeping outside in close proximity. Chronotype refers to one’s circadian rhythm with accompanying preferred sleep–wake pattern. Chronotype is the result of both genetic and environmental factors (Montaruli et al., 2021).

First of all, most primate species, including our own, are highly social (Frith & Frith, 2010; Kappeler & van Schaik, 2002; Wilson, 2012). Sleeping in small groups is common among non-human primates (Anderson, 1998, 2000; Bearder et al., 2003; Fruth et al., 2017). Similarly, we humans sleep in small groups, and sometimes in relatively large groups, at close proximity to each other. Sleeping arrangements include bonded adult pairs, mother-infant pairs, siblings, grandparents, extended family, and sometimes other group members who are not biological relatives (e.g., Mileva-Seitz et al., 2017). In most of the world, and throughout most of human history, group sleeping in close proximity has been and continues to be the norm (Worthman & Melby, 2002). By close proximity, we mean sleeping closely enough to touch at least one other person. Ekirch documents bed-sharing, even among biologically unrelated adults, as a common practice among people during the early modern era (Ekirch, 2005). This historical practice promoted not only feelings of security, but also assisted in staying warm during the cold winter months.

Some contemporary examples of group sleeping in non-industrial communities can be found among the Warlpiri of northwestern Australia (Musharbash, 2013), the Asabano of Papua New Guinea (Lohmann, 2013), the Hadza of Tanzania (Samson et al., 2017b), the Efe of Zaïre (Worthman & Melby, 2002), the Himba of Namibia (Prall et al., 2018), and the Melanesians of Vanuatu (Smit et al., 2019). One subdivision of group sleeping is bed-sharing, which in the contemporary literature goes beyond adult couples, and typically refers to parents sharing a sleeping surface with their children. It can encompass other types of pairs as well, including siblings, grandparents-grandchildren, etc. This practice is quite prevalent throughout the world, especially given the modest economic circumstances under which most humans live. In their review of bed-sharing practices across 45 different countries, Mileva-Seitz et al. (2017) found the median prevalence rate of bed-sharing in those surveyed was over 50%. Even in contemporary Western homes, which emphasize sleep as a private activity meriting an individual sleeping space apart from the rest of the family, other family members are still not far away.
With such proximity, if anyone in the group awakens, they are able to monitor the immediate environment for external threats. If a threat is imminent, other members of the group can awaken and quickly assist in responding to the threat. Safety diminishes with smaller numbers sleeping greater distances apart, although there may be circumstances under which that arrangement is advantageous, as discussed later.

Variation in chronotypes within a group contributes to the probability that someone will be awake at any given time, thus enhancing the probability of detecting threats (Samson & Nunn, 2015; Samson, Crittenden, I. Mabulla, A. Mabulla, & Nunn, 2017b). Such variation is evident in our own species (Fischer et al., 2017; Samson et al., 2017b; Skeldon et al., 2016). Infancy, childhood, and late life are characterized by early bedtimes and early awakening times. In contrast, most adults tend to have later bedtimes and later awakening times, in the absence of work demands. Adolescents and young adults display the latest bedtimes and latest awakening times of all across the human lifespan (Fischer et al., 2017). At the extreme end of the later chronotype is delayed sleep–wake phase disorder, where sleep onset and wake time may be delayed for up to 3–6 h compared to conventional times (Abbott et al., 2017).

At the opposite end of the spectrum, the elderly in many cases have very early bedtimes and very early awakening times, relative to adults and sometimes even relative to children. An early onset counterpart for delayed sleep–wake phase disorder exists, which is called advanced sleep–wake phase disorder (Abbott et al., 2017). Individuals with this disorder may awaken 2 h earlier than societal averages, with complaints of early morning awakenings between 0200 and 0500, even when sleep onset is intentionally delayed. These variations in sleep–wake cycles across the lifespan can contribute to an increase in the total percentage of time spent in wakeful, nighttime vigilance for one’s sleeping group as a whole, potentially enhancing the chances of detecting external threats and increasing group survival. On this note, Samson, Crittenden, I. Mabulla, A. Mabulla, and Nunn’s (2017b) study of chronotype variations among the Hadza of Tanzania, a hunter-gatherer society, is revealing. These investigators carried out actigraphic recordings on 33 participants over 20 days with up to 22 participants wearing actigraphs on any given day. Over this 20-day period, the authors found only 18 min in which virtually everyone in the group showed evidence of being asleep. Thus, with the exception of this 18-min window, at least one person was awake at all times, enabling them to monitor the external environment for any threats. This finding led Samson and co-workers to suggest a sentinel hypothesis for the evolution of chronotype variations.

Another interesting finding from the anthropological literature is that men have more variation than women in nighttime sleep onset and duration (Yetish & McGregor, 2019). This enhanced variation might serve multiple functions, at both individual and group levels. For one, it potentially increases the chances that at least one man in the group is awake at any given time. It would be adaptive to have the largest and strongest people in one’s social group awake at any given time in terms of confronting predators and other external threats. On the other hand, there’s the greater propensity of women to experience insomnia in modern, industrial societies compared to men. It may be a stretch to consider these sex differences a biological division of wakefulness labor as opposed to responses to different cultural stressors, but the possibility is worth considering.

One can come away from the discussion on chronotypes with the impression that they are primarily, if not exclusively determined by genetic/biological pressures. However, cultural factors can, under some conditions, take precedence. For example, de Souza et al. (1991) report on an Amazonian community that imposes a morning chronotype on its members. So chronotypes are not biologically unyielding predispositions immune to cultural influences. One might view occupations that demand early rising (e.g., restaurant work, building construction) in the same light.

One additional and important point of discussion is warranted with respect to group sleeping. As already suggested, an infant or small child sleeping close to one’s parents would have made it less likely in our evolutionary past that the child would be snatched by a predator (Boyden et al., 2018). This kind of co-sleeping arrangement is the norm throughout the world and presumably throughout human history (Crittenden et al., 2018; McKenna et al., 1993; Mileva-Seitz et al., 2017; Worthman & Melby, 2002). Such co-sleeping contrasts sharply with the Western practice, especially in the USA, of having infants and small children sleep alone in a separate bedroom.

Although there are legitimate concerns about increased risk of sudden infant death syndrome and asphyxiation when infants sleep in the same bed as their parents, this increased risk may be the result of factors like overheating, soft pillows/surfaces, and adults whose own alarm systems are compromised by intoxication or extreme fatigue (American Academy of Pediatrics Task Force, 2005). McKenna et al. (1993) make the case that co-sleeping actually reduces the chances of sudden infant death by inducing lighter sleep and increasing the number of arousals across the night for both the infant and their mother. Nevertheless, the American Academy of Pediatrics currently recommends room-sharing during the first year of life, but no bed sharing until infants are at least four months of age (Moon, 2021).

Group sleeping has been discussed recently by Samson (2021) in his Social Sleep Hypothesis, which directly addresses the question of vulnerability during sleep. He proposes that group sleeping promoted short, intense, and flexible sleeping patterns in ancestral human groups. These shorter but intense sleeping patterns would have efficiently fulfilled all of the
necessary biological functions, while giving humans additional wake time to strengthen social bonds and group cohesion. Stronger social groups might have translated into even greater feelings of security, leading to a further diminution in sleep duration and an increase in sleep quality.

Overall, ancestral humans would likely have benefitted from group sleeping and chronotype variation. These two characteristics would arguably have enhanced vigilance and served a protective function for both individuals and the groups to which they belonged.

**Costs of Group Sleeping and Chronotype Variation**

Although group sleeping allows for rapid defense of one’s group members in the face of external threats, too many people sleeping in close proximity could be problematic. In the case of attack by a group of enemies, whether they be carnivores or other humans, it would be easier to surround a concentrated group of sleepers than a group that’s at least somewhat dispersed. Dispersal increases the chances for escape by at least some members of a group under attack. Concentrated sleeping would also increase group vulnerability to natural threats, like falling trees, fires, and rapidly flowing water.

With respect to chronotypes, at the individual level those with an early morning chronotype are at a social disadvantage with respect to participation in evening activities. At the other extreme, night owls are at a disadvantage when it comes to activities that are best served by early awakening (e.g., fishing). The costs and benefits of chronotype variation arguably depend on how a specific society is organized. In contemporary industrial societies, an evening chronotype is advantageous in occupations and educational settings that require early start times.

In summary, a biological tendency towards group sleeping would likely have served a protective role in our evolutionary past compared to the absence of such a tendency, both in terms of coping with external threats as well as providing warmth. The appearance and persistence of chronotype variations within a group would likely have augmented this protective role, increasing the total amount of wakefulness and potential threat detection across the group. Admittedly, group sleeping might be viewed most parsimoniously as simply one more behavior characteristic of a social species. In any case, the combined effect of group sleeping and chronotype variation is potentially a beneficial one with respect to reducing vulnerability at night.

**Potential Adaptation No. 12: Choosing Safe Sleeping Locations**

As mentioned already, one can mitigate the need for enhanced vigilance by choosing sleeping sites that are relatively safe from predators and hostile conspecifics, while still enabling vigilance for the detection of approaching threats. For example, many non-human primate species will sleep in tree branches, tree cavities, the ledges of cliffs (e.g., Anderson, 1998, 2000; Ellison et al., 2019; Li et al., 2011; Pruetz et al., 2008) or even in caves (e.g., Brain, 1981; McGrew et al., 2003). Some non-human primates build sleep platforms in trees, which reduces the risk of predation and enhances stability while sleeping (Samson & Hunt, 2014; van Casteren et al., 2012). We humans are too large and heavy to adopt most of the above practices, but sleeping in caves may have afforded some degree of protection in our evolutionary past (Ullman et al., 2013). Interestingly, Wadley et al. (2020) recently reported evidence for burned grass bedding in Border Cave, South Africa suggesting construction and maintenance of a comfortable and protected sleeping site some 200,000 years ago. But cave sites are not impervious to predators; some paleontological evidence points to caves as being sites of attack by carnivorous predators, for both non-human primate species and ancient hominids (Hart & Sussman, 2009). Among modern hunter-gatherers, construction of shelters dug into the ground help to serve an anti-predator function (Samson & Nunn, 2015).

In contemporary industrial societies, sleeping locations are conflated with housing selection. Many individuals choose housing that contains the option of sleeping on higher floors, a greater barrier for entry to those with ill intent. Recent work by Spörrle and Stich (2010) shows that when experimental participants are asked to imagine bed positioning in a hypothetical bedroom, they make choices that maximize their ability to monitor entry into the bedroom from either windows or doors.

As was the case with group sleeping, an additional consideration in terms of sleeping locations is sleeper density. Sleeping apart involves risks, but too many people sleeping too closely together could also be risky for a group as a whole.

Nevertheless, it is important to recognize that security is not the only factor involved in the choice of sleeping locations in the animal kingdom, especially among primates. Access to food and water, territory defense, physical stability, thermoregulation, and comfort are also critical factors (Anderson, 1998, 2000; Brividoro et al., 2019; Li et al., 2011; Wang et al., 2011). Furthermore, cultural factors obviously interact with instinctual forces when it comes to choosing sleeping locations within our own species.

Ancestral humans might have selected their sleeping locations based on both instinct and experience, informed by cognition of anticipated outcomes. Their selections may well have been driven by attempts to maximize security and increase vigilance, while taking into account access to resources like food and water.
Costs Involved with Choosing Sleeping Locations

It is difficult to imagine how “choosiness” with respect to sleeping locations could backfire. However, it is possible that groups that were/are too choosy about sleeping locations might expend too many resources looking for the perfect location, subjecting the group to risks of hunger, dehydration, and hypothermia, while simultaneously increasing exposure to predators and fomenting internal dissension.

In summary, a biological tendency towards choosing specific kinds of sleeping locations could have increased our chances of survival as a species in our evolutionary past, particularly in light of our vulnerability to nighttime predators.

This concludes the section on potential biological/instinctual characteristics that may be served to reduce vulnerability during sleep and the nighttime in our evolutionary past. Next, I consider more recent cultural adaptations in the arc of human history that may also have supported enhanced vigilance and reduced vulnerability during sleep and the nighttime.

Cultural Developments/Emerging Adaptations?

In this section, I will present three recent developments in human history that could also have reduced vulnerability during sleep and the nighttime. Although these are cultural rather than primarily biological in nature, I include them because of their ability to promote individual and group survival, specifically with respect to enhancing vigilance.

Cultural Adaptation No. 1: Controlled Fire

One of the oldest cultural adaptations for promoting vigilance during the night is the use of controlled fire (Twomey, 2011; Worthman & Melby, 2002; Wrangham & Carmody, 2010). Fire can serve multiple functions besides promoting vigilance at night: it can ward off nocturnal predators and insect pests, provide warmth, expand human dietary options via cooking, and facilitate conversation, storytelling, and social cohesion (Burton, 2009; Gowlett, 2016; Wiessner, 2014; Worthman & Melby, 2002; Wrangham & Carmody, 2010). By illuminating the night, fire has also been seen as giving people an edge against evil spirits, for whom night and darkness were believed to be times of maximum activity, at least during the early modern era in Europe (Ekirch, 2005; Koslofsky, 2011; Millar, 2018). Across many non-industrial cultures sampled, fire is reported to be psychologically comforting (Worthman & Melby, 2002). In addition, fire appears to produce ancillary physiological benefits: Watching a simulated campfire and listening to crackling sounds has been found to lower blood pressure (Lynn, 2014).

Humans and even pre-humans have been using fires for hundreds of thousands of years (Wadley et al., 2020; Wrangham & Carmody, 2010). Controlled fire may have played a significant role in the evolution of the human brain and correspondingly, human cognition (Burton, 2009). Controlled fire may have made ground sleeping viable, as our ancestors moved from sleeping in trees to terrestrial sleeping sites (Wrangham & Carmody, 2010). Ground sleeping may have changed the quantity and quality of human sleep, accelerating the advancement of human cognition (Coolidge & Wynn, 2006).

The work of Goren-Inbar et al. (2004) at the Gesher Benot Ya’aqov excavation site in Israel shows evidence of controlled fire dating back to approximately 790,000 years ago. Even earlier in hominin history, Berna et al. (2012) have collected evidence from Wonderwerk Cave in Northern Cape province, South Africa, dating controlled fire back approximately one million years ago. Finally, preliminary results from the Homo erectus site FxJ20 AB, Koobi Fora, Kenya, push the date of controlled fire in hominins even further back, to 1.5 million years ago (Hublik et al., 2017). Before the publication of this latest work by Hublik et al., a detailed defense that Homo erectus was the first species adapted to the control of fire was put forth by Wrangham and Carmody (2010), although others have discussed the possibility as well (e.g., Burton, 2009).

Controlled fire continues to be used in the contemporary world while people sleep (Worthman & Melby, 2002; Samson et al., 2017b). For example, Samson et al. (2017a) recently investigated the effect of fire, along with several other variables, on the physiologically recorded sleep of contemporary Hadza hunter-gatherers in Tanzania. In this study, fire was present on 67% of the nights (295/436). Fire had no effect on sleep parameters, even though 88% of those who responded to surveys (32/36) said that fire helped their sleep. It is possible, though, that the wake-promoting effects of light from fires, along with enhanced noise from nighttime conversation, may have canceled any sleep-promoting effects delivered by the enhanced perception of security that fire brings. Despite these drawbacks, fire facilitates socializing and storytelling, which translates into staggered sleep/wake schedules and greater group vigilance, among other benefits (Wiessner, 2014). Twomey (2013) has argued that controlling fire implies a certain level of human cognition—the ability to plan for the future, the ability to inhibit one’s responses, and group cooperation. In addition, fire-making and fire-maintaining may have played a significant role in facilitating the development of language, consciousness, social complexity, and cooperation. Finally, fire may have influenced circadian rhythms, sleep onset, and perhaps sleep duration as well, in our hominin past (Atttewell et al., 2015; Burton, 2009). Light acts as a zeitgeber, i.e., a biological cue, modulating activity in the suprachiasmatic nucleus and
pineal gland, two brain areas important for regulating biochemical rhythms (Gooley & Saper, 2017). Firelight could, in principle, have led to the suppression of melatonin, a key neuroactive substance in the pineal gland, at least for those closest to the fire, delaying sleep onset, and possibly contributing over a great expanse of time to alterations in circadian rhythms and human sleep–wake cycles in at least some percentage of our hominin ancestors (Burton, 2009).

Not only does fire promote vigilance, but it requires vigilance as well. The danger exists of being burned if one sleeps too close to a fire. Fires can get out of control if not monitored. Finally, fires can be extinguished if not properly tended, which would increase the chances of being attacked by predators (Worthman & Melby, 2002).

One last point related to fire and sleep merits consideration. If 32 of 36 respondents in the Samson et al. (2017a) study say that fire helped their sleep, one must consider the possibility that sleep quality may be determined by some other variable(s) independent of conventionally measured sleep parameters, such as sleep efficiency and duration. As discussed earlier, the literature on insomnia indicates that some people report unsatisfying sleep even when objective sleep measurements show no evidence of awakening or deviations from the norm (Lichstein et al., 2017; Rizaie et al., 2018). In any case, more systematic work is needed on the variable of fire before definitive conclusions can be drawn concerning its effects on sleep.

Because controlled fire extends so far back in human history, it is not unlikely that positive feelings about fire have become part of our genetic as well as cultural inheritance.

**Costs Associated with Fire**

Besides the need to expend energy and time in order to find wood and other combustible materials, there are significant risks attached to fire use. A fire can quickly go from controlled to uncontrolled status, especially in windy, dry conditions. Under such conditions an out-of-control fire could easily threaten the lives of individuals and groups that start them, erase any benefits fire might otherwise bring.

**Cultural Adaptation No. 2: Intentional Deployment of Human Sentinels**

In many parts of the world and throughout history, we humans have assigned sentinels the job of staying awake and monitoring the external environment while others sleep. Contrary to popular belief, the nightwatch may very well be the “the world’s oldest profession” according to historian Ekirch (2005, p. 75). It is possible that human sentinels originated with the role of tending fires throughout the night in the social groups that used them (Twomey, 2011, 2013), though such a role certainly would not preclude being a night watch independent of fire tending.

In the contemporary world, some anthropological work relevant to the sentinel role is worth mentioning. Musharbash (2013) has noted that the Warlpiri Aboriginal people of northwestern Australia commonly engage in group sleeping practices, with sleepers arranged in rows known as yunta. Socially senior members of the group sleep in the outermost positions. Their job is to guard the row of sleepers throughout the night. Even if they do not stay up all night, they are expected to be alert and vigilant for any external threats or developments, including snakes, rain, and even evil spirits. An absence of people with the ability to decode nighttime noises may result in entire camp moving to another one which contains socially senior and presumably “skilled” nighttime sentinels. To compensate for nighttime sleep loss, sentinels can sleep during the day, with the expectation that other group members will return the favor and watch over them while they are asleep.

One might reasonably predict that group sleeping, coupled with nighttime sentinels, would lead to better quality sleep overall as people would feel safer than they otherwise would, and freer to sleep as deeply as they wished. Building on the cultural adaptation of controlled fire, a group sentinel role would be a presumed byproduct of people telling stories around the fire into the night (Attwell et al., 2015; Wiessner, 2014). For those not around the fire, listening to human voices after dark might provide reassurance and feelings of safety that override the noise of voices, producing a net facilitation of sleep, or at least the perception of improved sleep.

An interesting and probably related finding emerges from studies of sleep and dreaming in modern laboratory contexts. It is notoriously difficult for clinicians to observe nightmares, night terrors, and other negative parasomnias when patients come to sleep labs for nighttime sleep monitoring, even when those parasomnias are what brings them to the sleep lab (e.g., Fisher et al., 1970; Krakow et al., 2002; Woodward et al., 2000). Hartmann (1970) noted several decades ago the rarity of nightmares in his own laboratory, observing only one nightmare involving a spontaneous awakening out of over 500 nights of sleep investigation in normal subjects. In addition, his group failed to observe a single nightmare in over 400 awakenings from REM sleep. One explanation for this phenomenon is that the patients feel safer and “watched over” in the laboratory setting compared to their own homes (Woodward et al., 2000). Consistent with this line of discussion, Sikka et al. (2018) found a greater prevalence of negative emotions in dream reports collected at home than in the sleep laboratory. On the other hand, the previously discussed “first night effect” seems to be at odds with the reduced probability of seeing night terrors and nightmares in the sleep laboratory environment.
In contemporary industrialized societies, the job of human sentinels has been replaced, or at least supplemented, by electronic security systems. But even before the advent of these systems, humans would have begun to use animal sentinels, which are discussed in the next section.

Lastly, a sentinel function is an unintentional byproduct of chronotype variation, as pointed out by Samson et al. (2017b) and discussed above.

Costs of Human Sentinels

Human groups would need to compensate individuals for the job of night time sentinel, in cases where no one volunteers for the job. Alternatively, groups could assign the role to one or more individuals, a process that might conceivably entail considerable time and energy in less autocratic groups. Human sentinels who are awake most of the night would need to sleep during the day, rendering them unavailable for daytime activities. Being awake and sleeping at times that go against one’s biological rhythms can incur significant costs. As already noted, night shift work in modern industrialized societies is associated with a number of negative health consequences (Moreno et al., 2019; Ramin et al., 2015; Torquati et al., 2019; Wegryzyn et al., 2017).

Cultural Adaptation No. 3: Domestication of Dogs

Another more recent adaptation of relevance here is the domestication of dogs, whose superior auditory and olfactory range compared to our own species (Miklosi, 2015) can provide an enhanced sphere of vigilance. Humans began to domesticate dogs approximately 14,000 years ago, and perhaps even much earlier than that (Galeta et al., 2021). It is likely that our species quickly discovered how much benefit dogs could provide in terms of vigilance, especially nighttime vigilance. Dogs are especially suited to this role, given their close attachment to humans, their sensitivity to sound and smell, and their enhanced tendency, compared to wild canids, to engage in barking (Clutton-Brock, 1999). Barking in response to intruders and other unusual events makes them quite helpful in terms of nighttime vigilance, especially while their owners are sleeping. In their study of guard dogs, Adams and Johnson (1995) found that 70% of barking sessions appeared to be triggered by human activity. Importantly, and perhaps not surprisingly, humans can discriminate different kinds of barks (e.g., those indicating aggression vs. fear) (Miklosi, 2015). Moreover, dogs are more responsive to their external environment than wolves, as evidenced by mean heart rates, both during resting (which includes periods of sleeping) and inactive wakefulness (Kortekaas & Kotrschal, 2019). That is, the mean heart rates of dogs in this preliminary study were higher than the mean heart rates of the wolves, which could be the result of higher sympathetic nervous system activation. Also, dogs spend a high percentage of time in a state of low-attention drowsiness (Campbell & Tobler, 1984) with short sleep cycles averaging 21 min in length; thus, they awaken about three times per hour (Adams & Johnson, 1994). Although dogs respond to a range of auditory stimuli, they are more likely to bark in response to the barking of other dogs than to any other auditory stimulus. Not surprisingly, they are more responsive to such stimuli while they are awake than when they are asleep. The type of sleep (active or quiet) does not seem to matter.

We do not know precisely when dogs began to serve as nighttime sentinels for humans. But it is likely that dogs have been involved in a multitude of activities in service to humans dating back to 8000 to 10,000 years ago (Miklosi, 2015). The historical record shows the use of guard dogs in Roman times (Clutton-Brock, 1999; Coren, 1994) and during the early modern era in Europe (Ekirch, 2005). In the contemporary world, dogs are used to protect livestock from carnivorous predators (Andelt & Hopper, 2000; Green et al., 1984), and farms, businesses, and homes from theft (Adams & Johnson, 1995; Bunei et al., 2014; Grooms & Biddle, 2018). It is not simply an impression that dogs ward off predators and intruders; the data support this idea. For example, urban homes with registered dogs in them are less likely to experience property crime (Grooms & Biddle, 2018). Today, many people rely on dogs to alert them to possible intruders, especially at nighttime when most or all of the household is asleep and in a state of heightened vulnerability.

Although a relatively recent arrival on the human cultural scene, the ability of dogs to evoke strong positive feelings in us suggest that they tap into brain circuitry that’s far older than the estimated time of their domestication some 14,000 years ago.

Costs of Using Dogs as Night Sentinels

Dogs obviously require resources to house and feed. But they entail other costs as well. For example, barking throughout the night can disrupt the sleep of those nearby, with attendant negative consequences. Even without barking, dogs can awaken nearby humans and disrupt their sleep.

Integration and Synthesis

Whatever positive biological functions sleep may have, it is inherently a state of vulnerability for the organism. In this paper I have argued that a number of variations in human sleep characteristics could have served to reduce vulnerability during the nighttime of the ancestral environment, and improved chances for survival, reproduction, and continuity of our species. In particular, these variations could
have reduced vulnerability by enhancing vigilance oriented toward the external environment. But just because these variations could have enhanced vigilance does not mean that they evolved for that “purpose.” Rather, these characteristics could have been associated with some other feature that had an adaptive function in our evolutionary past, i.e., they could be exaptations of evolutionary older adaptations. They could also have arisen by chance and remain with us because they were not selected against. Nevertheless, humans could have put these variations to use and may continue to do so into the present day. This paper argues that one such use of each of the discussed variations is to enhance vigilance during the hours of darkness and sleep, thus reducing vulnerability in our species inherent to this time of day and to this behavioral state.

As already noted, sleep is a biological necessity, with evidence for roles in memory consolidation, neural plasticity, immune function, metabolism, emotional adaptation, and toxin clearance. Sleep alterations and reductions are often associated with negative medical consequences and reduced mortality. On the other hand, reductions in sleep length and continuity may also have served, throughout human history, to benefit individuals and the groups to which they belonged. At least some of the conditions we label as sleep disorders today, such as insomnia, could have conferred positive benefits in our evolutionary past, specifically promoting vigilance during the nighttime hours and reducing vulnerability to external threats, at both the individual and group level. Increased wakefulness could also have provided positive opportunities in our evolutionary past for activities such as hunting, fishing, socializing, and sex, among others.

Although one can make a theoretical argument for the plausibility of each of the previously proposed adaptations, it is difficult to know whether any of them in fact enhanced reproductive fitness throughout the history of our species. The evidence for and against the adaptive fitness of each of these discussed elements within human populations may be found potentially in data collected from families and social groups across the globe. It will be a significant undertaking to collect, analyze, and interpret these data. Despite the challenges, it is possible to generate specific, testable hypotheses for each of the aforementioned proposed adaptations. If any of the hypotheses are supported, such support is consistent with the possibility that the given characteristic evolved so as to reduce vulnerability during sleep, but by no means proves that it did so. At the very least, however, a case can be made that the variation is an exaptation. On the other hand, if a given hypothesis is not supported, then the case is weakened that the described characteristic evolved, at least in part, to solve the problem of vulnerability during sleep. In the next section, I present testable hypotheses for evaluating each of the proposed adaptations discussed earlier. For these hypotheses, I focus on the group level. As I argue in an earlier section, many variations that are problematic at the individual level may serve to benefit the larger groups to which individuals belong. Importantly, I expect the data to follow an inverted U-shaped function for most if not all of the predictions. Sleep variations at the extreme ends are likely to introduce significant psychological and medical costs that override any benefits they might confer with respect to enhanced vigilance and ultimately group fitness.

Instinctual Adaptations

1. REM sleep as a state that enhances vigilance during sleep and reduces vulnerability.
   - **Hypothesis 1**: All other things being equal, groups with higher amounts of REM sleep as a percentage of total sleep time are predicted to have lower mortality rates and greater longevity than groups with less REM sleep as a percentage of total sleep time.
   - **Hypothesis 2**: All other things being equal, groups with higher amounts of REM sleep as a percentage of total sleep time are predicted to have greater reproductive success than groups with lower amounts of REM.

   Increased REM frequency and duration means a greater percentage of sleep time spent in an immobile state, one that is less likely to attract the attention of predators and human enemies, due to reduced movement and attendant noise. Increased REM also means that the brain has a greater probability of being primed for action if awakened. A further possible benefit of increased REM is greater overall vigilance. However, at the extreme ends of REM frequency and duration other costs may come into play that reduce this benefit.

   Increased REM should also be associated with greater reproductive success overall, for two reasons: (1) Increased REM means increased threat detection, faster reactions to threats, and greater chances of surviving to sexual maturity and (2) Increased REM frequency in particular means more bouts of sexual arousal at night, potentially resulting in more instances of sexual intercourse, conception, and eventually birth.

2. A reduced ability to initiate sleep.
   - **Hypothesis 1**: All other things being equal, groups that experience difficulty initiating sleep are predicted to have lower mortality rates and greater longevity than groups that have no difficulty initiating sleep, up to a point.
   - **Hypothesis 2**: All other things being equal, groups that experience difficulty initiating sleep are predicted to have greater reproductive success than groups that have no difficulty initiating sleep, up to a point.
Such groups would include more individuals awake for longer periods of time into the night. That translates potentially into more collective vigilance as well as more time for positive activities, such as hunting, fishing, socializing, sex, etc. However, at the extreme end, excess difficulty initiating sleep may incur costs that decrease overall chances of survival, both for the individual and for the group. This is more likely to occur if the individual is unable to compensate by sleeping later and longer, rendering them susceptible to all of the problems associated with inadequate sleep. The costs include impaired performance in daytime tasks, especially those requiring sustained attention. An additional set of potential costs involve enhanced eating, weight gain, diabetes, and related conditions, thus reducing lifespan and survival rates, as discussed earlier. However, this constellation of conditions is expected to be less relevant in societies that approximate the human ancestral environment.

3. Frequent awakenings.

**Hypothesis 1**: All other things being equal, groups that experience more frequent awakenings are predicted to have lower mortality rates and greater longevity than groups that experience less frequent awakenings, up to a point.

**Hypothesis 2**: All other things being equal, groups that experience more frequent awakenings are predicted to have greater reproductive success than groups that have less frequent awakenings, up to a point.

In particular, groups with more members who awaken frequently would have greater collective vigilance across the night than groups with fewer members who awaken frequently. This effect may be expected to be magnified in groups with members who awaken frequently and have difficulty getting back to sleep. Again, this characteristic could translate into more time for beneficial waking activities, such as sexual activity. On the other hand, a group with too many members having difficulty returning to sleep might incur negative consequences that offset the benefits of enhanced vigilance and positive waking opportunities.

4. Reduced sleep duration.

**Hypothesis 1**: All other things being equal, groups with a lower average sleep duration are predicted to have lower mortality rates and greater longevity than groups with a higher average sleep duration. However, this advantage would be expected to disappear at the extreme low end of the sleep duration continuum.

**Hypothesis 2**: All other things being equal, groups with lower average sleep durations are predicted to have greater reproductive success than groups with higher average sleep durations, up to a point.

Again, these hypotheses derive from two factors: (1) enhanced vigilance but also (2) more time to carry out activities that may enhance group survival, such as food gathering and sexual opportunities. However, reduced sleep duration may be beneficial only up to a certain point. To repeat, if the average sleep duration goes too low, negative psychological and medical consequences may ensue that offset any benefits conferred by reduced sleep duration.

5. “Lighter” sleeping, which would enhance sensory responsiveness to external events and motor responsiveness, if the sleeper is awakened.

**Hypothesis 1**: All other things being equal, groups whose average percentage of deep slow-wave sleep (i.e., N3 sleep) relative to total sleep is lower are predicted to have lower mortality rates and greater longevity than groups whose average percentage of N3 sleep is higher, but only up to a point.

**Hypothesis 2**: All other things being equal, groups that experience lighter sleep, on average, awakenings are predicted to have greater reproductive success than individuals and groups that have less frequent awakenings, up to a point.

A greater percentage of deeper sleep (i.e., N3 sleep) would be expected to result in less sensitivity to external events and slower responding, if the sleeper is awakened. However, too little N3 sleep may result in negative medical, cognitive, and psychological consequences that increase mortality. For example, if it turns out that the greatest amounts of toxin clearance occur during N3 sleep in humans, insufficient N3 sleep might result in medical issues that reduce longevity and the chances of reproductive success. That is, an optimum amount of N3 sleep percentage would be expected.

Lighter sleep could also result in greater likelihood of awakening in response to movement and touch by bed partners, thus increasing the chances of sexual intercourse for heterosexual couples.

6. Continuous sensory monitoring of the external environment during sleep.

**Hypothesis 1**: All other things being equal, groups with greater sensitivity to external events while asleep are predicted to have lower mortality rates and greater longevity than groups with less sensitivity to external events while asleep, up to a point.

**Hypothesis 2**: All other things being equal, groups that experience greater sensitivity to external events, on average, are predicted to have greater reproductive
success than groups that have less sensory monitoring of the external environment during sleep.

Proposed adaptations 5 and 6 above are closely related, but separable. It is possible, at least in theory, to have a greater level of sensory monitoring without changes in the percentages of sleep stages. Continuous sensory monitoring of the external environment enhances the potential for threat detection, as well as alerting the individual and the group to positive opportunities, e.g., an animal wandering nearby that can serve as a potential food source, or a potential sexual partner. However, extreme sensitivity to external events may disrupt sleep to the point where negative medical considerations come into play.

7. Redistribution of sleep across the 24 h cycle so that some of it occurs during the daylight hours, when humans are less vulnerable—at both individual and group levels.

**Hypothesis 1:** All other things being equal, groups that shift some of their sleep time to the daylight hours are predicted to have lower mortality rates and greater longevity compared to groups that do not.

**Hypothesis 2:** All other things being equal, groups that shift some of their sleep to the daylight hours are predicted to have greater reproductive success compared to groups that do not.

Less nighttime sleep and more daytime sleep means more vigilance during the most vulnerable period of the 24-h cycle for humans. That means greater survival to sexual maturity. Napping cultures, especially in areas with high daytime temperatures, can benefit from energy conservation, water conservation, and the other positive benefits that sleep confers.

However, too much sleep during the day may be disadvantageous for groups, resulting in reduced time for group activities that enhance survival, such as hunting, fishing, and foraging.

8. Increased fear and anxiety responses at night and during sleep, which would promote vigilance and readiness to act upon awakening.

**Hypothesis 1:** All other things being equal, groups that experience higher levels of fear and anxiety associated with darkness/nighttime and/or greater frequency of nightmares, night terrors, and other negative emotional experiences associated with sleep, are predicted to have lower mortality rates and greater longevity than groups with lower levels of fear and anxiety at night and/or nightmares, night terrors, and other negative emotional experiences.

**Hypothesis 2:** All other things being equal, groups that experience higher levels of fear and anxiety associated with darkness and the nighttime and/or greater frequency of nightmares, night terrors, and other negative emotional experiences associated with sleep, are predicted to have greater reproductive success.

Increased fear of the night/darkness and an increased number of negative dream experiences would presumably translate into a greater probability of vigilance and threat detection. Greater vigilance would be expected to occur before falling asleep and after awakening from a nightmare, night terror, or other kind of negative dream experience.

However, at the extremes, an excess of negative dream experiences may have psychological and medical costs that work to the detriment of the individual and the group.

Increased fear of the dark and an increased number of negative dream experiences might be expected to decrease the probability of sexual activity for the individual experiencing them. However, more fear of the dark and negative dreams experiences translates potentially into greater vigilance and threat detection for the group. Thus, more people in such groups would be expected to live long enough to reach sexual maturity, increasing the overall chances of reproduction within that group.

9. Localized sleep: Having some brain areas remain awake while other brain areas sleep.

**Hypothesis 1:** All things being equal, groups with more members who experience blendings of sleep/wake states are predicted to have lower mortality rates and greater longevity than groups fewer members who experience such blendings, up to a point.

**Hypothesis 2:** All other things being equal, groups with more members who experience blendings of sleep/wake states are predicted to have greater reproductive success.

Localized sleep permits blendings of sleep states. That means greater potential monitoring of the environment for threats. However, in the extreme, blended states may result in behaviors that reduce individual and group survival, such as nighttime wandering that could attract the attention of predators or mistaking benign group members for threatening animals or human enemies and subsequently attacking them. On the other hand, blended states permit more opportunities for initiating sexual activity, as observed in the parasomnia known as sexsomnia (Dubessy et al., 2017), which could translate into greater reproductive success.
10. Sleeping in groups, at close proximity.

Hypothesis 1: All other things being equal, groups whose members sleep close together are predicted to have lower mortality rates and greater longevity than groups whose members sleep far apart, up to a point.

Hypothesis 2: All other things being equal, groups whose members sleep close together are predicted to have greater reproductive success than groups whose members sleep far apart, up to a point.

However, in the extreme, too many people sleeping in too close proximity could be problematic. As discussed earlier, sleeping too “densely” could make it easier for a group’s human enemies to exterminate them. Also, a natural event, like a rapidly moving fire or water, is more likely to kill a group occupying a densely packed space than a distributed space. However, group sleeping in general should lead to greater collective responses in the event of an environmental threat, such as a predator, human enemy, or natural threat like a fire or flood. As a result, more members of groups that sleep relatively close together should survive to sexual maturity, enhancing the chances of reproduction.

11. Having a variety of chronotypes within one’s group.

Hypothesis 1: All other things being equal, groups that contain a variety of chronotypes (including both morning larks and night owls) are predicted to have lower mortality rates and greater longevity than groups that do not.

Hypothesis 1: All other things being equal, groups that contain a variety of chronotypes are predicted to have greater reproductive success than groups that do not.

More chronotypes means more time across the day/night cycle within a group for vigilance and threat detection. That translates, potentially, into a greater number of members of that group living long enough to reproduce.

However, too much diversity in terms of chronotypes could result in excess movement and noise across the night that disrupts the overall sleep quantity and quality of a group, nullifying the beneficial effects provided by chronotype variation.

12. Choosing sleeping locations that promote safety and enhance vigilance.

Hypothesis 1: All other things being equal, groups that are more selective about sleeping locations are predicted to have lower mortality rates and greater longevity than groups that are less selective about sleeping locations, especially when it comes to feelings of security.

Hypothesis 1: All other things being equal, groups that are more selective about sleeping locations are predicted to have greater reproductive success than groups that are less selective about sleeping locations.

Greater selectivity, especially when it comes to feelings of security, would be expected to decrease the chances of attack by animal predators and human enemies, along with reduced risk of exposure to natural threats. Such selectivity would be expected to translate into more people surviving to sexual maturity, increasing the chances of reproduction. However, excessive selectivity could prove detrimental, as already discussed.

In summary, we can generate testable hypotheses for each of the proposed adaptations that might have reduced vulnerability during sleep in our evolutionary past.

Culturally Based Innovations: Emerging Adaptations?

Although they are qualitatively different from the biologically-based sleep traits discussed so far, culturally-based innovations that might have reduced vulnerability during sleep in our historical past are also amenable to hypothesis testing and, I believe, worth discussing. These culturally-based innovations might be regarded as emerging adaptations:

1. Controlled fire, which would partially compensate for reduced nighttime vision and ward off predators.

Hypothesis 1: All other things being equal, groups that employ controlled fire at night are predicted to have lower mortality rates and greater longevity than groups that do not.

Hypothesis 2: All other things being equal, groups that employ controlled fire at night are expected to have greater reproductive success than groups that do not.

Controlled fire means more opportunities for nighttime vigilance and reduced exposure to predators and insect pests. It could also mean reduced sleep time, along with the positive opportunities that wakefulness brings, including increased opportunities for sexual intercourse.

Over the long run, the use of controlled fire would be expected to result in more people within a group surviving to sexual maturity, increasing the chances for reproduction. On the down side, groups that start fires as a standard nightly practice are also at risk of losing control of the fire under dry conditions, putting their group at risk. Overall, one would expect controlled fire to deliver net benefits.
2. The intentional deployment of human sentinels during the night while most are sleeping.

   **Hypothesis 1**: All other things being equal, groups that deploy human sentinels at night are predicted to have lower mortality rates and great longevity than groups that do not.

   **Hypothesis 2**: All other things being equal, groups that deploy human sentinels at night are predicted to have greater reproductive success than groups that do not.

   It is difficult to imagine this strategy backfiring, unless the deployment of too many nighttime sentinels results in too many people sleeping during the day, rendering the group less able to handle daytime responsibilities and potential threats. Overall, one would expect that the regular practice of using nighttime sentinels would enhance vigilance and threat detection, increasing the numbers of people surviving until sexual maturity.

3. The use of domesticated animals, especially dogs, as nighttime guards.

   **Hypothesis 1**: All other things being equal, groups with domesticated dogs are predicted to have lower mortality rates and greater longevity than groups without them.

   **Hypothesis 2**: All other things being equal, groups with domesticated dogs are predicted to have greater reproductive success than groups without them.

   Having dogs within one’s group might be expected to result in enhanced vigilance at night, improving threat detection and group survival. That would be expected to translate into more individuals surviving until sexual maturity, increasing the chances of reproduction.

   However, if a dog is barking all night long, it could disrupt the sleep of the group, rendering them less able to handle daytime responsibilities and potential threats. Disruptions in sleep continuity and reduced sleep duration could produce a number of negative cognitive and medical consequences, as discussed above.

**General Comments About Proposed Adaptations**

The amount, type, and timing of sleep that characterize each species presumably reflects an equilibrium point that maximizes the benefits that sleep provides versus the benefits that wakefulness provides, while minimizing the costs of sleep (Siegel, 2009). One cost of sleep that this paper examines is vulnerability to external threats, with a focus on our own species. For any of the adaptations proposed here, in particular the instinctual, evolutionary ancient ones, one would expect something approximating an inverted U-shaped curve: The hypothesized trait in moderation would be expected to produce net benefits, while too little or too much of the trait would be expected to produce net costs that override those benefits.

**Testability and Limitations**

Most of the proposed adaptations I have enumerated above are quite difficult to test in practice. Moreover, it is not apparent that any single study can adjudicate between the variation in question being an adaptation or an exaptation. Each of the proposed adaptations could easily merit a separate, lengthy research program by itself. Controlled experiments are ethically out of the question. Correlative studies are possible, but costly, especially in terms of appropriate study timespans. The most relevant populations for testing the majority of these hypotheses are likely to be indigenous peoples whose lifestyles more closely match those likely to have existed under ancestral conditions. Another possible source of data would be non-human primate groups living in their natural environments. In either case, a wide range of factors influence mortality rates, so keeping other variables constant would be enormously challenging and likely to require large numbers of participants and data sets. It is an empirical question whether there are enough groups with enough variation to test any of these hypotheses in an adequate manner. It will also be difficult to provide conclusive proof that any of the adaptations proposed in this paper evolved specifically to reduce vulnerability or were selected for some other reason, but subsequently “co-opted” to reduce vulnerability during sleep. In any case, the function that was adapted later in time might serve to perpetuate that trait even if the original function of the trait no longer applies. It is also possible that some of the instinctual variations proposed in this paper might fall under the definition of a spandrel. The cultural innovations introduced here, *prima facie*, certainly seem to qualify.

**Future Directions**

In addition to evaluating the hypothesized adaptations that could have reduced vulnerability during sleep in our evolutionary past while (1) increasing opportunities for beneficial waking activities and (2) fulfilling the necessary biological functions that sleep provides, the questions raised in this paper lend themselves to additional research directions. For example, further examination of short-sleeping cultures is warranted, especially in light of the apparent (so far) absence of negative consequences.
in these cultures compared to the experiences of modern, industrial societies with similar sleep durations. It is possible that differences in diet, lifestyle, and the type and number of social/psychological threats and stressors experienced on a daily basis account for the relative paucity of negative effects observed among the Hadza and other short-sleeping groups. Slavich’s (2020) social safety theory may be relevant in this regard. In particular, it would be useful to examine the impact of social threats on the immune system of humans living in modern, industrial societies compared to non-industrial groups, given the close connections among sleep, emotions, and the immune system (Besedovsky et al., 2019; Slavich, 2020). It would also be worthwhile to examine more closely the impact of artificial light on circadian rhythms, sleep parameters, and immune system regulation (see Samson, 2021).

Social threats, artificial light, and other aspects of living in modern, industrial societies may be contributing to an evolutionary mismatch (Manus, 2018) between sleep-related adaptations that evolved in the ancestral environment and the conditions under which so many humans live today. Modern living conditions may be “converting” natural variations that evolved in the ancestral environments (e.g., insomnia, delayed sleep phase syndrome) into what we label as clinical sleep disorders today. Modern conditions may be creating new sleep disorders (e.g., obstructive sleep apnea) as well. Building on these points, attempts to “fix” some conditions labeled as sleep disorders appears to have unintended consequences. For example, treatment of insomnia with some sleep medications, such as zolpidem, can in rare cases lead to hybrid states of sleep and wakefulness in which those who are medicated leave their beds and proceed to operate motor vehicles in the absence of conscious awareness, sometimes resulting in accidents (Pressman, 2011). It is plausible to suggest that using medications to reduce insomnia and promote sleep may lead to reduced nighttime vigilance for oneself and one’s family, with potentially negative consequences. Future research programs could examine the down side of manipulations that aim to correct these perceived sleep problems, in terms of reduced vigilance and increased vulnerability to external threats. In any event, a Darwinian perspective on sleep disorders and their treatments may help identify unintended consequences that could, in the long run, prove maladaptive (Williams & Nesse, 1991).

Conclusions

The goal of this paper has been to address a fundamental problem: How do we humans, or any species for that matter, survive when our biology demands a period of time throughout the 24-h day when we are immobile, relatively unconscious, and unable to monitor environmental threats? Building on previous work (e.g., Samson, Yetish, and their collaborators), I have attempted to identify a number of variations in sleeping patterns and behaviors at the individual and group levels that may have reduced vulnerability in our ancestral environment and may continue to do so today. This paper has also offered a number of recent cultural developments that may have augmented these putative biological adaptations. Although the instinctual and cultural variations are treated separately, they obviously overlap and, in combination, could have led to enhanced vigilance at the individual and group levels, thus promoting survival. For example, the development of controlled fire could have amplified the range of biologically driven chronotype variations, and cultural factors could have been introduced that expanded this range even further. Perhaps the end result of this process is what we see in the case of the Hadza, a group that experiences on average only 18 min a night when virtually everyone in their group is asleep (Samson et al., 2017b). But even in this case, it remains an empirical question whether such minimal concurrent sleeping translates into enhanced probability of survival and greater reproductive success.

But regardless of where one lives, how one lives, and the particular environmental conditions to which one is exposed, most of us are still sleeping less on average than what phylogenetic modeling predicts, as discussed earlier. To review, Nunn and Samson’s (2018) model predicted that humans should have average sleep durations of 9.55 h. The fact that average human sleep durations are much less than 9.55 h suggests that human sleep evolved to be more “intense” than the sleep of other primates. Thus, we humans have been able to fulfill the biological needs that sleep delivers in a highly efficient manner, while maximizing waking time. The increased availability of waking time provides additional opportunities for a variety of cognitive, social, and creative functions that characterize our species (Samson, 2021). Many of the variations discussed in this article could have enhanced waking time even further, enhancing opportunities for waking activities important for survival, such as nighttime hunting and fishing, mating, and socializing opportunities—which could have cemented emotional bonds among members of the group. Enhanced emotional bonds could have translated into greater cooperation and group loyalty, with positive ramifications for individual and group survival, as noted by Samson’s (2021) social sleep hypothesis. In his words:

To help explain how early Homo overcame risks arising from the transition to terrestrial sleep, the social sleep hypothesis puts forward the idea that early humans engaged in a type of sociotechnological niche construction that enabled short and flexibly timed, high-quality sleep. Thus the capacity for flexibly timed, high-quality sleep was permitted by the extended structure of camp- and band-level social groups that emerged approximately 1.8 mya and by
technologies, such as fire and sheltered dwellings, that supported humans’ survival and increased fitness. Specifically, the sleep site secured by sentinels (i.e., a few individuals who are awake and vigilant during the most vulnerable sleep period for the majority of individuals in a sleeping group) and environmentally buffered domiciles produced an exophenotype that was highly mobile within which to withdraw from immediate ecological challenges and attain deep, restorative sleep. Moreover, once established secure sleep sites may have supported in-group prosociality and intragroup coalitionary alliance building…it stands to reason that the positive feedback loop of better sleeping and more cooperative ancestral camps and bands would have led to increased fitness (p. 268).

I would add that this more efficient pattern of human sleep could also have served to enhance vigilance and reduce vulnerability to external threats. At the end of the day (no pun intended), two critical questions remain for each of the proposed adaptations that may have enhanced vigilance and reduced vulnerability during human sleep in our evolutionary past: (1) Did they enhance individual and group survival in human populations? And (2) did these adaptations evolve initially for the purpose of enhancing vigilance, or are they variations that were simply “re-purposed” to serve that function? At a practical level, the obstacles confronting any serious attempt to answer these questions are immense, but the potential scientific and intellectual payoffs are, in this author’s opinion, well worth the effort. It is my hope that this paper, despite its limitations, will stimulate further thinking and research on the evolution of sleep.

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