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Impacts of artificial light at night on sleep: A review and prospectus

Anne E. Aulsebrook¹  | Therésa M. Jones¹  | Raoul A. Mulder¹  |
John A. Lesku² 

¹The University of Melbourne, School of BioSciences, Melbourne, Victoria, Australia

²La Trobe University, School of Life Sciences, Melbourne, Victoria, Australia

Correspondence

Anne E. Aulsebrook, The University of Melbourne, School of BioSciences, Parkville, VIC 3010, Australia.
Email: aulsebrook@gmail.com

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Abstract

Natural cycles of light and darkness govern the timing of most aspects of animal behavior and physiology. Artificial light at night (ALAN)—a recent and pervasive form of pollution—can mask natural photoperiodic cues and interfere with biological rhythms. One such rhythm vulnerable to perturbation is the sleep–wake cycle. ALAN may greatly influence sleep in humans and wildlife, particularly in animals that sleep predominantly at night. There has been some recent evidence for impacts of ALAN on sleep, but critical questions remain. Some of these can be addressed by adopting approaches already entrenched in sleep research. In this paper, we review the current evidence for impacts of ALAN on sleep, highlight gaps in our understanding, and suggest opportunities for future research.

KEYWORDS

anthropogenic light, ALAN, circadian rhythms, electroencephalogram, pollution, urbanization

1 | INTRODUCTION

Endogenous daily (or circadian) rhythms underpin almost all biological processes and are critical for maximizing fitness (Aschoff, 1989; DeCoursey, Walker, & Smith, 2000; Greives et al., 2015). Circadian rhythms evolved under a predictable, 24-hr cycle of light and darkness, and allow organisms to synchronize their biology with predictable daily changes in their environment (Aschoff, 1989; Kronfeld-Schor, Visser, Salis, & van Gils, 2017). Coordination with the environment is achieved via environmental cues, called *zeitgebers*, which entrain or synchronize the internal pacemaker system (Aschoff, 1965). The most important *zeitgeber* is light (Aschoff, 1989; Berson, Dunn, & Takao, 2002; Czeisler et al., 1986; Panda, Hogenesch, & Kay, 2002). Loss or disruption of circadian rhythms, and the subsequent desynchronization of physiological processes, can have detrimental outcomes for health (Alibhai, Tsimakouridze, Reitz, Pyle, & Martino, 2015; Martino et al., 2008) and survival (DeCoursey et al., 2000).

In animals, the sleep–wake cycle is arguably the most conspicuous, ubiquitous, and important circadian rhythm. All animals—even simple animals, including jellyfish (Nath et al., 2017) and flatworms (Omond et al., 2017)—sleep. Sleep can have important benefits for development and learning (Derégnaucourt, Mitra, Fehér, Pytte, & Tchernichovski, 2005; Kayser, Yue, & Sehgal, 2014), attention, motivation and emotional reactivity (Van Dongen, Maislin, Mullington, & Dinges, 2003), hand–eye coordination (Dawson & Reid, 1997), memory (Diekelmann & Born, 2010), immune function (Imeri & Opp, 2009), neurological

waste clearance (Xie et al., 2013), and energy homeostasis (Schmidt, 2014; Schmidt, Swang, Hamilton, & Best, 2017). However, sleep also precludes other vital activities, such as foraging, antipredator vigilance, and mating (Kronfeld-Schor & Dayan, 2003; Lesku et al., 2012; Lima, Rattenborg, Lesku, & Amlaner, 2005; Roth, Rattenborg, & Pravosudov, 2010). To balance these requirements, species have evolved diverse patterns of sleep and wakefulness (Lesku, Roth, Amlaner, & Lima, 2006), shaped by complex interactions with predators, competitors, food availability, and other factors (Acerbi & Nunn, 2011; Lesku, Roth, Rattenborg, Amlaner, & Lima, 2009). These daily sleep–wake patterns, whether nocturnal or diurnal, are often regulated, at least in part, by light (Dijk & Archer, 2009; Fisher, Foster, & Peirson, 2013).

Within the past century, natural light cycles have become distorted by the presence of artificial light at night (ALAN; Gaston, Davies, Nedelec, & Holt, 2017). Moreover, light pollution has become a rapidly increasing and global phenomenon (Davies & Smyth, 2018; Falchi et al., 2016; Kyba et al., 2017), prompting concerns about the possible negative impacts of ALAN on sleep in humans (Czeisler, 2013; Erren & Reiter, 2009; Navara & Nelson, 2007; Pauley, 2004; Stevens & Zhu, 2015; Stevens et al., 2007) and wildlife (Dominoni, Borniger, & Nelson, 2016; Dominoni, Goymann, Helm, & Partecke, 2013a; Gaston et al., 2017; Randler, 2014). In species that sleep predominantly at night, sleep is particularly likely to be disrupted by ALAN, and there is now evidence that diurnal songbirds exposed to ALAN commence their activity earlier (Da Silva, Samplonius, Schlicht, Valcu, & Kempnaers, 2014; Da Silva, Valcu, & Kempnaers, 2016; de Jong et al.,

2016; Kempnaers, Borgstrom, Loës, Schlicht, & Valcu, 2010; Nordt & Klenke, 2013; Spoelstra, Verhagen, Meijer, & Visser, 2018; but see Da Silva et al., 2017a) and are active for longer each day (Da Silva, Diez-Méndez, & Kempnaers, 2017b; de Jong et al., 2016; Dominoni, Helm, Lehmann, Dowse, & Partecke, 2013b; Russ, Rüger, & Klenke, 2014). The intensities of ALAN experienced by some urban birds, mammals, and fish (approximately 0.3–1 lx.) can also suppress their production of melatonin (Brüning, Hölker, Franke, Preuer, & Kloas, 2015; Dominoni et al., 2013a; Robert, Lesku, Partecke, & Chambers, 2015), a hormone that promotes sleep in diurnal species (Gandhi, Mosser, Oikonomou, & Prober, 2015; Tan et al., 2010).

While a connection between ALAN and sleep has been deemed “intuitive” (Chepesiuk, 2009), research outcomes are often conflicting and our understanding is far from complete. For example, some studies indicate that ALAN reduces sleep duration in humans (Cho et al., 2016; de la Iglesia et al., 2015; Ohayon & Milesi, 2016), whereas others show no such effect (Beale et al., 2017; Chang, Aeschbach, Duffy, & Czeisler, 2014; Cho, Joo, Koo, & Hong, 2013; Samson et al., 2017b; Wams et al., 2017). Even without affecting the duration of sleep, exposure to ALAN can disrupt the timing and composition of sleep (Beale et al., 2017; Chang et al., 2014; Chellappa et al., 2013; Cho et al., 2016; Cho et al., 2013; Santhi et al., 2012; Wams et al., 2017), but few studies have investigated such impacts in real-world settings (Aulsebrook, Jones, Rattenborg, Roth, & Lesku, 2016; but see Wams et al., 2017). Furthermore, interspecific variation and methodological differences between studies—including different light exposures and methods for measuring sleep—can make results difficult to compare and generalize. Nevertheless, there is mounting evidence from laboratory animals, humans, and wildlife demonstrating impacts of ALAN on sleep. Here, we summarize the existing evidence, focusing mostly on diurnal animals, whose sleep is most likely to be adversely affected by light at night. We then highlight the current gaps in our understanding and provide a prospectus for future research.

2 | LABORATORY-BASED SLEEP STUDIES: MECHANISMS AND PHYSIOLOGY

Our understanding of sleep comes primarily from the laboratory, where sleep is easiest to record. Sleep is typically characterized by a rapidly reversible, homeostatically regulated state of reduced responsiveness, accompanied by behavioral quiescence, and changes in the electrical activity of the nervous system (Joiner, 2016). In neuroscientific studies, the “gold-standard” approach to measuring sleep is with recordings of electrical activity in the brain, often the electroencephalogram (EEG). These recordings show that mammals and birds have two main sleep states: rapid-eye movement (REM) and non-REM sleep (Lesku & Rattenborg, 2014; Vyazovskiy & Delogu, 2014). REM sleep is characterized by small, fast waves of electrical activity, whereas non-REM sleep (referred to as slow wave sleep in non-human animals) is characterized by large, slow brain waves. The size and incidence of slow waves during non-REM sleep (i.e., low-frequency power density, or “slow wave activity”) is used as a proxy for sleep depth and intensity, as greater slow wave activity is associated with deeper,

more intense sleep (Tobler, 2011). Until recently, it was only possible to record brain activity in a laboratory setting, owing to technological constraints in the size of recording equipment (Aulsebrook et al., 2016; Rattenborg et al., 2017).

Light can affect sleep in several ways. First, exposure to light entrains sleep's circadian rhythm, primarily by suppressing the photosensitive pathway of melatonin (Axelrod, Wurtman, & Snyder, 1965; Berson et al., 2002; Reiter, Tan, & Fuentes-Broto, 2010). This pathway is most sensitive to short or blue (460–480 nm) wavelengths of light (Berson et al., 2002; Czeisler et al., 1986; Reiter et al., 2010). Light at night can therefore disrupt circadian rhythms (Dominoni et al., 2016; Stevens & Zhu, 2015; Yadav, Verma, & Singh, 2017), which not only shifts the timing of the sleep–wake cycle, but also dampens its rhythm (Dijk & Archer, 2009; Fisher et al., 2013). Second, exposure to light can have direct effects on sleep and wakefulness, without necessarily affecting circadian rhythms (Altimus et al., 2008; Cajochen, Zeitzer, Czeisler, & Dijk, 2000; Chang, Scheer, Czeisler, & Aeschbach, 2013; Chen et al., 2017; Gandhi et al., 2015; Rattenborg, Obermeyer, Vacha, & Benca, 2005). Finally, light at night can allow animals that are normally diurnal to extend their activity into the night (e.g., Bakken & Bakken, 1977; Gaston et al., 2017; Santos et al., 2010; Stracey, Wynn, & Robinson, 2014; reviewed by Gaston et al., 2017). Thus, there is compelling reason to expect impacts of ALAN on sleep, although the relative contributions of different mechanisms can be difficult to disentangle.

To investigate how exposure to light affects sleep, many studies have used nocturnal rodents as laboratory models. Such studies have typically compared more naturalistic light cycles (12:12 light:dark) with constant light, constant darkness, or exposure to bright daytime light during the usual dark phase (e.g., Benca, Gilliland, & Obermeyer, 1998; Phillips, Savenkova, & Karatsoreos, 2015; Stephenson, Lim, Famina, Caron, & Dowse, 2012; Tobler, Franken, Alfvöldi, & Borbély, 1994). In addition, two studies have investigated the effects of more ecologically relevant “dim” ALAN on sleep. These studies found no effects of “dim” ALAN (5 lx.) on total sleep duration in rats (Stenvers et al., 2016) or mice (Borniger, Weil, Zhang, & Nelson, 2013), which is consistent with the idea that ALAN may have little or no negative effect on sleep in nocturnal animals (Borniger et al., 2013). However, exposure to “dim” ALAN affected sleep–wake rhythms in rats, causing them to redistribute daytime sleep into the night (Stenvers et al., 2016). Such effects on sleep timing could have important ecological consequences, including increased competition between diurnal and nocturnal species. Nevertheless, the degree to which observations can be generalized to other contexts is unclear (Calisi & Bentley, 2009; Horne, 2013). Effects of light exposure can vary even among different rat strains, with albino rats showing different responses to disruptive light cycles than pigmented rats (Benca et al., 1998). Many strains of laboratory mice are also melatonin-deficient (Kasahara, Abe, Mekada, Yoshiki, & Kato, 2010), which could influence study outcomes. Importantly, nocturnal rodents are also very limited as a model for how ALAN affects humans and other diurnal species, given that light affects nocturnal and diurnal species in different ways.

In diurnal species, laboratory studies have typically found effects of ALAN on sleep. In pigeons (*Columba livia*), continuous exposure to

artificial light strongly suppresses or even eliminates sleep (Berger & Phillips, 1994; Phillips & Berger, 1992), although the classification of sleep in these studies likely affected the interpretation of the results (Martinez-Gonzalez, Lesku, & Rattenborg, 2008). Another study of pigeons found that changing from a 12:12 light:dark cycle to a 3:3 cycle also reduced sleep behavior (defined by eye closure; Rattenborg et al., 2005). However, laboratory research has generally neglected the effects of more realistic ALAN exposures on diurnal species, besides humans. In humans, exposure to artificial light in the evening or throughout the night can variously delay sleep onset (Chang et al., 2014; Santhi et al., 2012; reviewed by Cho et al., 2015), cause more frequent awakenings from sleep (Chellappa et al., 2013; Cho et al., 2013), decrease total sleep duration (Cho et al., 2016) or sleep intensity (Chellappa et al., 2013), and alter the relative proportions of REM and non-REM sleep (Chang et al., 2014; Cho et al., 2016; Cho et al., 2013). Nevertheless, exact outcomes vary between studies. For example, Cho et al. (2013) found no effect of bright bedside light (40 lx.) on total sleep duration, whereas Cho et al. (2016) found that comparatively dim light at night (5 or 10 lx.) decreased total sleep duration. Similarly, Chang et al. (2014) found that use of a light-emitting e-Reader before bedtime increased the time needed to fall asleep (sleep latency) and decreased REM sleep, yet Rångtjell et al. (2016) observed no effect of e-Reader use on sleep.

Inconsistent findings could be explained by multiple factors. They may be partly due to small sample sizes, given that many studies have been of fewer than 20 subjects. In addition, the effects of light at night on sleep and alertness can depend on the spectra (Ayaki et al., 2016; Chellappa et al., 2013; Santhi et al., 2012), timing (Carrier & Dumont, 1995), duration (Chang et al., 2012), and intensity (Cajochen et al., 2000) of the light exposure, as well as prior exposure to light (Chang et al., 2013; Chang, Scheer, & Czeisler, 2011). It is therefore critically important for studies to report this information to facilitate comparisons between studies and replication of research. Notably, many studies (of humans and other species) fail to provide sufficient spectral information, even though short (blue) wavelengths of light are known to have the greatest impact on melatonin production, circadian rhythms, and alertness (Berson et al., 2002; Czeisler et al., 1986). A final consideration is that there are also limitations of recording sleep in the laboratory. Homogenous laboratory lighting may not capture the spatial and temporal heterogeneity of light exposure in urban environments and homes (Gaston, Duffy, Gaston, Bennie, & Davies, 2014). Furthermore, in the laboratory, an individual's behavior may be restricted or otherwise influenced by their unusual sleeping environment. To understand the impacts of ALAN, we therefore also need to complement these studies with research in real-world settings (Aulsebrook et al., 2016).

3 | HUMAN SLEEP: REAL-WORLD COMPARISONS

Historical research indicates that prior to the introduction of electric light, human sleep patterns differed from those of today. Instead of sleeping in a single consolidated episode each night (monophasic

sleep), people slept in two bouts (biphasic sleep), each of which lasted a few hours with a bout of wakefulness in between (Ekirch, 2001; 2015, 2015, 2016). This has led to conjecture that artificial light has caused an “unnatural” shift in human sleep, whereby people now stay awake later and condense their sleep into a shorter period. Accordingly, a laboratory study found that people adopted biphasic sleep when exposed to 14 hr of darkness each night (Wehr, 1992). There is also evidence of biphasic sleep in some contemporary communities without electricity (Samson et al., 2017b), but not others (Beale et al., 2017; de la Iglesia et al., 2015; Peixoto, da Silva, Carskadon, & Louzada, 2009; Samson, Crittenden, Mabulla, Mabulla, & Nunn, 2017a; Yetish et al., 2015). Despite some dispute about the likely origins of biphasic sleep in humans (Ekirch, 2016; Yetish et al., 2015), sleep in western societies has clearly changed in recent history (Ekirch, 2015). However, since the invention and widespread use of electric light, there have been other social, cultural, and technological changes that are also likely to have affected sleep (e.g., Gradisar et al., 2013). It is therefore difficult to isolate the role of artificial light on sleep from historical records alone.

Cross-sectional and comparative studies provide additional support for impacts of artificial light on sleep. People in communities with access to electricity tend to go to sleep later than those without (Beale et al., 2017; de la Iglesia et al., 2015; Peixoto et al., 2009) and, in some cases, also sleep less (de la Iglesia et al., 2015). In the United States, people exposed to higher-intensity outdoor light at night also report delayed bedtimes, later wake-up times, shorter sleep durations, and increased daytime sleepiness (Ohayon & Milesi, 2016). Similarly, the use of light-emitting technology before sleep is associated with increased sleep latency and decreased sleep duration (Hysing et al., 2015), while exposure to light later in the evening is associated with delayed sleep times and increased awakenings, but no difference in sleep duration (Wams et al., 2017). Such studies are somewhat limited by the methods used to measure sleep; almost all rely on actigraphy or questionnaires (but see Wams et al., 2017). These techniques are valuable, but less accurate and comprehensive than measurements of brain state (Marino et al., 2013; Paquet, Kawinska, & Carrier, 2007; Westerlund, Lagerros, Kecklund, Axelsson, & Akerstedt, 2016). Moreover, sleep need builds as a function of prior sleep-wake history and the intensity of brain use during that wakefulness (Huber et al., 2006; Lesku, Vyssotski, Martinez-Gonzalez, Wilzeck, & Rattenborg, 2011b; Tobler, 2011). If exposure to light at night is associated with different waking experiences, this could have a confounding effect on the timing and duration of sleep. For example, in a study by Beale et al. (2017), people from a rural community without electricity were also doing much more intense physical labor than those in the urban community with electricity. As with historical studies, it is therefore challenging to isolate the effects of ALAN from other factors.

An alternative and powerful approach can be to experimentally manipulate evening or night-time light exposure in people's homes. Very few sleep studies have adopted this approach, presumably due to the combined challenges of recording sleep and adhering to experimental protocols in the home environment. Interestingly, when people “maximized” their home light exposure to 46–82 lx. in the evening, they went to bed only slightly later (average difference 14 min) than when

they “minimized” their exposure to 1–5 lx. and wore short-wavelength-blocking glasses (Burgess & Molina, 2014). Furthermore, there was no effect on wake time or total sleep duration, despite impacts on circadian timing. Similarly, in a rural community in Madagascar, the use of electric field lanterns for one week had no effect on participants’ sleep (Samson et al., 2017b). In another study, researchers took eight participants camping without electric lights (Wright et al., 2013). After 1 week of camping, the participants went to sleep earlier on average, and there was less between-individual variability in their sleep timing than when they were at home. Of course, as with comparative studies of human sleep, confounding factors such as increased fatigue associated with exercise may have influenced patterns of sleep in this study. Ongoing developments in our ability to record sleep at home, using reasonably cheap and unobtrusive technology (e.g., Winnebeck, Fischer, Leise, & Roenneberg, 2017), will hopefully facilitate further research. Such research could also help to address the extent to which outdoor illumination affects human sleep, and whether illumination from indoor lighting and light-emitting screens effectively overwhelms effects from external sources of illumination. It is also worth noting that many people are likely aware that light at night can disrupt sleep, and these expectations could influence study outcomes.

4 | SLEEP BEHAVIOR IN WILDLIFE

Sleep in diurnal animals is likely to be affected by illumination from streetlights, security lights, and other outdoor lighting intended for human security and entertainment. Research has demonstrated that ecologically relevant light intensities can affect sleep behavior in wildlife. These studies have so far been based exclusively on two songbird species: great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*). By video-recording wild blue tits inside their nest boxes, Steinmeyer, Schielzeth, Mueller, and Kempenaers (2010) observed behavioral and postural changes that are thought to be associated with sleep (Amlaner & Ball, 1983; Stuber, Baumgartner, Dingemanse, Kempenaers, & Mueller, 2016). Specifically, a bird was considered asleep when it had its beak tucked backwards beneath its scapulars for at least 30 sec, and awake when it had not assumed that posture for at least 10 sec. Assuming this to be true, birds woke earlier when exposed to higher intensities of light at night. Subsequent studies used LED lights *inside* nest boxes to experimentally manipulate light at night, and record the effects on sleep behavior using the same definition (Raap, Pinxten, & Eens, 2015; 2016; Raap, Sun, Pinxten, & Eens, 2017; Sun, Raap, Pinxten, & Eens, 2017). Interestingly, exposure to light at night decreased the duration of night-time sleep behavior in great tits, but not blue tits (Sun et al., 2017), and the effects on female great tits were much greater during the nestling period (Raap, Pinxten, & Eens, 2016).

Field-based studies represent a critical first step towards understanding how ALAN affects sleep in wildlife. However, while the resting behavior of animals is interesting and informative, it is not necessarily a good proxy for sleep (Aulsebrook et al., 2016). Some animals can adopt wake-like postures during sleep (Lesku et al., 2011a; Rattenborg et al., 2016), and others can be awake while in ostensibly sleep-like postures (Voinin et al., 2014). Furthermore, sleep behavior in great and blue tits

has not yet been verified with recordings of brain state, meaning that researchers must make assumptions about sleep onset and continuity. Critically, sleep behavior alone does not inform us about the impacts of ALAN on sleep composition or intensity. This is particularly important since ALAN can affect these factors without affecting total sleep duration (e.g. Chang et al., 2014; Cho et al., 2013; Stenvers et al., 2016). It is also possible that birds sleep less at night when exposed to ALAN, but compensate by sleeping more intensely, or by napping outside their nest box during the day.

To expand on observations of sleep behavior, future research will need to adopt other methods for measuring sleep in the wild. Advances in miniaturization have given rise to data loggers that can record brain activity in wild animals (Lesku et al., 2012; Rattenborg et al., 2016; Rattenborg et al., 2008; Scriba et al., 2013; Vyssotski et al., 2009). Such EEG data loggers are currently only suitable for animals larger than 100 g, which means that they are still too large for use on many songbirds, including blue and great tits, which weigh around 11 and 16 g, respectively. However, EEG data loggers could be used in many other study systems, and ongoing miniaturization of technology is likely to provide further opportunities in the future. Interestingly, the discovery of a biomarker for sleep loss, oxalic acid (Weljie et al., 2015), also shows some promise for determining effects of ALAN on sleep. However, results from two studies in wild great tits are equivocal. Ouyang et al. (2017) found that birds in their “white light treatment” (roosting up to 160 m from experimental white LED streetlights) were more active at night than birds in their dark control, red or green light treatments. Greater nocturnal activity was associated with decreasing oxalic acid over the course of the 3-month study, potentially reflecting a sleep-deprived condition (but see Raap, Pinxten, & Eens, 2017). Conversely, Raap, Pinxten, and Eens (2018) found that exposure to white ALAN inside the nest box caused an unexpected *increase* in oxalic acid concentrations in male, but not female, nestlings. Since oxalic acid has so far only been validated as a biomarker for sleep loss in humans and rodents experiencing relatively severe sleep deprivation (Weljie et al., 2015), further validation is required.

5 | PROSPECTUS FOR FUTURE RESEARCH

The combined evidence from laboratory experiments, correlational field studies, and field experiments suggests that light at night has the capacity to affect most, and perhaps even all aspects of sleep in diurnal species. Nevertheless, there are other critical questions that still need to be addressed. What are the impacts of real-world light exposures on sleep? Are people and wild animals able to ameliorate such impacts, by retreating to darker refuges to sleep at night? How is sleep in other animals, beyond humans, songbirds and laboratory rodents, affected by ALAN? When ALAN disrupts sleep, what are the “downstream” costs, and how can these be mitigated? Below, we discuss these questions and possible approaches in further detail.

Investigating how ecologically relevant ALAN affects sleep is fundamental for understanding the scale of its impact. Experimental studies often use light exposures that have unrealistic timing, or that are more intense and spatially homogenous than would be

experienced in real-world settings (Santhi et al., 2012). In some studies, light is also presented in an unrealistic manner that might influence sleep via other mechanisms. For example, the introduction of artificial light into a nest box, which is typically darker than the outside environment at night, may create a novel situation that disrupts sleep, rather than the alerting effects of light *per se*. “Daylight” in laboratory studies is also typically much dimmer than natural sunlight, which is likely to have subsequent effects on sleep (Wams et al., 2017). On the other hand, field studies that measure the effects of real-life light at night are often correlational, and typically rely on behavioral proxies or questionnaires to measure sleep. The use of experimental protocols in real-world settings, together with more advanced techniques for measuring sleep (Aulsebrook et al., 2016), should help to address this major gap in our understanding.

To better understand how ALAN affects sleep in wildlife, we also need to understand how diurnal animals behave in the presence of ALAN. Since ALAN is spatially heterogeneous, diurnal animals might actively avoid exposure to light at night by retreating to refugia (Dominoni, Carmona-Wagner, Hofmann, Kranstauber, & Partecke, 2014; Longcore & Rich, 2004). Avoidance behavior could ameliorate some of the negative impacts on sleep, but at the cost of reduced habitat availability, increased competition, increased searching time for suitable sleeping sites, or the use of suboptimal sites. Conversely, if animals do not avoid light when sleeping, then they might face a greater risk of predation from visually orienting predators. Animals might also be able to compensate for lost sleep by sleeping more deeply or sleeping during the day, as observed in migratory Swainson's thrushes (*Catharus ustulatus*; Fuchs, Haney, Jechura, Moore, & Bingman, 2006) and white-crowned sparrows (*Zonotrichia leucophrys gambelii*; Rattenborg et al., 2004). However, the thrushes and sparrows were wild-caught birds brought into a laboratory environment, such that it is unknown how they might respond to nocturnal sleep loss in the wild. Even if animals can compensate for nocturnal sleep loss, this behavior could also lead to other costs, such as decreased foraging time and increased predation risk during the day (Lima et al., 2005).

While we assume that impacts of ALAN on sleep are costly, there is currently little evidence to indicate the specific costs or their extent, or how (if present) they might be mitigated. Behavioral studies typically focus on sleep duration, but sleep intensity and composition might be equally important for fulfilling sleep functions (Joiner, 2016). Furthermore, if sleep requirements vary in wild animal populations, such that some individuals cope better with less sleep than others, then there could be scope for natural (or sexual) selection to favor reduced sleep need (Lesku et al., 2012). It is also unknown whether humans or animals can habituate to ALAN, allowing the impacts of ALAN on sleep to lessen over time. Given the known physiological pathways by which light at night affects melatonin, circadian rhythms, alertness, and sleep, complete habituation appears unlikely, yet the possibility is worthy of investigation. In humans, the impacts of ALAN might also increase over time, as our ability to work and socialize after sunset alters societal expectations (Jakle, 2001).

Importantly, current research also lacks taxonomic diversity, as most studies have been restricted to humans, laboratory rodents,

and a few species of songbirds. ALAN can have major impacts on the behavior and activity of diverse taxonomic groups, including insects (Knop et al., 2017), which suggests it could also have critical impacts on their sleep. Even closely related species or strains may respond differently to ALAN (Benca et al., 1998; also see Da Silva & Kempnaers, 2017; Sun et al., 2017). Expanding the phylogenetic breadth of study species, and investigating how ecological factors may contribute to different responses, would provide a broader understanding of the costs of ALAN and lead to better management outcomes.

From a practical perspective, further research is required to determine how to minimize any impacts of ALAN on sleep. The most obvious and effective solution would be to eliminate ALAN wherever it is not necessary. However, there are conflicting opinions about what is “necessary,” and many contexts where ALAN may have actual or perceived benefits for humans. In such contexts, mitigation is likely the best solution. Smarter lighting designs can reduce the penetration of light into unwanted or unnecessary areas, such as bedrooms and nature reserves (Gaston, Davies, Bennie, & Hopkins, 2012). Since blue wavelengths of light have the greatest impact on melatonin and circadian rhythms, reducing or filtering out these wavelengths could also reduce impacts of ALAN on sleep. However, studies testing this approach for humans have reported mixed results (Ayaki et al., 2016; Heath et al., 2014; van der Lely et al., 2015), and little is known about whether it would benefit wildlife (Dimovski & Robert, 2018). Other possible solutions include dimming lights or simply switching them off when they are of least benefit to humans (Davies & Smyth 2018). The success of these solutions will depend on how sleep is affected by different timings, durations, and intensities of light, for which further research is needed. In all likelihood, the best outcome will involve a combination of approaches, adapted for specific contexts. Importantly, while there are still some critical gaps in our understanding, there is sufficient evidence to warrant strategic minimization of ALAN to reduce its harmful impacts.

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ORCID

Anne E. Aulsebrook  <http://orcid.org/0000-0002-9217-7043>

Therésa M. Jones  <http://orcid.org/0000-0002-5300-0018>

Raoul A. Mulder  <http://orcid.org/0000-0002-2710-0947>

John A. Lesku  <http://orcid.org/0000-0001-5073-6954>

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