SYMPOSIUM ARTICLE

Light at Night and Disrupted Circadian Rhythms Alter Physiology and Behavior

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Synopsis Life on earth has evolved during the past several billion years under relatively bright days and dark nights. Virtually all organisms on the planet display an internal representation of the solar days in the form of circadian rhythms driven by biological clocks. Nearly every aspect of physiology and behavior is mediated by these internal clocks. The widespread adoption of electric lights during the past century has exposed animals, including humans, to significant light at night (LAN) for the first time in our evolutionary history. Importantly, endogenous circadian clocks depend on light for synchronization with the external daily environment. Thus, LAN can derange temporal adaptations. Indeed, disruption of natural light–dark cycles results in several physiological and behavioral changes. In this review, we highlight recent evidence demonstrating how LAN exposure can have serious implications for adaptive physiology and behavior, including immune, endocrine, and metabolic function, as well as reproductive, foraging, and migratory behavior. Lastly, strategies to mitigate the consequences of LAN on behavior and physiology will be considered.

Introduction—circadian rhythms

Prior to the past century, life on this planet evolved under bright, sunlit days and dark, and moon- and starlit nights. Early during the evolution of life on earth, the daily rhythm of our rotating planet was internalized in the form of self-sustaining temporal rhythms that approximate the solar day (Reppert and Weaver 2002). The approximately 24-h circadian rhythms are set to precisely 24 h by exposure to bright light at the beginning and throughout the day. In plants, for example, such clocks likely evolved to forecast light and dark to optimize photosynthesis or counteract harmful redox reactions on a daily basis (Guadagno et al. 2018). As organisms became more complex, metabolism and nearly all other physiological and behavioral processes were regulated by circadian clocks. Thus, physiological processes such as gene expression (Eckel-Mahan et al. 2012), cellular division (Farshadi et al. 2020), endocrine (Gamble et al. 2014), metabolic (Reinke and Asher 2019), and immune function (Logan and Sarkar 2012), as well as behavioral processes such as sleep and locomotor activities (Antle and Silver 2016), foraging (Challet 2019), and reproduction (Boden and Kennaway 2006) are all coordinated by internal clocks entrained to the solar day. Although other entraining agents (or *zeitgebers*) have been documented, bright day and dark night cycles appear to be the most potent environmental factor that synchronizes internal clocks with the external world.

At the molecular level, circadian rhythms arise from the cyclical transcription and translation system of a set of core clock genes, which in vertebrates includes *Clock*, *Bmal1*, *Per*, and *Cry*, among others. In essence, heterodimers of these clock genes act as transcriptional activators and repressors of one another to form an autoregulatory transcriptional–translational feedback loop. These genes are expressed in nearly every tissue, and they drive

circadian rhythms by activating and repressing the transcription of other genes within the genome. The intricate details of clock genes and their feedback loop have been detailed elsewhere (Partch et al. 2014). Importantly, a complete cycle of this loop takes approximately 24-h to occur, and the timing, or phase, of the loop is coordinated by environmental *zeitgebers*.

Light entrains circadian rhythms

In mammals, internal circadian rhythms are synchronized via the orchestration of core clock gene loops within the suprachiasmatic nuclei (SCN) of the anterior hypothalamus (Evans and Silver 2015). The SCN maintains internal synchrony with the external world by receiving and interpreting photic signaling from the retina. Photosensitive cells in the retina, including rods, cones, and the signal relaying melanopsin-containing intrinsically photosensitive retinal ganglion cells (ipRGCs) transduce photic information for signaling to the SCN along the retinohypothalamic tract (Lucas et al. 2012). ipRGCs exhibit peak sensitivity to short-wavelength (blue) light, which has potent effects on the rhythmicity of the circadian system. A diverse population of neurons and astrocytes in the SCN comprise circuits that interpret retinal photic signaling information and provide direct and indirect rhythmic signaling cues to the rest of the body (Silver et al. 2018).

Light exposure can discretely and continuously modulate the activity of neurons, glial cells, and molecular pathways within the SCN. As with all rhythms, cellular and molecular activity within the SCN fluctuates across a period of about 24-h, even in the absence of external synchronizing cues. It is the connection with the retina that allows light to synchronize SCN activity with the solar day. As measured by calcium imaging or c-fos expression, neuronal activity in the SCN is modulated and inducible by light exposure throughout the day (Kornhauser et al. 1990; Jones et al. 2018). For example, VIP-containing neurons in the SCN exhibit greatest spontaneous activity during the light phase and are acutely sensitive to light pulses in the hours before and after the onset of the dark phase in mice (Jones et al. 2018). Astrocytic microdomains in the dorsal SCN exhibit circadian rhythms in calcium spikes (Brancaccio et al. 2017), and astrocytic clock gene rhythms in the SCN are entrained by photic signaling, even when clock gene transcriptional/translational loops are exclusively eliminated in neurons (Brancaccio et al. 2019). Given that astrocytes alone are capable of producing circadian rhythms in the SCN, current evidence strongly suggest that astrocytic activity is modulated by light in a manner similarly to SCN neurons (Brancaccio et al. 2019). Finally, clock gene expression in SCN neurons can be modulated by light. Aberrant exposure to light during various portions of the dark phase can induce expression of *Per1* and *Per2*, as well as *Clock* (Albrecht et al. 1997; Shigeyoshi et al. 1997; Abe et al. 1999; Miyake et al. 2000).

Taken together, the fundamental synchronization properties of the mammalian SCN demonstrate the vital importance of appropriately timed light to the circadian system. Proper rhythmicity of SCN function, internal molecular and physiological rhythms, as well as behavioral rhythms all depend on consistent external light–dark cycles.

Artificial light at night

After the commercialization of artificial electric lighting at the turn of 20th century, the integrity of light–dark cycles has rapidly diminished to the point where the majority (>80%) of humans do not experience naturally dark nights (Falchi et al. 2016). In 2016, artificial light at night (LAN) covered over 23% of the earth's landmass between 75°N and 60°S (Falchi et al. 2016). The disappearance of dark nights will likely continue to expand in the foreseeable future, as LAN coverage is growing at a rate of about 2% per year due to continued global population growth, urbanization, and industrialization (Kyba et al. 2017). Illuminating the night with electrical lighting has facilitated anthropic industrial and societal development, but the environmental and ecological cost of artificial lighting has been dramatic.

Although LAN may appear to be an innocuous facet of modern life, nighttime light above natural levels can have negative consequences for the health of exposed organisms (Gaston et al. 2017). As suggested above, LAN exposure can alter the timing and integrity of the transcription–translation feedback loop and cellular activity within the SCN. Rhythmic and synchronous activity of the SCN is important for the coordination of numerous behavioral and physiological processes throughout the body. When the timing of SCN or peripheral rhythms is altered or disrupted by improperly timed synchronizing cues—such as LAN—circadian rhythms can become disrupted and internally desynchronized (Vetter 2020).

LAN alters clock gene loops

Numerous laboratory experiments have demonstrated that low levels of LAN (<10 lux) can disrupt clock gene expression. It is worth re-stating that unnatural exposure to light during various portions of the dark phase can induce expression of *Per1* and *Per2*, as well as *Clock*, thereby disrupting typical biological clock function (Albrecht et al. 1997; Shigeyoshi et al. 1997; Abe et al. 1999; Miyake et al. 2000). LAN directly alters PER1 and PER2 rhythms in the SCN (Shuboni and Yan 2010; Bedrosian et al. 2013b; Fonken et al. 2013b), *Clock* and *Cry1* rhythms in the hippocampus (Walker et al. 2020), and *Rev-erbα* rhythms in white adipose tissue (Fonken et al. 2013b) of laboratory rodents. LAN reduces the diurnal mean (MESOR) and peak amplitude of *Per2* expression in the liver of zebra finches (*Taeniopygia guttata*) (Batra et al. 2019) and alters *Period* expression in *Drosophila* heads (Honnen and Hölker 2019). Disruption of central and peripheral clock gene loops leads to internally desynchronized, blunted, or abolished circadian rhythms that are generated by the expression of core clock genes (Logan and Sarkar 2012; Gamble et al. 2014).

LAN alters immune function

LAN modulates the immune system of organisms in the laboratory and in the field, yet the effects are inconsistent. In some instances, LAN exposure exaggerates immune function and responsiveness to immune challenges. Several studies have demonstrated that LAN exposure exaggerates delayed-type hypersensitivity (Fonken et al. 2012; Bedrosian et al. 2013a) and increases antibody production in response to novel antigens (Fonken et al. 2012; Cissé et al. 2017b). Further, LAN can increase the bactericidal capacity of blood in both mice (*Mus musculus*) and quails (*Excalfactoria chinensis*) (Fonken et al. 2012; Saini et al. 2019) and can heighten innate immune response to lipopolysaccharide injections (Fonken et al. 2013c). Peripheral and central inflammation are also commonly observed following short and prolonged periods of LAN exposure (Walker et al. 2020; Bedrosian et al. 2013c; Becker et al. 2020).

Other research has demonstrated contrasting effects, in which LAN reduces immune function. For example, LAN can reduce adaptive and innate immune responses of rodents (Bedrosian et al. 2011; Aubrecht et al. 2014). These effects can even be transgenerational; maternal LAN exposure reduces adaptive immunity of male hamster offspring

(Cissé et al. 2017b). Crickets exposed to LAN exhibit reduced hemocyte concentrations but unchanged hemolymph lytic or phenoloxidase activity (Durrant et al. 2020). Juncos (*Junco hyemalis*) exposed to LAN across a full simulated annual photoperiod cycle display increased parasitemia with concurrent compensatory increased leukocyte counts, suggesting overall impaired immune function (Becker et al. 2020).

LAN can have inconsistent modulatory effects on organisms even within single studies. LAN disrupts rhythmic expression of *Il-6*, *Il-1β*, or *Il-10* profiles in various central and peripheral tissues of zebra finches without a clear pro- or anti-inflammatory effect (Mishra et al. 2019). Similarly, male Wistar rats exposed to 2-weeks of LAN exhibited reduced circulating monocytes and heightened circulating T cells across the day. After 5-weeks of LAN exposure in the same animals, time of day × LAN interactions lead to various increases and decreases of circulating leukocytes (Okuliarova et al. 2021). Together these contrasting data suggest that LAN exposure dysregulates the function of the immune system with context specific effects. The consequences of this modulation on survival and fitness in the field remain unspecified.

LAN alters endocrine function

LAN is a common and potent environmental endocrine disruptor (Russart and Nelson 2018) and recent research has continued to support this assertion. In the laboratory, LAN can both elevate and disrupt the rhythmic secretion of plasma corticosterone in zebra finches (Mishra et al. 2019); this is true for varying wavelengths and spectrums of light, including blue and green wavelengths and 5000 K spectrum white light (Pilorz et al. 2016; Alaasam et al. 2018; Mishra et al. 2019). Great tits (*Parus major*) nesting near white LED lights also exhibit elevated serum corticosterone (Ouyang et al. 2015). LAN exposure for only seven nights is capable of elevating corticosterone in great tit nestlings (Grunst et al. 2020). Lastly, juvenile American toads (*Anaxyrus americanus*) exposed to LAN in the larval stage have greater whole body corticosterone concentrations, but this effect does not persist when LAN exposure is limited to the juvenile stage (Cope et al. 2020). Given the sensitivity of the pineal gland to light, melatonin secretion is also disrupted by LAN. Diel melatonin rhythms in zebra finches are abolished by only 3 lux of blue LAN exposure (Mishra et al. 2019). Diel melatonin levels are also reduced in

Eurasian tree sparrows exposed to LAN (*Passer montanus*) (Jiang et al. 2020).

One informative study demonstrated that 1-h LAN pulses reduce mean and daily pineal allopregnanolone synthesis and secretion in chicks (*Gallus gallus*; LAN levels were not reported) (Haraguchi et al. 2019). Reduced allopregnanolone secretion resulting from LAN exposure led to a reduction of pituitary adenylate cyclase-activating polypeptide (PACAP) and increased neuronal death in the cerebellum. Restoration of allopregnanolone levels via daily injections in the second week of life in chicks exposed to LAN restored cerebellar PACAP levels and Purkinje cell numbers (Haraguchi et al. 2019).

The reproductive hormone axis can be altered by LAN. For example, LAN exposure reduced pituitary expression of luteinizing hormone β (LH) and follicle stimulating hormone β mRNA in perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) living in field enclosures (Brüning et al. 2018). Similarly, both sexes of perch and roach exposed to LAN had significantly reduced serum concentrations of 17β-estradiol and 11-ketotestosterone (Brüning et al. 2018). Another study examined the effects of three levels of LAN—85, 150, and 300 lux—on the hypothalamus–pituitary–gonadal axis of female tree sparrows (*P. montanus*) (Zhang et al. 2019). LAN at 85 lux stimulated activation of the HPG axis by increasing plasma estrogen and LH, whereas 150 and 300 lux blunted HPG activation and reduced plasma estrogen and LH concentrations (Zhang et al. 2019). In contrast, one report suggests that LAN has no discernable effects on salivary testosterone concentrations in toads (*Bufo bufo*) (Touzot et al. 2020). Together, this research adds to an already extensive field of literature demonstrating the hormonally disruptive effects of LAN.

LAN alters reproductive fitness

Recent reports suggest that LAN has generally negative effects on reproductive fitness in animals with several contradictory exceptions. *Drosophila* housed in 10 lux of LAN take longer to copulate after the onset of courtship; however, other courtship behaviors were not altered (McLay et al. 2018). LAN exposure further reduces fecundity in *Drosophila* by lowering the probability of egg laying and decreasing the number of eggs produced during oviposition (McLay et al. 2017). Common toads (*B. bufo*) exposed to LAN displayed increased latency to achieve successful amplexus and reduced fertilization success in males (Touzot et al. 2020). In a field-experiment, LAN repelled and inhibited successful mating behavior of a species of winter moth (*Operophtera brumata*) (van Geffen et al. 2015). Crickets (*Teleogryllus commodus*) exposed to LAN in a mating chamber paradigm took slightly longer to initiate movement toward mating calls, but LAN had no other discernible effects on movement or attraction toward the mating song (Thompson et al. 2019). Several studies have demonstrated that LAN reduces flashing frequency and mating success of fireflies (*Photuris versicolor* and *Photinus pyralis*) (Costin and Boulton 2016; Firebaugh and Haynes 2016).

In contrast, LAN can have beneficial effects on reproductive fitness in some species. For example, adult great tits exposed to low levels of LAN (0.5–5 lux) have increased testes volume and seminiferous tubule diameter (Dominoni et al. 2018). Additionally, LAN elevated testicular transcriptional activity indicative of heightened germ cell development and Sertoli cell activity (Dominoni et al. 2018). In a laboratory experiment, environmentally relevant LAN levels (determined empirically; 23–44 lux) also improved reproductive fitness in brown anole lizards (*Anolis sagrei*) (Thawley and Kolbe 2020). LAN increased the mean growth of these lizards, advanced egg laying time, increased eggs laid by smaller females, and increased egg laying frequency of smaller females without impacting the health of hatchlings (Thawley and Kolbe 2020). LAN can also have indirect fitness consequences. Exposure to as little as 1 lux of LAN delays the time to maturity in crickets (*T. commodus*) but increases femur and body size (Durrant et al. 2018).

LAN alters foraging behavior and food webs

LAN alters animal foraging behavior and food webs; this may lead to both beneficial and detrimental consequences for affected species. In laboratory settings, LAN shifts the timing of food intake such that animals eat more in their inactive phases, commonly resulting in increased gains of body mass (Fonken et al. 2010; Borniger et al. 2014; Aubrecht et al. 2015; Cissé et al. 2017a; Batra et al. 2019). LAN can also both suppress and improve foraging activity in laboratory settings. For example, LAN suppressed nocturnal sugar-water feeding behavior in three moth species housed in small plastic containers (van Langevelde et al. 2017). Contrastingly, perch (*P. fluviatilis*) exposed to 2 lx of LAN displayed increased foraging efficiency, foraging activity, and predatory attacks on invertebrate prey regardless of habitat complexity (Czarnecka et al. 2019).

In the natural environment, LAN can be both beneficial and disruptive to foraging behavior. Similar to the laboratory, LAN exposure can shift foraging activity

into the inactive phase of pigeons (*Columba livia f. domestica*) (Leveau 2020) and great tits (Silva et al. 2017). This effect appears to be species dependent, as LAN did not shift foraging timing in 5/6 examined songbird species in the latter study (Silva et al. 2017). Stephens' kangaroo rats (*Dipodomys stephensi*) exposed to LAN had reduced foraging activity (Shier et al. 2020). Jerboas (*Allactaga sibirica*) foraging in LAN covered patches are able to locate food more quickly, but the animals eat less, abandon searches more frequently, and display increased vigilance (Zhang et al. 2020). Together these results suggest an overall detrimental effect of LAN on foraging efficiency. LAN can conversely improve foraging behavior in some species. Orb-web spiders (*Eriophora biapicata*) are attracted to building nests near LED sources, and in the field this behavior results in greater prey captures (Willmott et al. 2019). But LAN also reduced web relocations in these spiders, which may be detrimental depending on prey abundance (Willmott et al. 2019). LAN alters the foraging behavior of bats, leading to increased and decreased moth or beetle consumption, depending on prey preference (Cravens et al. 2018). Redshanks (*Tringa totanus*) that live in areas covered by LAN exhibit increased foraging behavior and a preference toward sight-, rather than tactile-based, scavenging (Dwyer et al. 2013).

Food web composition and abundance can be directly affected by LAN exposure by altered selective pressure. A 2-year long field study demonstrated that streetlamps increase emergence of aquatic insects and altered ground dwelling arthropod populations (Manfrin et al. 2017). Introduction of artificial high-pressure sodium street lighting increased the abundance of invertebrates and increased the number of observed predators and scavengers (Davies et al. 2012). LAN reduced observed abundance of tree and cave weta (*Hemideina thoracica* and *Rhaphidophoridae*, respectively) in Waikato, New Zealand caves (Farnworth et al. 2018). Further, LAN either directly or indirectly can alter the biomass and ground coverage of grass vegetation across the year (Bennie et al. 2018). In all, LAN should be considered as an environmental disruptor that directly alters foraging behavior and food webs.

LAN alters metabolic function

LAN consistently impairs metabolic function (Fonken and Nelson 2014; Nelson and Chbeir 2018). As discussed in the foraging section, LAN exposure modulates the timing of feeding of animals in laboratory and natural environments, often leading to increased body masses. Naturally, altered timing of food-intake and disrupted metabolism are related. For example, LAN exposure in rodents is associated with altered energy expenditure in the hours before and after the onset of the dark phase and an increased preference for carbohydrate over lipid metabolism (Borniger et al. 2014). Further, zebra finches exposed to LAN exhibited altered nocturnal glucose levels and disrupted metabolic gene expression in the liver (Batra et al. 2019). However, the metabolic consequences of LAN are not dependent on changes in body mass. For example, 2-h pulses of white and green light in ZT14-16 of the dark phase result in elevated blood glucose following glucose tolerance tests compared with red LAN controls (Opperhuizen et al. 2017). Two weeks of LAN exposure increased triacyl glyceride levels in the liver, increased nocturnal plasma insulin, reduced plasma leptin, and disrupted lipid metabolism gene expression in the liver without altering body mass (Okuliarova et al. 2020). Lastly, toads (*B. bufo*) exposed to 20 lux of LAN increased standard metabolic rates, decreased activity energy expenditure, and increased standard energy expenditure (Touzot et al. 2019).

Metabolic hormones are also affected by LAN. For example, LAN can alter insulin secretion in rodents (Fonken et al. 2013a). Triiodothyronine (T3) levels are reduced in Eurasian perch (*P. fluviatilis*) with a concurrent increase in body mass following LAN exposure (Kupprat et al. 2020). In another laboratory setting, LAN also reduced plasma leptin and nocturnal insulin levels (Okuliarova et al. 2020).

When considering human health, the effects of LAN on metabolism are unfavorable (Fleury et al. 2020). However, when considering how LAN may affect metabolic function in the natural environment—particularly its effects on increased body mass with similar caloric intakes—the consequences may not be obviously adaptive or nonadaptive. Increased body mass gains may be seen as favorable in some environmental settings, but the associated dysregulated metabolic consequences may override the favorable mass increase.

LAN alters migratory behavior and movement

LAN can disrupt migratory patterns. LAN disrupts the movement and stopover patterns of nocturnal migrating birds (McLaren et al. 2018). Regional stopover density increases near LAN sources, but stopover density decreases in close proximity to light sources (McLaren et al. 2018; Cabrera-Cruz et al. 2020). In other words, these studies suggest that nocturnal migratory birds are drawn toward light

sources, but spend extra time finding appropriate landing areas with suitable low light levels. Purple martin (*Progne subis*) migratory birds exposed to at least 10 nights of LAN in their overwintering sites in South America end up departing 8 days earlier on average to their summer habitats (Smith et al. 2021). Lastly, migratory eels (*Anguilla anguilla*) in simulated downstream flow environments were less likely to enter illuminated channels and swam more rapidly in illuminated routes (Vowles and Kemp 2021).

Locomotor activity rhythms can be both suppressed and stimulated by LAN exposure. Activity onset is commonly altered by LAN. Bats (*Rhinolophus hipposideros*) exposed to street lighting exhibit delayed activity onset (Stone et al. 2009). LAN of various wavelengths phase advances activity patterns in great tits by up to 2 h by a masking effect (Spoelstra et al. 2018; Ulgezen et al. 2019). Diel activity is also altered by LAN in some species. Both overall and nocturnal activity of great tits is increased by LAN exposure (Ulgezen et al. 2019; Dominoni et al. 2020). Similarly, LAN exposure increased guppy (*Poecilia reticulata*) emergence activity from a starting box in a memory test (Kurvers et al. 2018). Conversely, LAN reduces diel activity in toads (*B. bufo*) by a mean 73% across the day (Touzot et al. 2019) and reduces nocturnal down-shore movement and diel activity in a sandy beach isopod (*Tylos spinulosus*) (Duarte et al. 2019).

Crosstalk between field and laboratory studies

It is becoming increasingly apparent that the effects of LAN on environmental health urgently need to be addressed. How can circadian rhythm disruption research inform LAN-reduction techniques to improve ecological and laboratory animal health? Work cited in this review and other previous research demonstrate how LAN may unintentionally alter the results of laboratory research (Dauchy et al. 1997; Dauchy et al. 2010, 2011). Accordingly, it should be commonplace for researchers to eliminate all blatant sources of LAN in vivarium rooms (Emmer et al. 2018). Any unnatural LAN in the environment is disruptive, but the current rate of societal industrialization dictates its implementation. As such, researchers should use field studies to inform policy on maximally acceptable levels of LAN that result in the least amount of environmental disruption possible. For example, efforts should be made to reduce skyward glow, contain ground light dispersion, and eliminate unnecessary LAN sources in the environment. Lastly, another avenue to mitigate environmental LAN disruption is the modification of LAN source spectrums. We will discuss the possibilities of this modification below.

Wavelength matters?

Light has wavelength dependent effects on the circadian system; as such, reduction of specific LAN wavelengths may improve environmental health. In humans, rodents, and other organisms, blue LAN is thought to have the most potent effects on the circadian system (Fleury et al. 2020). For example, nighttime light pulses of white LEDs with blue wavelength peaks, but not 'blue-cut' LEDs, can alter clock gene expression in the SCN of laboratory rodents (Nagai et al. 2019), and blue and white, but not red, LAN can consistently alter rodent behavior (Bedrosian et al. 2013d). Because of this, numerous organizations and experts have called for the reduction of blue LAN sources as a palliative remedy for LAN-mediated ecological disruption.

Yet, the efficacy of limiting blue LAN exposure has been challenged by research demonstrating that red and other wavelengths of light are also capable of disrupting the circadian system, especially at elevated intensities (Dauchy et al. 2015; Fleury et al. 2020). One-hour nighttime pulses of violet, blue, and green light can increase plasma cortisol and alter *Per1* expression, but in this context blue light had the greatest discernable effect and was the only wavelength to alter *Per2* expression (Pilorz et al. 2016). White, blue, and green LAN exposure can also elevate c-fos expression in the SCN, but white light was observed to have the greatest effect (Masís-Vargas et al. 2020). In the field, one group reported limited negative consequences of retrofitting high-pressure sodium lamps with LED lights in an urban setting (McNaughton et al. 2021). Avian populations were not affected by these LEDs, but LED-lit areas exhibited increased richness of overall and introduced species (McNaughton et al. 2021). Another study demonstrated similarly limited consequences of cool versus warm LED lights on insect and bat populations (Bolliger et al. 2020). However, given that the history of selective pressure induced by historical LAN exposure in the examined area may have already altered animal populations, the authors and others still advocate for blue LAN reduction efforts (Hopkins et al. 2018; Bolliger et al. 2020). Of note, the contradictory effects of these discussed studies may be not only due to wavelength effects, but they may reflect differences in the intensity or duration of

LAN exposure, as both play a role in typical circadian rhythm synchronicity (Comas et al. 2006).

Aside from eliminating LAN in the environment and the laboratory (which seems impossible for the former), limiting wavelength spectrums appears to be the best option for reducing collateral damage to animal fitness and health. However, additional field and laboratory studies are needed to explore the true efficacy of modifying LAN source wavelengths, that is, eliminating blue/green LAN.

Conclusion

LAN is a pervasive and ever-growing facet of modern-day urban, suburban, and indoor life. The majority of humans are exposed to LAN, and a growing percentage of animal populations in the wild are becoming exposed as well. LAN acts as an environmental disruptor with generally negative (with few positive exceptions) consequences on the brain, physiology, and behavior, including disruptions of clock gene rhythms, neuronal activity, immune function, hormone function, reproductive behavior, metabolic function, foraging activity, and migratory behavior. Although total elimination of LAN is an impossible task, field and laboratory research can continue to elucidate the consequences and characteristics of LAN. These efforts could in turn improve our ability conduct ecologically relevant laboratory experiments with reduced variability and improve our ability to implement environmental LAN sources that have the least amount of ecological impact.

Data availability statement

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References

Abe H, Honma S, Namihira M, Tanahashi Y, Ikeda M, Yu W, Honma K. 1999. Phase-dependent induction by light of rat clock gene expression in the suprachiasmatic nucleus. Brain Res Mol Brain Res 66:104–10.

Alaasam VJ, Duncan R, Casagrande S, Davies S, Sidher A, Seymoure B, Shen Y, Zhang Y, Ouyang JQ. 2018. Light at night disrupts nocturnal rest and elevates glucocorticoids at cool color temperatures. J Exp Zool A Ecol Integr Physiol 329:465–72.

Albrecht U, Sun ZS, Eichele G, Lee CC. 1997. A differential response of two putative mammalian circadian regulators, mPer1 and mPer2, to light. Cell 91:1055–64.

Antle MC, Silver R. 2016. Circadian insights into motivated behavior. Curr Top Behav Neurosci 27:137–69.

Aubrecht TG, Jenkins R, Nelson RJ. 2015. Dim light at night increases body mass of female mice. Chronobiol Int 32:557–60.

Aubrecht TG, Weil ZM, Nelson RJ. 2014. Dim light at night interferes with the development of the short-day phenotype and impairs cell-mediated immunity in Siberian hamsters (Phodopus sungorus). J Exp Zool A Ecol Genet Physiol 321:450–6.

Batra T, Malik I, Kumar V. 2019. Illuminated night alters behaviour and negatively affects physiology and metabolism in diurnal zebra finches. Environ Pollut 254:112916.

Becker DJ, Singh D, Pan Q, Montoure JD, Talbott KM, Wanamaker SM, Ketterson ED. 2020. Artificial light at night amplifies seasonal relapse of haemosporidian parasites in a widespread songbird. Proc Biol Sci 287:20201831.

Bedrosian TA, Aubrecht TG, Kaugars KE, Weil ZM, Nelson RJ. 2013a. Artificial light at night alters delayed-type hypersensitivity reaction in response to acute stress in Siberian hamsters. Brain Behav Immun 34:39–42.

Bedrosian TA, Fonken LK, Walton JC, Nelson RJ. 2011. Chronic exposure to dim light at night suppresses immune responses in Siberian hamsters. Biol Lett 7:468–71.

Bedrosian TA, Galan A, Vaughn CA, Weil ZM, Nelson RJ. 2013b. Light at night alters daily patterns of cortisol and clock proteins in female Siberian hamsters. J Neuroendocrinol 25:590–6.

Bedrosian TA, Weil ZM, Nelson RJ. 2013c. Chronic dim light at night provokes reversible depression-like phenotype: possible role for TNF. Proc Natl Acad Sci USA 18:930–6.

Bedrosian TA, Vaughn CA, Galan A, Daye G, Weil ZM, Nelson RJ. 2013d. Nocturnal light exposure impairs affective responses in a wavelength-dependent manner. J Neurosci 33:13081–7.

Bennie J, Davies TW, Cruse D, Bell F, Gaston KJ. 2018. Artificial light at night alters grassland vegetation species composition and phenology. J Appl Ecol 55:442–50.

Boden MJ, Kennaway DJ. 2006. Circadian rhythms and reproduction. Reproduction 132:379–92.

Bolliger J, Hennet T, Wermelinger B, Blum S, Haller J, Obrist MK. 2020. Low impact of two LED colors on nocturnal insect abundance and bat activity in a peri-urban environment. J Insect Conserv 24:625–35.

Borniger JC, Maurya SK, Periasamy M, Nelson RJ. 2014. Acute dim light at night increases body mass, alters metabolism, and shifts core body temperature circadian rhythms. Chronobiol Int 31:917–25.

Brancaccio M, Edwards MD, Patton AP, Smyllie NJ, Chesham JE, Maywood ES, Hastings MH. 2019. Cell-autonomous clock of astrocytes drives circadian behavior in mammals. Science 363:187–92.

Brancaccio M, Patton AP, Chesham JE, Maywood ES, Hastings MH. 2017. Astrocytes control circadian timekeeping in the suprachiasmatic nucleus via glutamatergic signaling. Neuron 93:1420–35.e5.

Brüning A, Kloas W, Preuer T, Hölker F. 2018. Influence of artificially induced light pollution on the hormone system of two common fish species, perch and roach, in a rural habitat. Conserv Physiol 6:coy016.

Cabrera-Cruz SA, Cohen EB, Smolinsky JA, Buler JJ. 2020. Artificial light at night is related to broad-scale stopover distributions of nocturnally migrating landbirds along the Yucatan Peninsula, Mexico. Remote Sens 12:395.

Challet E. 2019. The circadian regulation of food intake. J Neurosci Res 15:393–405.

Cissé YM, Peng J, Nelson RJ. 2017a. Effects of dim light at night on food intake and body mass in developing mice. Front Neurosci 11:294.

Cissé YM, Russart KL, Nelson RJ. 2017b. Parental exposure to dim light at night prior to mating alters offspring adaptive immunity. Sci Rep 7:45497.

Comas M, Beersma DGM, Spoelstra K, Daan S. 2006. Phase and period responses of the circadian system of mice (Mus musculus) to light stimuli of different duration. J Biol Rhythms 21:362–72.

Cope KL, Schook MW, Benard MF. 2020. Exposure to artificial light at night during the larval stage has delayed effects on juvenile corticosterone concentration in American toads, Anaxyrus Americanus. Gen Comp Endocrinol 295:113508.

Costin KJ, Boulton AM. 2016. A field experiment on the effect of introduced light pollution on fireflies (Coleoptera: Lampyridae) in the piedmont region of Maryland. Coleopt Bull 70:84–6.

Cravens ZM, Brown VA, Divoll TJ, Boyles JG. 2018. Illuminating prey selection in an insectivorous bat community exposed to artificial light at night. J Appl Ecol 55:705–13.

Czarnecka M, Kakareko T, Jermacz Ł, Pawlak R, Kobak J. 2019. Combined effects of nocturnal exposure to artificial light and habitat complexity on fish foraging. Sci Total Environ 684:14–22.

Davies TW, Bennie J, Gaston KJ. 2012. Street lighting changes the composition of invertebrate communities. Biol Lett 8:764–7.

Dauchy RT, Dauchy EM, Tirrell RP, Hill CR, Davidson LK, Greene MW, Tirrell PC, Wu J, Sauer LA, Blask DE. 2010. Dark-phase light contamination disrupts circadian rhythms in plasma measures of endocrine physiology and metabolism in rats. Comp Med 60:348–56.

Dauchy RT, Dupepe LM, Ooms TG, Dauchy EM, Hill CR, Mao L, Belancio VP, Slakey LM, Hill SM, Blask DE. 2011. Eliminating animal facility light-at-night contamination and its effect on circadian regulation of rodent physiology, tumor growth, and metabolism: a challenge in the relocation of a cancer research laboratory. J Am Assoc Lab Anim Sci 50:326–36.

Dauchy RT, Sauer LA, Blask DE, Vaughan GM. 1997. Light contamination during the dark phase in "photoperiodically controlled" animal rooms: effect on tumor growth and metabolism in rats. Comp Med 47:511–8.

Dauchy RT, Wren MA, Dauchy EM, Hoffman AE, Hanifin JP, Warfield B, Jablonski MR, Brainard GC, Hill SM, Mao L. 2015. The influence of red light exposure at night on circadian metabolism and physiology in Sprague–Dawley rats. J Am Assoc Lab Anim Sci 54:40–50.

Dominoni D, Smit JAH, Visser ME, Halfwerk W. 2020. Multisensory pollution: artificial light at night and anthropogenic noise have interactive effects on activity patterns of great tits (Parus major). Environ Pollut 256:113314.

Dominoni DM, de Jong M, Bellingham M, O'Shaughnessy P, van Oers K, Robinson J, Smith B, Visser ME, Helm B. 2018. Dose–response effects of light at night on the reproductive physiology of great tits (Parus major): Integrating morphological analyses with candidate gene expression. J Exp Zool A Ecol Integr Physiol 329:473–87.

Duarte C, Quintanilla-Ahumada D, Anguita C, Manríquez PH, Widdicombe S, Pulgar J, Silva-Rodríguez EA, Miranda C, Manríquez K, Quijón PA. 2019. Artificial light pollution at night (ALAN) disrupts the distribution and circadian rhythm of a sandy beach isopod. Environ Pollut 248:565–73.

Durrant J, Botha LM, Green MP, Jones TM. 2018. Artificial light at night prolongs juvenile development time in the black field cricket, Teleogryllus commodus. J Exp Zool B Mol Dev Evol 330:225–33.

Durrant J, Green MP, Jones TM. 2020. Dim artificial light at night reduces the cellular immune response of the black field cricket, Teleogryllus commodus. Insect Sci 27:571–82.

Dwyer RG, Bearhop S, Campbell HA, Bryant DM. 2013. Shedding light on light: benefits of anthropogenic illumination to a nocturnally foraging shorebird. J Anim Ecol 82:478–85.

Eckel-Mahan KL, Patel VR, Mohney RP, Vignola KS, Baldi P, Sassone-Corsi P. 2012. Coordination of the transcriptome and metabolome by the circadian clock. Proc Natl Acad Sci USA 109:5541–6.

Emmer KM, Russart KLG, Walker IIW, Nelson RJ, DeVries AC. 2018. Effects of light at night on laboratory animals and research outcomes. Behav Neurosci 132:302–14.

Evans J, Silver R. 2015. The suprachiasmatic nucleus and the circadian timekeeping system of the body. In: Pfaff DW, editor. Neuroscience in the 21st century. New York (NY): Springer New York. p. 1–49.

Falchi F, Cinzano P, Duriscoe D, Kyba CCM, Elvidge CD, Baugh K, Portnov BA, Rybnikova NA, Furgoni R. 2016. The new world atlas of artificial night sky brightness. Cancer Res 2:e1600377.

Farnworth B, Innes J, Kelly C, Littler R, Waas JR. 2018. Photons and foraging: artificial light at night generates avoidance behaviour in male, but not female, New Zealand weta. Environ Pollut 236:82–90.

Farshadi E, van Der Horst GTJ, Chaves I. 2020. Molecular links between the circadian clock and the cell cycle. J Mol Biol 432:3515–24.

Firebaugh A, Haynes KJ. 2016. Experimental tests of light-pollution impacts on nocturnal insect courtship and dispersal. Oecologia 182:1203–11.

Fleury G, Masís-Vargas A, Kalsbeek A. 2020. Metabolic implications of exposure to light at night: lessons from animal and human studies. Obesity (Silver Spring) 28(Suppl. 1):S18–S28.

Fonken LK, Lieberman RA, Weil ZM, Nelson RJ. 2013a. Dim light at night exaggerates weight gain and inflammation associated with a high-fat diet in male mice. Endocrinology 154:3817–25.

Fonken LK, Aubrecht TG, Meléndez-Fernández OH, Weil ZM, Nelson RJ. 2013b. Dim light at night disrupts molecular circadian rhythms and increases body weight. J Biol Rhythms 28:262–71.

Fonken LK, Haim A, Nelson RJ. 2012. Dim light at night increases immune function in Nile grass rats, a diurnal rodent. Chronobiol Int 29:26–34.

Fonken LK, Workman JL, Walton JC, Weil ZM, Morris JS, Haim A, Nelson RJ. 2010. Light at night increases body mass by shifting the time of food intake. Proc Natl Acad Sci USA 107:18664–9.

Fonken LK, Weil ZM, Nelson RJ. 2013c. Mice exposed to dim light at night exaggerate inflammatory responses to lipopolysaccharide. Brain Behav Immun 34:159–63.

Fonken LK, Nelson RJ. 2014. The effects of light at night on circadian clocks and metabolism. Endocr Rev 35:648–70.

Fleury G, Masís-Vargas A, Kalsbeek A. 2020. Metabolic implications of exposure to light at night: lessons from animal and human studies. Obesity 28:S18–S28.

Gamble KL, Berry R, Frank SJ, Young ME. 2014. Circadian clock control of endocrine factors. Nat Rev Endocrinol 10:466–75.

Gaston KJ, Davies TW, Nedelec SL, Holt LA. 2017. Impacts of artificial light at night on biological timings. Annu Rev Ecol Evol Syst 48:49–68.

Grunst ML, Raap T, Grunst AS, Pinxten R, Parenteau C, Angelier F, Eens M. 2020. Early-life exposure to artificial light at night elevates physiological stress in free-living songbirds. Environ Pollut 259:113895.

Guadagno CR, Ewers BE, Weinig C. 2018. Circadian rhythms and redox state in plants: till stress do us part. Front Plant Sci 9:247.

Haraguchi S, Kamata M, Tokita T, Tashiro K-i, Sato M, Nozaki M, Okamoto-Katsuyama M, Shimizu I, Han G, Chowdhury VS, et al. 2019. Light-at-night exposure affects brain development through pineal allopregnanolone-dependent mechanisms. eLife 8:e45306.

Honnen K, Hölker M. 2019. Artificial light at night influences clock-gene expression, activity, and fecundity in the mosquito Culex pipiens f. Molestus. Sustainability 11:6220.

Hopkins GR, Gaston KJ, Visser ME, Elgar MA, Jones TM. 2018. Artificial light at night as a driver of evolution across urban-rural landscapes. Front Ecol Environ 16:472–9.

Jiang J, He Y, Kou H, Ju Z, Gao X, Zhao H. 2020. The effects of artificial light at night on Eurasian tree sparrow (Passer montanus): Behavioral rhythm disruption, melatonin suppression and intestinal microbiota alterations. Ecol Indic 108:105702.

Jones JR, Simon T, Lones L, Herzog ED. 2018. SCN VIP neurons are essential for normal light-mediated resetting of the circadian system. J Neurosci 38:7986–95.

Kornhauser JM, Nelson DE, Mayo KE, Takahashi JS. 1990. Photic and circadian regulation of c-fos gene expression in the hamster suprachiasmatic nucleus. Neuron 5:127–34.

Kupprat F, Kloas W, Krüger A, Schmalsch C, Hölker F. 2020. Misbalance of thyroid hormones after two weeks of exposure to artificial light at night in Eurasian perch Perca fluviatilis. Conserv Physiol 9:coaa124.

Kurvers RHJM, Drägestein J, Hölker F, Jechow A, Krause J, Bierbach D. 2018. Artificial light at night affects emergence from a refuge and space use in guppies. Sci Rep 8:10.

Kyba CCM, Kuester T, De Miguel AS, Baugh K, Jechow A, Hölker F, Bennie J, Elvidge CD, Gaston KJ, Guanter L. 2017. Artificially lit surface of earth at night increasing in radiance and extent. Cancer Res 3:e1701528.

Leveau LM. 2020. Artificial light at night (ALAN) is the main driver of nocturnal feral pigeon (Columba livia f. Domestica) foraging in urban areas. Animals 10:554.

Logan RW, Sarkar DK. 2012. Circadian nature of immune function. Mol Cell Endocrinol 349:82–90.

Lucas RJ, Lall GS, Allen AE, Brown TM. 2012. How rod, cone, and melanopsin photoreceptors come together to enlighten the mammalian circadian clock. In: Kalsbeek A, Merrow M, Roenneberg T, Foster RG, editors. Progress in brain research. Amsterdam: Elsevier. p. 1–18.

Manfrin A, Singer G, Larsen S, Weiß N, van Grunsven RHA, Weiß N-S, Wohlfahrt S, Monaghan MT, Hölker F. 2017. Artificial light at night affects organism flux across ecosystem boundaries and drives community structure in the recipient ecosystem. Front Environ Sci 5:61.

Masís-Vargas A, Ritsema WIGR, Mendoza J, Kalsbeek A. 2020. Metabolic effects of light at night are time- and wavelength-dependent in rats. Obesity (Silver Spring) 28(Suppl. 1):S114–25.

McLaren JD, Buler JJ, Schreckengost T, Smolinsky JA, Boone M, Emiel van Loon E, Dawson DK, Walters EL. 2018. Artificial light at night confounds broad-scale habitat use by migrating birds. Ecol Lett 21:356–64.

McLay LK, Green MP, Jones TM. 2017. Chronic exposure to dim artificial light at night decreases fecundity and adult survival in Drosophila melanogaster. J Insect Physiol 100:15–20.

McLay LK, Nagarajan-Radha V, Green MP, Jones TM. 2018. Dim artificial light at night affects mating, reproductive output, and reactive oxygen species in Drosophila melanogaster. J Exp Zool A Ecol Integr Physiol 329:419–28.

McNaughton EJ, Beggs JR, Gaston KJ, Jones DN, Stanley MC. 2021. Retrofitting streetlights with LEDs has limited impacts on urban wildlife. Biol Conserv 254:108944.

Mishra I, Knerr RM, Stewart AA, Payette WI, Richter MM, Ashley NT. 2019. Light at night disrupts diel patterns of cytokine gene expression and endocrine profiles in zebra finch (Taeniopygia guttata). Sci Rep 9:15833.

Miyake S, Sumi Y, Yan L, Takekida S, Fukuyama T, Ishida Y, Yamaguchi S, Yagita K, Okamura H. 2000. Phase-dependent responses of Per1 and Per2 genes to a light-stimulus in the suprachiasmatic nucleus of the rat. Neurosci Lett 294:41–4.

Nagai N, Ayaki M, Yanagawa T, Hattori A, Negishi K, Mori T, Nakamura TJ, Tsubota K. 2019. Suppression of blue light at night ameliorates metabolic abnormalities by controlling circadian rhythms. Invest Ophthalmol Vis Sci 60:3786–93.

Nelson RJ, Chbeir S. 2018. Dark matters: effects of light at night on metabolism. Proc Nutr Soc 77:223–9.

Okuliarova M, Rumanova VS, Stebelova K, Zeman M. 2020. Dim light at night disturbs molecular pathways of lipid metabolism. Int J Mol Sci 21:6919.

Okuliarova M, Mazgutova N, Majzunova M, Rumanova VS, Zeman M. 2021. Dim light at night impairs daily variation of circulating immune cells and renal immune homeostasis. Front Immunol 11:3548.

Opperhuizen AL, Stenvers DJ, Jansen RD, Foppen E, Fliers E, Kalsbeek A. 2017. Light at night acutely impairs glucose tolerance in a time-, intensity- and wavelength-dependent manner in rats. Diabetologia 60:1333–43.

Ouyang JQ, de Jong M, Hau M, Visser ME, van Grunsven RHA, Spoelstra K. 2015. Stressful colours: corticosterone concentrations in a free-living songbird vary with the spectral composition of experimental illumination. Biol Lett 11:20150517.

Partch CL, Green CB, Takahashi JS. 2014. Molecular architecture of the mammalian circadian clock. PLoS ONE 24:90–9.

Pilorz V, Tam SK, Hughes S, Pothecary CA, Jagannath A, Hankins MW, Bannerman DM, Lightman SL, Vyazovskiy VV, Nolan PM, et al. 2016. Melanopsin regulates both sleep-promoting and arousal-promoting responses to light. PLoS Biol 14:e1002482.

Reinke H, Asher G. 2019. Crosstalk between metabolism and circadian clocks. Nat Rev Mol Cell Biol 20:227–41.

Reppert SM, Weaver DR. 2002. Coordination of circadian timing in mammals. Nature 418:935–41.

Russart KLG, Nelson RJ. 2018. Light at night as an environmental endocrine disruptor. Physiol Behav 190:82–9.

Saini C, Hutton P, Gao S, Simpson RK, Giraudeau M, Sepp T, Webb E, McGraw KJ. 2019. Exposure to artificial light at night increases innate immune activity during development in a precocial bird. Comp Biochem Physiol A Mol Integr Physiol 233:84–8.

Shier DM, Bird AK, Wang TB. 2020. Effects of artificial light at night on the foraging behavior of an endangered nocturnal mammal. Environ Pollut 263:114566.

Shigeyoshi Y, Taguchi K, Yamamoto S, Takekida S, Yan L, Tei H, Moriya T, Shibata S, Loros JJ, Dunlap JC, et al. 1997. Light-induced resetting of a mammalian circadian clock is associated with rapid induction of the mPer1 transcript. Cell 91:1043–53.

Shuboni D, Yan L. 2010. Nighttime dim light exposure alters the responses of the circadian system. Neuroscience 170:1172–8.

Silva AD, Diez-Méndez D, Kempenaers B. 2017. Effects of experimental night lighting on the daily timing of winter foraging in common European songbirds. J Avian Biol 48:862–71.

Silver R, Taub A, Li A. 2018. Suprachiasmatic nucleus anatomy, physiology, and neurochemistry. In: Nelson RJ, editor. Oxford Research Encyclopedia of Neuroscience: Neuroendocrine and Autonomic Systems. Chief Murray Sherman. New York: Oxford University Press.

Smith RA, Gagné M, Fraser KC. 2021. Pre-migration artificial light at night advances the spring migration timing of a trans-hemispheric migratory songbird. Environ Pollut 269:116136.

Spoelstra K, Verhagen I, Meijer D, Visser ME. 2018. Artificial light at night shifts daily activity patterns but not the internal clock in the great tit (Parus major). Proc R Soc B 285:20172751.

Stone EL, Jones G, Harris S. 2009. Street lighting disturbs commuting bats. Curr Biol 19:1123–7.

Thawley CJ, Kolbe JJ. 2020. Artificial light at night increases growth and reproductive output in Anolis lizards. Proc Biol Sci 287:20191682.

Thompson EK, Cullinan NL, Jones TM, Hopkins GR. 2019. Effects of artificial light at night and male calling on movement patterns and mate location in field crickets. Anim Behav 158:183–91.

Touzot M, Teulier L, Lengagne T, Secondi J, Théry M, Libourel PA, Guillard L, Mondy N. 2019. Artificial light at night disturbs the activity and energy allocation of the common toad during the breeding period. Conserv Physiol 7:coz002.

Touzot M, Lengagne T, Secondi J, Desouhant E, Thery M, Dumet A, Duchamp C, Mondy N. 2020. Artificial light at night alters the sexual behaviour and fertilisation success of the common toad. Environ Pollut 259:113883.

Ulgezen ZN, Käpylä T, Meerlo P, Spoelstra K, Visser ME, Dominoni DM. 2019. The preference and costs of sleeping under light at night in forest and urban great tits. Proc Biol Sci 286:20190872.

van Geffen KG, van Eck E, de Boer RA, van Grunsven RHA, Salis L, Berendse F, Veenendaal EM. 2015. Artificial light at night inhibits mating in a Geometrid moth. Insect Conserv Diver 8:282–7.

van Langevelde F, van Grunsven RH, Veenendaal EM, Fijen TP. 2017. Artificial night lighting inhibits feeding in moths. Biol Lett 13:20160874.

Vetter C. 2020. Circadian disruption: what do we actually mean. Eur J Neurosci 51:531–50.

Vowles AS, Kemp PS. 2021. Artificial light at night (ALAN) affects the downstream movement behaviour of the critically endangered European eel, Anguilla anguilla. Environ Pollut 274:116585.

Walker WH, Borniger JC, Gaudier-Diaz MM, Hecmarie Meléndez-Fernández O, Pascoe JL, Courtney DeVries A, Nelson RJ. 2020. Acute exposure to low-level light at night is sufficient to induce neurological changes and depressive-like behavior. Semin Neurol 25:1080–93.

Willmott NJ, Henneken J, Elgar MA, Jones TM. 2019. Guiding lights: foraging responses of juvenile nocturnal orb-web spiders to the presence of artificial light at night. Ethology 125:289–97.

Zhang FS, Wang Y, Wu K, Xu WY, Wu J, Liu JY, Wang XY, Shuai LY. 2020. Effects of artificial light at night on foraging behavior and vigilance in a nocturnal rodent. Sci Total Environ 724:138271.

Zhang X, Yang W, Liang W, Wang Y, Zhang S. 2019. Intensity dependent disruptive effects of light at night on activation of the HPG axis of tree sparrows (Passer montanus). Environ Pollut 249:904–9.