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REVIEW

Hormonally mediated effects of artificial light at night on behavior and fitness: linking endocrine mechanisms with function

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ABSTRACT

Alternation between day and night is a predictable environmental fluctuation that organisms use to time their activities. Since the invention of artificial lighting, this predictability has been disrupted and continues to change in a unidirectional fashion with increasing urbanization. As hormones mediate individual responses to changing environments, endocrine systems might be one of the first systems affected, as well as being the first line of defense to ameliorate any negative health impacts. In this Review, we first highlight how light can influence endocrine function in vertebrates. We then focus on four endocrine axes that might be affected by artificial light at night (ALAN): pineal, reproductive, adrenal and thyroid. Throughout, we highlight key findings, rather than performing an exhaustive review, in order to emphasize knowledge gaps that are hindering progress on proposing impactful and concrete plans to ameliorate the negative effects of ALAN. We discuss these findings with respect to impacts on human and animal health, with a focus on the consequences of anthropogenic modification of the night-time environment for non-human organisms. Lastly, we stress the need for the integration of field and lab experiments as well as the need for long-term integrative eco-physiological studies in the rapidly expanding field of light pollution.

KEY WORDS: Light pollution, Urban ecology, ALAN, Hormones, Metabolism, Stress, Sleep, Glucocorticoid, Thyroid, Melatonin

Introduction

Organisms have evolved under a natural dark and light cycle for millions of years, so their ability to survive and reproduce depends on not only occupying a favorable spatial niche but also an optimal temporal one. The increasing use of electric light has modified the temporal niche of humans, allowing them to be active at night. This change comes with obvious benefits, but we are also starting to see the dark side of night lighting (Gaston et al., 2017; Navara and Nelson, 2007; Swaddle et al., 2015). Indeed, the synchronization of circadian (see Glossary) and circannual physiological functions depends on precise timing information (Sharma, 2003). For example, timing of reproduction, immunological and foraging activities all vary with seasonal changes in day length (Dawson et al., 2001; Moen, 1978; Nelson and Demas, 1996; Stevenson et al., 2015).

In the early 1900s, William Rowan noticed that birds breeding in urbanized London enlarged their gonads earlier and bred earlier than birds in rural areas (Rowan, 1938b), and he proposed that the

difference was dependent on seasonal photoperiod (see Glossary) that has been altered by artificial light (Rowan, 1938a). Since Rowan's time, rigorous experimental work has related reproductive events with changes in photoperiod (Farner, 1964; Farner and Wingfield, 1980; Menaker, 1968). In the decades following these earlier studies, the night-time environment has been drastically altered with rapid growth of urban areas and artificial light (Cinzano and Falchi, 2014; Falchi et al., 2016; Rich and Longcore, 2006). Not only has artificial light at night (ALAN; see Glossary) intensity and coverage increased (Falchi et al., 2016; Kyba et al., 2017), but lighting technology has also advanced (Fig. 1). Within just 30 years, night-time lighting has progressed from low-pressure sodium to light-emitting diodes (LEDs). These changes have occurred on a relatively short time scale, evolutionarily speaking. Whether organisms have been able to keep up with these changes is a key question for evolutionary biologists and conservationists. As governments and agencies begin to switch to LEDs for economic reasons, do we know enough about these alternative light sources to justify policy change?

The endocrine system (see Glossary) is particularly susceptible and sensitive to changes in the environment because it integrates internal condition with external cues. Hormone levels vary in accordance with light–dark cycles, corresponding to metabolic, immunological and reproductive functions (Atkinson and Waddell, 1997; Guchhait and Haldar, 1999), which is why we focus on ALAN as a potential endocrine disruptor for this review. We start by outlining organismal perception of ALAN. Then, we discuss how the organism perceives light at the brain and the eye and how those signals are translated into responses at different hormonal axes that affect reproduction and survival. We focus on the pineal, reproductive, adrenal and thyroid endocrine axes in vertebrate systems (Table 1). Lastly, we suggest avenues for future research and stress the importance of reporting results to policy makers to limit light pollution.

Light perception

Detecting and responding to changes in photoperiod requires photoreceptors to detect light in the environment (irradiance; see Glossary), a clock to measure the photoperiod duration and an effector system to relay photoperiod information to the rest of the body (Halford et al., 2009; Kuenzel et al., 2015). The location of photoreceptors differs between mammals and non-mammalian vertebrates. Photoreception by mammals takes place exclusively in the retina, and removing the eyes eliminates the photoperiodic response (Foster et al., 1991). In addition to the image-forming retinal photoreceptors, mammals have specialized neurons in the retina, called intrinsically photosensitive retinal ganglion cells (ipRGCs), which detect irradiance (Berson, 2003; Berson et al., 2002). Stimulation of these neurons is transmitted to the suprachiasmatic nucleus (SCN) in the hypothalamus of the brain, which is considered the location of the 'master clock' that

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Glossary

Adrenal glands
Endocrine glands located above the kidneys that produce hormones such as glucocorticoids and adrenaline.
Artificial light at night (ALAN)
Any type of anthropogenic illumination at night, both indoor and outdoor.
Circadian
Biological processes occurring naturally in roughly a 24 h cycle, even in the absence of any temporal information.
Diel
A period of 24 h.
Endocrine system
Collection of glands that produce hormones that regulate most bodily functions, from sleep to mood.
Hypothalamic–pituitary–adrenal (HPA) axis
A set of three interacting endocrine glands involved in maintaining body function. In vertebrates, the HPA axis mainly regulates metabolic activities.
Hypothalamic–pituitary–gonadal (HPG) axis
A set of three interacting endocrine glands involved in maintaining reproductive activities.
Illuminance
Total luminous flux incident on a surface, per unit area. It is a measure of how much the incident light illuminates the surface, wavelength-weighted by the luminosity function to correlate with human brightness perception.
Incandescent
Emitting light as a result of being heated.
Irradiance
Radiant flux (power) arriving at a surface per unit area, as opposed to radiance, which is light leaving a surface.
Photoperiod
Day length; time of the day that the animal receives light.
Pineal organ
A small endocrine gland found in nearly all vertebrates and located in the lower mid-brain, at the point where the spinal cord meets the thalamus. It is responsible for maintaining circadian rhythms through the rhythmic release of the hormone melatonin.
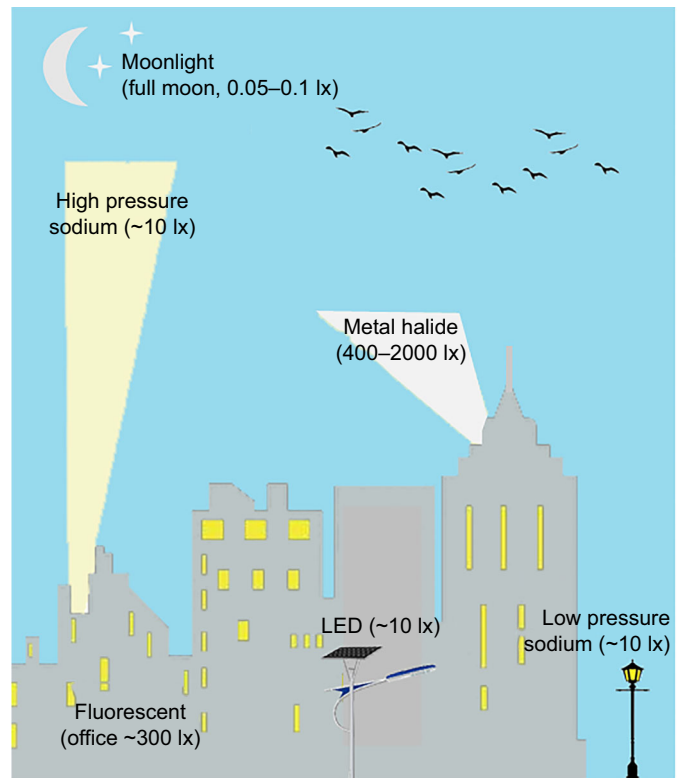**Scotophase**
The dark phase of the daily light–dark cycle.

Fig. 1. Sources of artificial light at night (ALAN) in an urbanized environment. Relative illuminance (see Glossary) is given in lux for estimates for human vision. Metal halide lights are usually used in stadiums. There is a general trend for all lighting to switch to LED given the versatile use of colors and cost savings.

regulates circadian rhythms (Kuenzel et al., 2015). The SCN ultimately regulates the synthesis and release of melatonin by the pineal gland (see Glossary), such that melatonin levels mirror the length of the scotophase (see Glossary). Melatonin then relays photoperiodic information to the rest of the body and can modulate the activity of the hypothalamic–pituitary axes (Hazlerigg and Loudon, 2008).

In contrast to mammals, non-mammalian vertebrates possess a range of non-retinal photoreceptors that can be located in various parts of the body, including the pineal gland, septum, hypothalamus, hindbrain and spinal cord (Hankins et al., 2014; Kuenzel et al., 2015). As well as being anatomically diverse, the photoreceptors in different locations can mediate separate aspects of physiology and behavior. As an example, in birds, the reproductive response to a changing photoperiod does not require the eyes, SCN or pineal gland (Kuenzel et al., 2015; Wilson, 1991). Instead, it appears that hypothalamic photoreceptors (Neuropsin and VA-opsin) with action spectrum peaking at either 420 or 490 nm, respectively, principally regulate the reproductive photoperiodic response in birds (Davies et al., 2012; Menaker and Keatts, 1968; Nakane et al., 2010).

To stimulate the non-retinal photoreceptors of non-mammalian vertebrates, light must penetrate the overlying tissues. The spectral composition of light that reaches the photoreceptors is, therefore, heavily determined by the transmission of the overlying tissues (Davies et al., 2012; Hankins et al., 2014). Incoming light is first modified by scattering due to the tissue, which results in more longer-wavelength than shorter-wavelength light penetrating to the photoreceptors. The spectral composition of incoming light is further modified by light-absorbing molecules in the tissue. In this respect, the most important light-absorbing molecule is hemoglobin, which has a transmission window that allows more light in the 460–540 nm range to penetrate to the photoreceptors (Foster et al., 1985; Hartwig and van Veen, 1979). For reference, the human eye can perceive light between 380 and 700 nm. This transmission window likely created a selection pressure for the spectral sensitivity of photoreceptors, such that many non-image-forming photoreceptors are maximally sensitive to light around 480 nm (with a spread ranging from 360 to 530 nm; Hankins et al., 2014). In the context of ALAN, the spectral sensitivity of the non-image-forming photoreceptors has important implications for how – and, in fact, whether – vertebrates perceive and respond to a given type of ALAN. The spectral composition of artificial light must overlap the spectral sensitivity of a given photoreceptor to be perceived and elicit a response. If the two do not overlap, then it is unlikely that artificial light will be perceived. Owing to a lack of studies on different types of ALAN, it is currently unclear which sources of ALAN [e.g. LED, low- and high-pressure sodium, incandescent (see Glossary), etc.] are perceived by vertebrates and, hence, are responsible for the apparent effects of ALAN.

Table 1. Studies on the effect of ALAN on the endocrine function of non-model vertebrates*

Species	Scientific name	Taxa	Location	Type of light	Intensity	Hormone	Effect	Citation
Great tit	*Parus major*	Bird	Lab	LED white, full spectrum	0.05–5 lx	Melatonin	Dose-dependent decrease with intensity	de Jong et al., 2016
Blackbird	*Turdus merula*	Bird	Lab	Dimmable incandescent	0.3 lx	Melatonin	Reduced under light	Dominoni et al., 2013a,b,c
Senegal sole	*Solea senegalensis*	Fish	Lab	Fluorescent violet, white or red	3.3–51.9 µW cm^{-2}	Melatonin	Decreased under violet and white ALAN, but not under red ALAN	Oliveira et al., 2007
Anole lizard	*Anolis carolinensis*	Reptile	Lab	Fluorescent white	24.1 lx	Melatonin	Not reduced after exposure to 1–2 h of light pulses at mid-dark	Underwood, 1986
Tammar wallabies	*Macropus eugenii*	Mammal	Field	Naval base lighting	0–0.015 W cm^{-2}	Melatonin	Decreased at naval base	Robert et al., 2015
European perch	*Perca fluviatilis*	Fish	Lab	LED (red, green, blue, white)	0–100 lx	Melatonin	Decreased by white, blue, green and red LEDs	Brüning et al., 2015, 2016
						Gonadal hormones	Suppressed by white light >1 lx, not by blue, green, and red	Brüning et al., 2015, 2016
Siberian hamster	*Phodopus sungorus*	Mammal	Lab	NA	0–5 lx	Gonadal hormones	ALAN increased gonadal size compared with short day	Ikeno et al., 2014
						Thyroid hormones	Gene expression higher in ALAN exposed	Ikeno et al., 2014
						Melatonin	Gene expression higher in ALAN exposed	Ikeno et al., 2014
European blackbird	*Turdus merula*	Bird	Lab	Dimmable incandescent	0.3 lx	Testosterone	Advanced under light	Dominoni et al., 2013a,b,c
Florida scrubjay	*Aphelocoma californica*	Bird	Lab	NA	NA ('low')	Testosterone, estradiol, LH, melatonin	ALAN affected all hormones, but with notable sex differences	Schoech et al., 2013
Gray mouse lemur	*Microcebus murinus*	Mammal	Lab	LED white	0.3–51.5 lx	Estradiol	ALAN increased estradiol and advanced estrus	LeTallec et al., 2015
Siberian hamster	*Phodopus sungorus*	Mammal	Lab	NA	5 lx	Cortisol	ALAN blunted diurnal fluctuations	Bedrosian et al., 2013
Atlantic salmon	*Salmo salar*	Fish	Lab	Blue/white LED	0–2.75 W m^{-2}	Cortisol	Increased under blue high intensity and decreased post treatment	Migaud et al., 2007
Great tit	*Parus major*	Bird	Field	LED (red, green, white)	8 lx at ground	Corticosterone	White higher than other, decreasing effect farther from light source	Ouyang et al., 2015
Red drum	*Sciaenops ocellatus*	Fish	Lab	Fluorescent	2.05×10^{17} quanta s^{-1} cm^{-2}	T$_4$	Free-running T$_4$ under dim constant light	Leiner and MacKenzie, 2001

*Note that the focus for this table is on ALAN rather than photoperiodic studies. Studies are grouped according to the hormone studied. For reviews on model organisms, see text. ALAN, artificial light at night; LED, light-emitting diode; LH, luteinizing hormone; NA, not applicable.

From hormonal axes to function

To fully appreciate how different endocrine axes might mediate individual responses to ALAN, we must first understand how hormones can affect behavioral and physiological function. Hormonal systems are powerful physiological mechanisms by which organisms can flexibly adjust their behavior, morphology and physiology to varying environmental conditions (Zera et al., 2007). Therefore, they are one of the first mediators of the effects of ALAN, and the disruption of endocrine responses may also have pleiotropic effects on whole organism function (Table 1; Fig. 2). After light has been perceived by the organism, hormones act as part of an effector system that will transmit information on light to the rest of the body. In this section, we will review the effects of ALAN on four endocrine axes, and how organismal fitness is affected by changes in their function.

Pineal axis

The pineal gland plays a crucial role in the regulation of daily and seasonal rhythms of vertebrates. This organ is found in all vertebrate classes, from fishes (Falcón et al., 2003) to amphibians (Dodt and Heerd, 1962), reptiles (Underwood, 1977), birds (Cassone, 2014) and mammals (Arendt and Skene, 2005). The most important function of the pineal gland is to produce and release the hormone melatonin, which conveys information about light–dark cycles and day length, thereby maintaining temporal organization of physiology and behavior. Importantly, in many species such rhythms are endogenously produced, and persist when the animal is placed in constant environmental conditions, such as constant darkness or constant light (Daan and Aschoff, 1975). Changes in the light environment synchronize, or 'entrain', such endogenous rhythms to the optimal time of day, night or even season, when they are supposed to be expressed. Although the pineal gland and the function of melatonin have been extensively studied in birds and mammals, here we attempt to broaden the field of reference to other vertebrate groups wherever possible. In this section, we focus on the effects of ALAN only on pineal functions that modify daily rhythms. We will consider seasonal rhythms in the next section, which will concern reproduction, as these are not always mediated by melatonin.
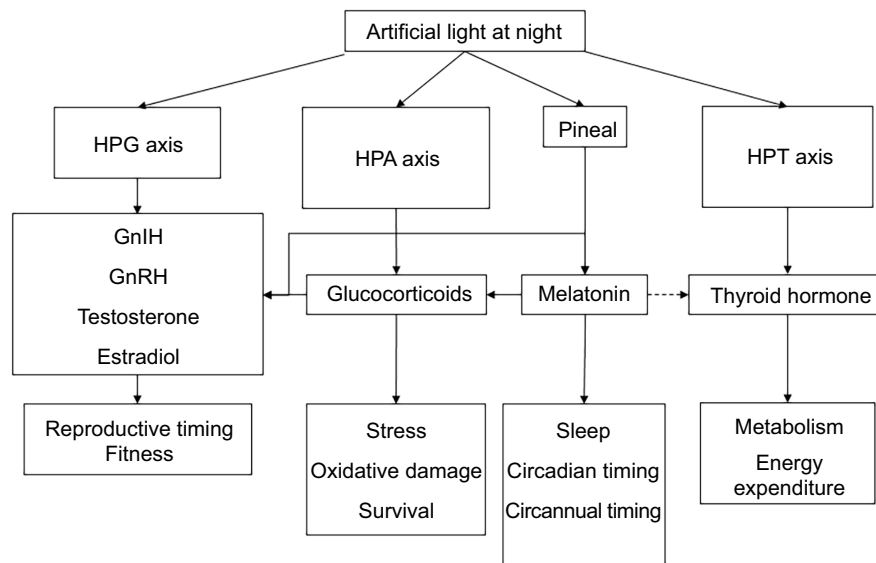
Fig. 2. Different endocrine axes affected by artificial light at night that lead to changes in potential fitness components. Solid lines indicate direct causal pathways and dashed lines indicate indirect pathways. GnIH, gonadotrophin-inhibitory hormone; GnRH, gonadotrophin-releasing hormone; HPA, hypothalamic–pituitary–adrenal; HPG, hypothalamic–pituitary–gonadal; HPT, hypothalamic–pituitary–thyroid.

Daily timing and light at night

The pineal gland exhibits strong endogenous regulation of its rhythm of melatonin synthesis and secretion in lower vertebrates, whereas in mammals the pineal rhythm is driven by a neural input. For instance, in birds it is possible to culture pineal cells *in vitro* without the cells losing their endogenous circadian release of melatonin (Arendt, 1998; Brandstätter et al., 2000; Gaston and Menaker, 1968; Robertson and Takahashi, 1988). Experiments both *in vivo* (in plasma samples) and *in vitro* (cultured pineal cells) have demonstrated that rhythms of melatonin are comparable (Brandstätter et al., 2001). This is not possible for the mammalian pineal gland as pinealectomy does not lead to disrupted circadian rhythms unless the animal is kept in constant bright light (Valdés-Tovar et al., 2015; Vinogradova et al., 2010), when animals present signs of splitting, fragmentation or damping of activity rhythms (Cassone, 1990).

The daily timing of melatonin secretion is highly conserved across all vertebrates (Reiter et al., 2014). Melatonin is secreted by the pineal gland during the night and is suppressed by light during the daytime. In mammals, the secretion of melatonin is largely controlled by the SCN, which then regulates pineal rhythms via neural inputs. In birds, the pineal gland possesses its own set of photoreceptors (Peirson et al., 2009), and is therefore able to produce melatonin independently of the SCN (Bell-Pedersen et al., 2005). However, in non-mammalian vertebrates it is also clear that melatonin is not an exclusive product of the pineal gland, but it can be synthesized by other organs and tissue. For instance, in birds, amphibians and fishes, the eyes are also capable of melatonin production (Underwood et al., 1984).

The duration of melatonin release varies between species, but it is generally assumed to reflect the length of the night and thereby the photoperiod (Arendt, 1998; Gwinner et al., 1997). Light pulses of different duration and intensity, delivered at night, can suppress melatonin levels in humans and other vertebrates (Arendt, 1998; Wikelski et al., 2008). Therefore, ALAN has been suggested to alter the perception of day length and influence the regulation of daily and seasonal rhythms (Dominoni, 2015; Dominoni and Partecke, 2015). Indeed, exposure to ALAN has been associated with changes in diel (see Glossary) activity patterns in several species across all vertebrate taxa (Bird et al., 2004; de Jong et al., 2016; Dominoni et al., 2014; Kempenaers et al., 2010; Migaud et al., 2007; Ouyang

et al., 2017b; Perry et al., 2008; Raap et al., 2015; Rotics et al., 2011). In humans, partial suppression of melatonin can be achieved by exposure to 100–300 lx for 2 h, although for complete suppression, an intensity of 2500 lx is required (Fig. 1) (Arendt, 1998; Dauchy et al., 2014; Stevens and Zhu, 2015). In captive birds, it has long been known that light pulses during the night can reduce melatonin concentrations (Gwinner et al., 1997; Vakkuri et al., 1985). Two recent studies in captivity have tested the hypothesis that nocturnal light of an intensity comparable to that found in urban environments can suppress melatonin rhythms. The first study showed that whole-night exposure to a light intensity of 0.3 lx is able to suppress melatonin concentrations to baseline values in the European blackbird (*Turdus merula*), especially in the early morning, with milder effects in the early and mid-night (Fig. 3; Dominoni et al., 2013b). The second study, on great tits (*Parus major*), revealed that increasing levels of light intensity given over the whole night are linearly associated with a decrease in plasma melatonin levels (de Jong et al., 2016). Similar results have been found in fishes, where exposure to as little as 2 lx of light for 1 h in the middle of the night is able to decrease melatonin levels in serum, and this decrease is linearly related to light intensity (Bayarri et al., 2002; Zachmann et al., 1992). However, in reptiles, which are phylogenetically closer to birds, light pulses during the night are, surprisingly, unable to reduce melatonin levels. This negative result has been found in both lizards and turtles (Underwood, 1986; Vivien-Roels et al., 1988), and the investigators suggest that, in these species, light might affect pineal-originated melatonin indirectly via its synchronizing effect of circadian oscillators, rather than directly via changes in the activity of N-acetyltransferase, the enzyme that initiates melatonin production in birds and mammals. Importantly, the degree of melatonin suppression by ALAN not only depends on the light intensity, but also on the light spectrum. Indeed, in humans, short wavelengths corresponding to blue light have been shown to elicit a much stronger suppressive effect on melatonin levels than longer wavelengths, such as orange-red light (Aubé et al., 2013; Cajochen et al., 2005; Navara and Nelson, 2007). This wavelength-dependent effect of light on melatonin suppression is used by some computer monitors and electronic devices, which can shift the spectrum of light emitted toward more orange and less blue light during the night time. Similar wavelength-dependent effects
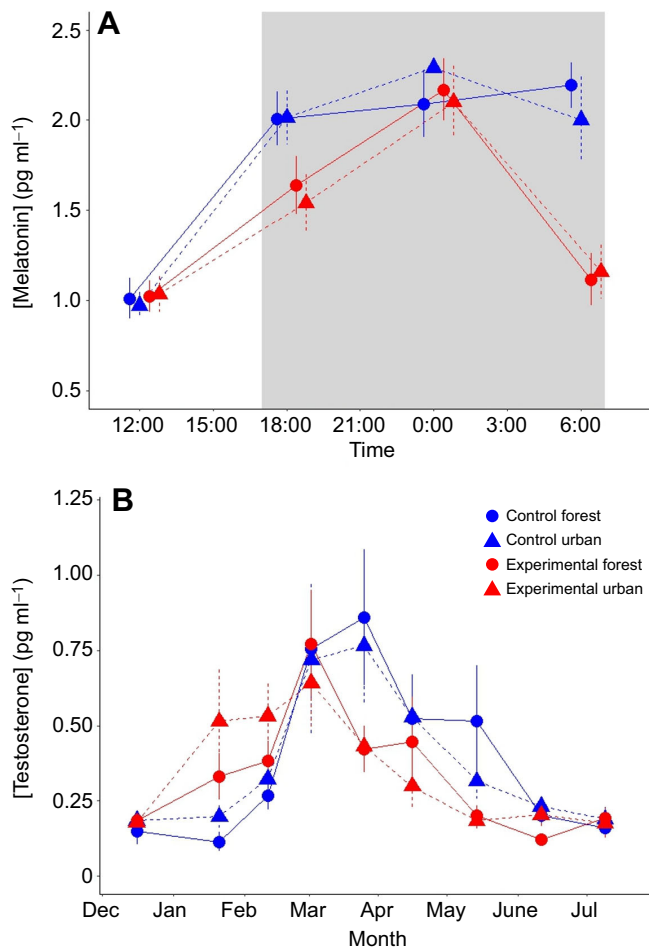
Fig. 3. Effects of exposure to ALAN on daily and seasonal concentration of melatonin and testosterone in male urban and forest European blackbirds (*Turdus merula*). Melatonin (A) and testosterone (B) levels in plasma from an equal number of forest and urban birds exposed to two different treatments: either dark nights (control) or artificial light at night (experimental). Experimental birds were exposed to a constant intensity of artificial light level throughout the night, equal to 0.3 lx, and produced by an incandescent light bulb with a wavelength range between 450 and 950 nm. Control birds were exposed to dark nights. Photoperiod followed the natural variation in daylength in Radolfzell, Germany and was changed on a daily basis. Daytime light intensity was ~600 lx and was provided by fluorescent white bulbs. Both hormones were analysed on plasma samples obtained from the same individuals at different times. Blood sampling for melatonin was conducted in winter (Jan 25 to 29, 2011). Blood sampling for testosterone was conducted approximately every 3 weeks during the period of Dec 2010 to Aug 2011. Figures adapted from Dominoni et al. (2013a,b).

have also been found in rodents (Nelson and Takahashi, 1991; Zubidat et al., 2011), birds (Lewis et al., 2001; Surbhi and Kumar, 2015) and fishes (Oliveira et al., 2007; Vera et al., 2010; Ziv et al., 2007). Therefore, it is generally accepted that short to mid wavelengths can suppress melatonin levels, and thus affect circadian physiology to a greater extent than longer wavelengths.

Circadian homeostasis is essential for the maintenance of body function and health. When circadian rhythms are disrupted, for instance through sleep deprivation or shift work, negative health consequences can appear. This has been demonstrated in cross-sectional human studies as well as in more rigorous experiments in model species (Buxton et al., 2012; McFadden et al., 2014; Möller-Levet et al., 2013; Navara and Nelson, 2007; Stevens, 2009). Since ALAN is a potent agent of modification of circadian rhythms, it has

been implicated in the emergence of several human diseases, from metabolic syndrome and obesity (Fonken et al., 2010; Navara and Nelson, 2007), to depression (Bedrosian et al., 2013; Stevens and Zhu, 2015) and cancer (Stevens, 2009). However, this aspect is much less studied in wild animals (Dominoni et al., 2016). Recent work has suggested that wild species, and in particular birds, might be sleep deprived when exposed to ALAN, although with only mild physiological health consequences (Ouyang et al., 2017b; Raap et al., 2016, 2015). Whether such effects can impair fitness remains to be established.

Reproductive axis

The relationship between light, circadian rhythms and the perception of day length profoundly affects seasonal processes, and forms the basis for understanding the potential effects of ALAN on seasonal rhythms and reproduction. Central to photoperiodism is the role of the hypothalamic–pituitary–gonadal (HPG) axis (see Glossary) (Dawson, 2015), a well conserved system across vertebrates (Sower et al., 2009). HPG axis activity begins with secretion of gonadotropin-releasing hormone (GnRH) from the hypothalamus into the hypophyseal portal blood vessels. GnRH stimulates the anterior pituitary to secrete gonadotropins [luteinizing hormone (LH) and follicle stimulating hormone (FSH)], which elicit gonadal maturation and secretion of sex steroids (estrogens and androgens). The neural pathway that detects day length and transduces this information to the HPG axis varies between vertebrate classes (Ikegami and Yoshimura, 2016). In mammals, light is detected through the eyes, and the signals are transduced to the pineal gland, which then releases melatonin (as detailed above). In addition, recent work has elucidated the molecular mechanism behind the action of melatonin on mammalian seasonal reproduction (Hut, 2011). A specific area in the pituitary, the pars tuberalis (PT), is packed with melatonin receptors. Under long photoperiods (usually more than 14 h of light per day), a physiological cascade is initiated in the PT that stimulates the production of thyroid hormones in the adjacent basal hypothalamus, ultimately influencing the secretion of GnRH. A similar mechanism has been recently uncovered in birds (Nakao et al., 2008).

Studies on birds have also been instrumental in the understanding of the relationship between light, circadian rhythms and seasonal processes. Indeed, it has long been known that single, short light pulses in the middle of the night are able to trigger reproductive responses (gonadal growth, LH secretion) even when the animal is kept under short, non-stimulatory day lengths (Follett et al., 1974; Te Marvelde et al., 2012). These studies suggest the existence of a circadian rhythm in photosensitivity that mediates seasonal reproduction in birds. Importantly, the photoreceptors involved in such responses are located in the avian hypothalamus (Davies et al., 2012; Halford et al., 2009; Nakane et al., 2010). Thus, it is reasonable to hypothesize that even brief pulses of ALAN might directly affect reproductive timing via stimulation of deep brain photoreceptors. A competing or complementary hypothesis is that ALAN does not directly stimulate the photoreceptors, but instead indirectly affects seasonal reproduction by influencing other processes, such as foraging and social interactions. As discussed below, future research is necessary to establish which hypothesis is correct.

Seasonally breeding vertebrates that use photoperiod as the main reproductive cue can be broadly categorized into either long- or short-day breeders, depending on the day length when they are fertile. Long-day breeders (e.g. horses, hamsters, birds and most non-avian reptiles) are fertile during spring when day length is increasing, whereas short-day breeders (e.g. sheep, goats, foxes and

deer) are fertile during autumn when day length is decreasing. A growing number of studies have found that the timing of seasonal reproductive processes differs between vertebrates inhabiting areas with ALAN and their conspecifics inhabiting areas with little or no ALAN (Brüning et al., 2015; de Jong et al., 2015; Dominoni et al., 2013a; Ikeno et al., 2014; LeTallec et al., 2015; Schoech et al., 2013). Given the central role of day length in regulating seasonal reproduction, one hypothesis to explain these findings is that ALAN stimulates the photoreceptors that activate the HPG axis, thereby altering the perceived day length and modifying the timing of reproductive processes (Fig. 3). Following this hypothesis, ALAN should advance the increase in day length that long-day breeders use to initiate HPG axis activity. In turn, long-day breeders should advance the timing of reproductive maturation and breeding. By contrast, ALAN should delay or even completely inhibit the decrease in day length that short-day breeders use to time reproductive maturation and breeding. The available evidence from studies of free-ranging vertebrates is consistent with these predictions. Studies of long-day breeders have focused mainly on birds, and have generally found that birds living in areas with ALAN initiate seasonal reproductive processes earlier than birds in areas lacking ALAN (de Molenaar et al., 2006; Kempenaers et al., 2010; Russ et al., 2015). Among short-day breeders, Robert et al. (2015) found that female tammar wallabies (*Macropus eugenii*) living in areas with ALAN gave birth later than wallabies living in areas free of ALAN. The authors suggest that it is because ALAN masks the small decreases in day length following the summer solstice that wallabies use to time the reactivation of blastocysts. In European perch (*Perca fluvialis*), another short-day breeder, ALAN completely inhibits gonadotropins (LH and FSH) production. However, it is important to note that although the effects of ALAN on the reproductive physiology are generally strong and well established, this does not necessarily mean that the actual breeding time will be affected. For instance, although ALAN can stimulate gonadal growth in birds up to 1 month earlier than usual, this translates into egg-laying only a few days earlier than usual, and even this is not observed every year (de Jong et al., 2015; Kempenaers et al., 2010). This is likely because egg-laying date is mediated by supplementary cues other than photoperiod, such as temperature and availability of food (Schaper et al., 2012; Te Marvelde et al., 2012).

Although the studies in controlled conditions generally find that ALAN affects the timing of seasonal reproductive processes, they do not demonstrate that ALAN exerts its effects by directly stimulating the non-image-forming photoreceptors. As such, it still cannot be excluded that ALAN indirectly affects seasonal reproduction by influencing other processes, including foraging and social interactions. ALAN-induced increases in perceived day length potentially give vertebrates more time each day to forage and for social interactions. More time to forage could potentially improve the likelihood that animals have sufficient energy stores for breeding, which is thought to be particularly important for females (Davies and Deviche, 2014). Furthermore, ALAN has been shown to improve foraging efficiency of wading birds (Regular et al., 2011; Santos et al., 2010). Increases in apparent day length as a result of ALAN may also provide time for more social interactions between males and females. It is well known that the onset of dawn song is earlier in birds inhabiting areas with ALAN (Kempenaers et al., 2010; Miller, 2006). Changes in the timing of reproductive processes could, therefore, be related to ALAN-induced changes in the behavior of the opposite sex. Indeed, it is well established that social interactions between males and females can modulate

reproductive processes. For example, male song has rapid endocrine and behavioral effects on females (Maney et al., 2007, 2003) and can stimulate ovarian development (Bentley et al., 2000). Likewise, males can respond to estradiol-treated females by elevating their plasma testosterone (Wingfield and Monk, 1994).

A major limitation of studies in the wild is that it is difficult to separate the effects of ALAN from the effects of other environmental variables that often accompany ALAN. Most studies of ALAN compare vertebrates in urban areas against vertebrates in non-artificially illuminated rural areas (for an exception, see de Jong et al., 2015). In addition to increased ALAN, urban areas also tend to be warmer (the so-called 'urban heat island' effect), noisier, have higher human density, altered plant phenology and possibly also altered food availability (Buyantuyev and Wu, 2012; Deviche and Davies, 2013; Halfwerk and Slabbekoorn, 2013; Imhoff et al., 2010). Accordingly, urban populations of long-day breeders generally begin reproductive processes earlier than their rural conspecifics (Deviche and Davies, 2013; Partecke et al., 2005). Studies in controlled conditions aiming to test whether ALAN by itself is sufficient to modify the timing of seasonal reproductive processes generally support the hypothesis that ALAN alters reproductive physiology consistent with the predictions above (Brüning et al., 2015; Dominoni et al., 2013a; Ikeno et al., 2014; LeTallec et al., 2015; Schoech et al., 2013), and likely more strongly than other urban-specific factors, such as higher temperature and breeding density (Dominoni et al., 2015). Indeed, the effects of ALAN have been demonstrated at all levels of the HPG axis. However, these effects of ALAN are complex and can depend on which aspects of the HPG axis are considered and sex. This point is illustrated by the study of Schoech et al. (2013), which found differences in the responses of plasma LH, testosterone and estradiol to ALAN in male and female Western scrub jays (*Aphelocoma californica*). The cause of this variation between hormones and sexes remains to be determined.

Adrenal axis

The hypothalamic–pituitary–adrenal (HPA; see Glossary) axis is responsible for responding to external stressors or challenges in the environment (Romero et al., 2009). Glucocorticoid hormones (GCs; cortisol, corticosterone), released by the adrenals (see Glossary), are of particular importance for vertebrates as they serve diverse functions to maintain organismal energy balance (Hau and Goymann, 2015). GCs coordinate organismal response to predictable changes but also to acute, unpredictable challenges. Thus, they are mediators of individual phenotypic flexibility to changing environmental conditions (Hau et al., 2016).

An early study in rats found an elevation of corticosterone levels with constant exposure to fluorescent lighting (Scheving and Pauly, 1966). Interestingly, not only did the rats have elevated corticosterone levels, their diurnal rhythm of release was also disrupted. A series of laboratory studies in hamsters have shown that chronic light exposure decreases immune function and elevates cortisol levels (Bedrosian et al., 2011, 2013). In a laboratory study on fish, only salmon exposed to high-intensity blue LED light had increased cortisol levels whereas white LEDs and metal halide lights did not raise cortisol levels (Migaud et al., 2007). Free-living great tits breeding in white light at night had much higher GC levels than birds breeding in green, red or dark control sites (Ouyang et al., 2015). Differences in these two studies on the effects of LEDs can be attributed to study design or taxa-related ALAN perception and response. These elevated levels are typical for circulating levels seen after a restraint-and-capture stress series. This study was the first to

look at GC levels in a free-living species and there were no differences in survival, which suggests that long-term fitness effects in the wild could be balanced by other factors, such as increases of food availability in white light (Welbers et al., 2017). These studies illustrate the importance of investigating GC levels in other taxa and under different lighting conditions as not all species seem to react to ALAN with an elevation of the HPA axis.

As widespread artificial light is a relatively recent phenomenon, upstream effects on receptors and receptor densities in the HPA axis have not been studied. In order to understand the full impact of ALAN on the HPA axis, we should be testing HPA reactivity (how high GC levels originate), as well as negative feedback (how increasingly high levels of GCs may inhibit further secretion). It could be that ALAN only affects negative feedback and/or receptor levels, which causes the downstream effects of elevated GCs. But only by probing the whole axis will we be able to counteract the effects of ALAN.

Thyroid axis

Thyroid hormones show pronounced daily and/or seasonal rhythms, and have been shown to strongly respond to changes in photoperiod. Thus, ALAN can potentially affect the secretion of these molecules, and thereby many physiological processes. Here, we briefly review the role of thyroid hormones (THs) in daily and seasonal biology, and then describe potential consequences of exposure to ALAN on thyroid function.

The daily and seasonal regulation of THs is well understood in vertebrates. THs are important regulators of energy homeostasis, and thyroid hormone receptors (THRs) are present in virtually all tissues (Williams and Bassett, 2011). T4 is the first TH that is produced and released in significant concentrations in the blood. T4 is converted into its active form, T3, through the action of the enzyme type II iodothyronine deiodinase (DIO2) in target tissues (Williams and Bassett, 2011). T3 is involved in several physiological processes, including growth and development, metabolism, regulation of body temperature and heart rate, and can be considered the main thyroid hormone (Eales, 1988; Mullur et al., 2014; Williams and Bassett, 2011). Photoperiod synchronizes the production of THs. For instance, in fishes, diurnal rhythms of circulating THs appear to be synchronized to the light cycle rather than to time of feeding (Leiner and MacKenzie, 2001; Reddy and Leatherland, 2003). Importantly, such rhythms persist in constant conditions for several cycles, suggesting the involvement of a light-sensitive endogenous circadian clock that determines the activation or inhibition of the hypothalamus–pituitary–thyroid (HPT) axis (Leiner and MacKenzie, 2001). Similar findings have been found across all vertebrates, from anurans (Gancedo et al., 1997) to birds (Cogburn and Freeman, 1987) and mammals (Eales, 1988). The time of day at which levels of T3 and T4 peak appears to differ across seasons (Gancedo et al., 1996; Yoshimura, 2010), underlying the role of seasonal changes in photoperiod in regulating thyroid function. Indeed, THs are a key component of the photoperiodic response across all vertebrates (Hazlerigg and Loudon, 2008; Hut, 2011).

So how could ALAN affect thyroid function? The most obvious way is through indirect effects due to changes in melatonin levels. As we outlined above, ALAN changes day length perception, and more specifically it is interpreted as a long day. Thereby, exposure to ALAN fundamentally shifts the entire physiology to longer-day-length-like conditions. As for thyroid action, increased day lengths initiate a physiological cascade that promotes the conversion of T4 into T3 and ultimately gonadal activation. Indeed, long

photoperiods have been associated with increased levels of TSH and T3 in several species (Boeuf and Le Bail, 1999; Nakao et al., 2008; Yoshimura, 2010). Realistic levels of ALAN (5 lx) have been shown to increase the expression of TSH receptors in the hypothalamus and pars tuberalis of Siberian hamsters kept under short photoperiods, and this was accompanied by important physiological changes such as increased gonadal and body mass, suggesting that dim light at night can alter the molecular and physiological mechanisms underlying photoperiodic response, including thyroid function (Ikeno et al., 2014). However, chronic exposure to ALAN might have the opposite effect and reduce thyroid hormones to very low levels, as seen for testosterone in birds (Dominoni et al., 2013c). Indeed, studies on humans living in polar regions have highlighted the risk of the so-called 'polar T3 syndrome', a hallmark of which is chronically low levels of blood T3. Such syndromes are usually associated with psychological disorders such as depression and increased aggression, similar to seasonal affective disorders (SADs) (Palinkas and Suedfeld, 2008). Changes in thyroid hormone concentrations due to ALAN could also have indirect effects on a plethora of other physiological processes that are heavily regulated by thyroid action. In particular, energy metabolism is a key process that is under the influence of the thyroid (Mullur et al., 2014). A recent study has linked ALAN with reduced energy expenditure in wild birds (Welbers et al., 2017), but it is unclear whether thyroid hormones were at all involved in such metabolic changes. Overall, it is sensible to hypothesize several physiological consequences of light at night that could be mediated by changes in thyroid hormones. However, there is little empirical evidence for this so far, and some data point more to an indirect effect of ALAN on thyroid action via changes in circadian physiology and melatonin (Ikeno et al., 2014).

Future plans

We have highlighted differences between field and laboratory studies (Calisi and Bentley, 2009). In lab studies, it is clear that ALAN disrupts endocrine axes, which could indirectly affect phenotypic traits, leading to changes in fitness. However, conclusions from field studies where animals are potentially able to avoid ALAN are currently inconclusive due to the lack of studies on many taxa and standardized measurements of light sources. Furthermore, the findings from this small set of available studies to a certain extent can result from publication bias, and until more research is available for meta-analyses, endocrine disruption due to ALAN in the wild remains a black box (Ouyang et al., 2017a). Laboratory studies can illustrate the mechanistic 'dark' sides of ALAN, and these negative effects can be ameliorated by using alternative light spectra for LEDs, switching to different types of lights, or only using light at certain periods of the night. However, the light sources used during the day in the laboratory setting are not able to reach the same levels of intensity as sunlight, which might be a problem when studying the effects of ALAN on circadian rhythms (Bentley et al., 1998). In the few field studies conducted to date, causal relationships are more complex to demonstrate, and although short-term physiological changes are observed, long-term fitness effects are not as evident (Table 1). We are in dire need of more studies in the wild linking physiological mechanisms to organismal function and ultimately to fitness. As animals are freely able to move away from light sources, the question of avoidance and ability to do so is a necessary one. Adaptive processes, such as phenotypic plasticity and entrainment to environmental stimuli, may offset the impact of ALAN. Natural examples of species that are seasonally subjected to long photoperiods, e.g. arctic species, may thus offer

some insight into potential adaptation. We suggest combining laboratory and field studies to understand both mechanism and function in relation to ALAN.

As the section on reproduction illustrates, ALAN is associated with changes in reproductive physiology at all levels of the HPG axis and in the timing of breeding. Why, then, is it necessary to determine whether ALAN directly stimulates the photoreceptors that activate the HPG axis? There are currently efforts to mitigate the effects of ALAN on wildlife, for example by changing the color, intensity and/or type of outdoor lights. A deeper understanding of the pathway(s) by which ALAN affects reproductive processes will play a major role in deciding the most suitable type of outdoor lighting. The non-image-forming photoreceptors that initiate seasonal reproductive processes are sensitive to a narrow range of wavelengths and a higher light intensity is required for photo-induction of the HPG axis than is required to entrain circadian rhythms (Davies et al., 2012; Dawson, 2015; Menaker, 1968). Therefore, to stimulate the non-image-forming photoreceptors and affect activity of the HPG axis, ALAN must not only be of the correct spectral composition, but also of adequate intensity. It is possible that ALAN is sufficient to enable visually oriented vertebrates to be active for longer each day and to modify circadian rhythms, but is insufficient to stimulate the non-image-forming photoreceptors. ALAN is produced by a growing diversity of electric light bulbs, and the light produced by each bulb type has a unique spectral composition and intensity. The night-time environment is now a patchwork of different light spectrums and intensities (Fig. 1; Hale et al., 2013), but the effects of any given type of ALAN, relative to other types, are largely unknown. To date, studies of the effects of ALAN on reproductive processes commonly consider the effects of light produced by a single type of bulb (commonly LED or incandescent bulbs), and few have compared the responses to different types of light (Gaston et al., 2015). This gap in our knowledge hinders our ability to predict how vertebrate reproductive processes will respond to a given type of ALAN. If ALAN does indeed directly stimulate the photoreceptors, then the best predictor for how strongly a given type of ALAN will influence reproductive processes is likely to be the overlap between the action spectra of the photoreceptors and the spectral composition of the light. By contrast, this may be a poor predictor if ALAN indirectly affects reproductive processes by influencing foraging or social interactions. If this is the case, a better predictor of how ALAN affects vertebrates may be how well it stimulates visual photoreceptors. To make progress in understanding how ALAN affects the reproductive processes of vertebrates, we suggest that future studies should compare the responses to types of ALAN with diverse spectral compositions and at intensities similar to those experienced by free-ranging vertebrates (Dominoni and Partecke, 2015). Furthermore, studies designed to test whether ALAN directly or indirectly affects vertebrate reproductive processes have the potential to greatly improve our ability to predict how vertebrates will respond to the changing night-time environment.

Hormonal systems are pleiotropic: changes in one effector system often create downstream changes throughout the organism. We see some evidence of changes in melatonin having downstream impacts on GnIH and the reproductive axis. To have a complete view of endocrine systems affected by ALAN, we need more studies in which multiple endocrine axes are evaluated. We also have a paucity of studies on certain vertebrate taxa (Table 1); given the differences in light perception and pineal function for certain vertebrate classes, such as reptiles and amphibians, studies on these animals will be especially useful.

ALAN is a pressing ecological and economic concern, and we are seeing an exponential increase in research studies (Davies and Smyth, 2017). However, there is a current lack of consideration for seasonality and latitude (but see Da Silva and Kempenaers, 2017 for a recent example of latitudinal variation in singing behavior affected by ALAN). For example, high-latitude species may not be affected by ALAN in the summer but could be more heavily affected in the winter because of the longer night-time period, whereas lower latitude species may be more consistently affected throughout the year. These seasonal and latitudinal effects might only be evident if data are collected at non-traditional locations, such as the tropics or the arctic. With these data, we can then test hypotheses regarding geographical relationships between hormone levels and ALAN using macroanalyses. As large, global datasets of hormone measurements will soon be available (C. Francis and M. Vitousek, unpublished results), a macro-analytic approach will be particularly useful.

To conclude, in this Review we have highlighted several endocrine pathways that are affected by ALAN. As ALAN is increasingly recognized as a threat to biodiversity and ecosystem services, there is considerable interest in reducing its impact via informed policy decisions (Hölker et al., 2010; Knop et al., 2017). In order to do so, we are in desperate need of more mechanistic studies that measure both endocrine responses to ALAN as well as their fitness effects. The studies should be conducted in more taxa and in more natural environments. Before development plans begin for new urban areas, which are projected to increase by 50% by 2025 (United Nations, 2014), we should be assessing and implementing alternative lighting regimes (Gaston et al., 2012), in complement with consideration of other factors within an urban environment, such as temperature, noise or pollutants (Swaddle et al., 2015). In fact, 'orange' lighting with decreases in the blue spectrum range may be more aesthetically pleasing for humans as well as able to limit physiological costs (Figueiro et al., 2011; Heo et al., 2017). Therefore, we should be looking into alternatives to broad-spectrum intense lighting sources and advocate for these alternatives to improve the health and productivity of organisms that depend on daily and seasonal light–dark cycles.

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