Behavioural Processes 144 (2017) 13–19

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Disruptive effects of light pollution on sleep in free-living birds: Season and/or light intensity-dependent?

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ARTICLE INFO

Keywords:
Dose-dependent
Mitigation
Season
Urbanization
Wildlife

ABSTRACT

Light pollution or artificial light at night (ALAN) is an increasing anthropogenic environmental pollutant posing an important potential threat for wildlife. Evidence of its effects on animal physiology and behaviour is accumulating. However, in order to effectively mitigate light pollution it is important to determine which factors contribute to the severity of effects of ALAN.

In this experimental study we explored whether there are seasonal-dependent effects of ALAN on sleep in free-living great tits (*Parus major*), an important model species. Additionally, we looked at whether light intensity determined the severity of effects of ALAN on sleep. We therefore exposed animals to artificial light inside the nest box (3 lx) in December (winter) and February (pre-breeding season). Results from February were compared with the results from a previous study in February, using a lower light intensity (1.6 lx).

We found little evidence for a season-dependent response. Effects of ALAN hardly differed between high and low light intensity. ALAN disrupted sleep with as main effect a decrease in sleep duration (≈−40 min) as animals woke up earlier (≈−24 min). However, compared to a natural dark situation sleep onset was delayed by high but not by low light intensity of ALAN.

Our study underlines earlier found disruptive effects of ALAN on sleep of free-living animals. While we found no conclusive evidence for seasonal or light intensity-dependent effects of ALAN, additional experimental work using lower light intensities might show such differences. Examining potential management options is crucial in mitigating disruptive effects of light pollution, which will be an important focus for future studies.

1. Introduction

Light pollution or artificial light at night (ALAN) is an increasing worldwide anthropogenic environmental pollutant (Falchi et al., 2016). The loss of darkness poses a potentially important threat for wildlife, biodiversity and humans (Rich and Longcore, 2005; Navara and Nelson, 2007; Hölker et al., 2010; Gaston et al., 2013; Kyba and Hölker, 2013; Duffy et al., 2015). This disruption of our natural light and dark cycles, to which animals and plants have evolved, results in a wide range of physiological and behavioural responses. For example in songbirds, ALAN has been shown to reduce melatonin levels, advance dawn song (reviewed in Swaddle et al., 2015; Bedrosian et al., 2016) and to disrupt sleep (Raap et al., 2015, 2016c).

It is crucial to understand which factors contribute to the severity of negative environmental impacts of light pollution, in order to effectively mitigate them (Gaston et al., 2012, 2013, 2015). However, what determines the extent of these impacts on free-living animals is still unknown. Seasonal variability and intensity of light are both likely to be important and must be better understood to develop short and long-term solutions.

Variability in responses to artificial light across the year (see e.g. Meyer and Sullivan, 2013) may influence management options during a particular period. Reducing the intensity of lighting is another possible strategy to reduce effects of light pollution. Studies of effects of ALAN at different light intensities are of vital importance (Gaston et al., 2013) but are uncommon (but see e.g. Newman et al., 2015; de Jong et al., 2016), especially those using free-living animals.

While ALAN affects a range of animal behaviours (reviewed by Swaddle et al., 2015), the present study is focused on the effects of ALAN on sleep in songbirds in the wild, more specifically in free-living great tits (*Parus major*), a widely used model species. Studying the effects of light pollution on sleep in birds is of major importance for several reasons. First, sleep is an important animal behaviour widespread across the animal kingdom (Cirelli and Tononi, 2008; Siegel

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http://dx.doi.org/10.1016/j.beproc.2017.08.011
Received 15 June 2017; Received in revised form 21 August 2017; Accepted 23 August 2017

2008), and most if not all bird species show sleeping behaviour (Roth II et al., 2006; Lesku and Rattenborg, 2014; Libourel and Herrel, 2016). Second, it serves multiple purposes including energy conservation and memory consolidation (Gobes et al., 2010; Roth II et al., 2010). Third, avian sleep shares many characteristics of mammalian sleep, for example both consist of two types of sleep, REM and non-REM (Siegel 2008). Sleep is important for many organisms, plays a role in maintaining high levels of physical and cognitive functioning and is ideally suited to examine differences in effects of ALAN in the wild.

The severity of effects of ALAN may vary over time during the year (e.g. Meyer and Sullivan, 2013) and strategies for mitigating light pollution may need to be adjusted accordingly. Day length is an important cue for seasonal time-keeping in animals (Bradshaw and Holzapfel, 2010). For example, as the season progresses from December to February onwards, sleep behaviour of great and blue tits (*Cyanistes caeruleus*) changes, with birds waking up earlier (relative to sunrise) in both species (Steinmeyer et al., 2010; Stuber et al., 2015a). Under natural conditions light initiates a cascade of physiological effects associated with day length (Bradshaw and Holzapfel, 2010) and at the end of winter as day length starts to increase, this cascade prepares the animal for reproduction (Helm et al., 2013). In contrast with December, in February great tits are near the breeding season and therefore physiological events already prepare them for reproduction. Previously, we found that effects of ALAN on sleep were more severe during the nestling period, such as a 50% reduction in sleep of female great tits, instead of a reduction of about 5% in February. This may have been due to multiple factors (Raap et al., 2016c). For example, differences might have been due to direct effects of ALAN on female sleep or indirectly through increased nestling begging and parasite activity during the nestling period. The severity of ALAN due to season or other drivers (e.g., nestling or parasite activity) remains unclear and requires study.

Light intensity may influence the extent of sleep disturbance mediated by ALAN and is especially relevant due to the variation of exposure in free-living animals (Gaston et al., 2014). While laboratory studies showed dose-dependent effects of light on daily activity rhythms of great tits (de Jong et al., 2016), whether this is also true for free-living great tits and for other behaviours is not yet known. Environmental conditions outside of the laboratory may affect physiology and behaviour (Daan 2011) and experiments involving behaviour (such as sleep) are particularly susceptible to environmental influences (Calisi and Bentley, 2009; Stuber et al., 2015a; Aulsebrook et al., 2016). Sleep behaviour of captive animals can thus vary tremendously from the behaviour of wild individuals (Rattenborg et al., 2008). Consequently, responses to ALAN may differ between wild and captive animals and comparing behavioural responses to ALAN recorded in laboratory conditions to natural environments is necessary.

Here, we tested for a seasonal-dependent and light intensity-dependent effect of ALAN on sleep in free-living great tits. First, using a field experiment, we compared the effect of ALAN on sleep between December (winter) and February (pre-breeding season). We expected larger disruptive effects on sleep in February. Second, we tested whether light intensity and sleep disturbance by ALAN are associated. We compared results obtained from the current study using a light intensity of 3 lx in the nest box with our previous study, which was also done in February but used a lower light intensity of 1.6 lx (Raap et al., 2015). Under laboratory conditions, great tits' responses of daily activity rhythms to ALAN have been shown to be dose-dependent (de Jong et al., 2016) and so we expected that a higher light intensity (similar to those used by de Jong et al., 2016) would increase the disruptive effect of ALAN on sleep behaviour of free-living animals.

2. Method

2.1. Study area and general procedures

Data was collected during December 2015 (November 30th–December 28th) and February 2016 (February 22nd − March 3rd) in a resident nest box population of great tits in the surroundings of Wilrijk, Belgium (51°9′44″N, 4°24′15″E). This nest box population was established in 1997 and has been continuously monitored since then (see e.g. Van Duyse et al., 2000, 2005; Rivera-Gutierrez et al., 2010, 2012; Vermeulen et al., 2016; Thys et al., 2017). During previous winter- and breeding seasons great tits were caught inside nest boxes after which they were sexed and ringed (see e.g. Rivera-Gutierrez et al., 2010, 2012; Vermeulen et al., 2016; Casasole et al., 2017; Raap et al., 2017a). Since 2012, all adults have been provided with a ring containing a passive integrated transponder, also known as a PIT tag. This enabled the individual detection of birds sleeping in nest boxes without physically disturbing them.

2.2. Experimental procedure

Similar to a previous study on effects of ALAN on sleep behaviour (Raap et al., 2015), we used a within-individual design (or repeated measures) with two sequential nights of observed sleep behaviour. Using a within-individual design "controls" (Ruxton and Colegrave, 2010) for the large variation between individuals in sleep behaviour (Stuber et al., 2015a; Raap et al., 2016c). Birds slept with the light in the nest box turned off on the first night and turned on during the second night, which allowed us to observe the change in sleep behaviour caused by ALAN (see paragraph 2.3). In total we obtained paired data from 11 individuals (three females and eight males) in December and from 23 individuals (12 females and 11 males) in February. No individuals from our previous study (Raap et al., 2015) were re-used.

2.3. Sleep behaviour recordings and light treatment

We measured sleep behaviour and exposed great tits to artificial light following Raap et al. (2015). In short, nest boxes were checked for presence and identity of sleeping great tits prior to the first recording and during the experiment with a handheld transponder reader (FR-250 RFID Reader, Trovan, Aalten, Netherlands). To record sleeping behaviour we installed infrared sensitive cameras (Pakatak PAK-MIR5, Essex, UK) under the nest box roof lid. These were installed at least two hours before sunset and removed at the earliest about an hour after sunrise the next morning. In a previous study (Raap et al., 2015) we did not find a difference in sleep behaviour for great tits sleeping in a dark nest box on two subsequent nights. A masking effect would therefore seem unlikely.

Under each nest box roof lid we also placed a small white LED light (15 × 5 mm, taken from a RANEX 6000.217 LED headlight, Gilze, Netherlands). We successfully used this system to study the effects of ALAN on sleep and physiology (Raap et al., 2015, 2016a, 2016b, 2016c).

All LED lights were standardized to produce 3 lx at the bottom of the nest box (ISO-Tech ILM 1335 light meter; Corby, UK). Birds living in light polluted areas are exposed to similar and higher light intensities outside of nest boxes or cavities (Dominoni et al., 2013; Gaston et al., 2013). In the laboratory, large differences in daily activity rhythms were found when comparing 1.5 and 5 lx (de Jong et al., 2016). Using a 5 lx light intensity might cause not enough birds to enter the nest box as free-living great tits tend to not enter a nest box when it was lit with an interior light of 1.6 lx (Raap et al., 2015). Therefore, instead of the 5 lx light intensity (de Jong et al., 2016) we used 3 lx. With this light intensity we still expected to find differences in sleep behaviour but also that sufficient animals would enter the nest box when the light was turned on.

On the first night of recording the LED was present but off. During the second day/night the LED and the recording system were turned on, before 15:00 (at least two hours before sunset). This allowed animals to become accustomed to changed light conditions. The following morning the light was turned off when the recordings ended (about an