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Artificial light at night affects sleep behaviour differently in two closely related songbird species☆

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ABSTRACT

Artificial light at night (ALAN) or light pollution is an increasing and worldwide problem. There is growing concern that because of the disruption of natural light cycles, ALAN may pose serious risks for wildlife. While ALAN has been shown to affect many aspects of animal behaviour and physiology, few studies have experimentally studied whether individuals of different species in the wild respond differently to ALAN. Here, we investigated the effect of ALAN on sleep behaviour in two closely related songbird species inhabiting the same study area and roosting/breeding in similar nest boxes. We experimentally exposed free-living great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) to artificial light inside their nest boxes and observed changes in their sleep behaviour compared to the previous night when the nest boxes were dark.

In line with previous studies, sleep behaviour of both species did not differ under dark conditions. ALAN disrupted sleep in both great and blue tits. However, compared to blue tits, great tits showed more pronounced effects and more aspects of sleep were affected. Light exposed great tits entered the nest boxes and fell asleep later, woke up and exited the nest boxes earlier, and the total sleep amount and sleep percentage were reduced. By contrast, these changes in sleep behaviour were not found in light exposed blue tits. Our field experiment, using exactly the same light manipulation in both species, provides direct evidence that two closely related species respond differently to ALAN, while their sleep behaviour under dark conditions was similar. Our research suggests that findings for one species cannot necessarily be generalised to other species, even closely-related species. Furthermore, species-specific effects could have implications for community dynamics.

1. Introduction

The increase in the human population and the associated urbanization has caused a dramatic increase in artificial light at night (ALAN), or light pollution (Hölker et al., 2010; Bennie et al., 2014; Falchi et al., 2016). Light pollution is potentially an ecological threat due to the impact it can have on natural light cycles (Longcore and Rich, 2004; Rich and Longcore, 2005; Gaston et al., 2012, 2015). ALAN has been shown to disrupt animal physiology, e.g. levels of melatonin, testosterone, haptoglobin and nitric oxide (e.g. Bedrosian et al., 2011; Dominoni et al., 2013a; Schoech et al., 2013; Jones et al., 2015; Russ et al., 2015; Raap et al., 2016a, 2016c), as well as animal behaviour (reviewed in Swaddle et al., 2015). For example, ALAN causes changes in the timing of singing behaviour in songbirds (Miller, 2006; Kempenaers et al., 2010; Nordt and Klenke, 2013; Da Silva et al., 2014, 2015; but see Da Silva et al., 2017), changes daily activity patterns (e.g. Dominoni et al., 2013b, 2014; Dominoni and Partecke, 2015; Russ et al., 2015; but see Welbers et al., 2017) and alters breeding behaviour (Kempenaers et al., 2010; de Jong et al., 2015; Russ et al., 2015).

Light at night also disrupts sleep, an important and widespread animal behaviour (Cirelli and Tononi, 2008; Siegel, 2008), which plays an important role in many biological functions (Schmidt, 2014; Vorster and Born, 2015). For example, ALAN caused great tits (*Parus major*) to wake up earlier and sleep less during winter (Raap et al., 2015). The effect of ALAN was even more disruptive during the breeding season with female great tits showing a reduction in sleep of more than 50% (Raap et al., 2016b). However,

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to what extent the sleep of other free-living animal or bird species is affected is largely unknown.

Several studies suggest that the effects of light pollution differ among species. For example, songbird species that naturally sing early at dawn, e.g. blackbirds (*Turdus merula*) and robins (*Erithacus rubecula*), had more advanced singing in the morning with ALAN, compared to species that normally start singing later, e.g. blue tits (*Cyanistes caeruleus*) and chaffinches (*Fringilla coelebs*; Kempenaers et al., 2010). Dawn and dusk singing developed earlier in the year due to ALAN in robins, blackbirds, great and blue tits. Likewise, this effect was most pronounced in robins and blackbirds (Da Silva et al., 2015). As a consequence of ALAN, dawn song may potentially no longer be a reliable indicator of male quality (Kempenaers et al., 2010). Hence, species that naturally sing earlier at dawn appear to be the most affected by artificial light in terms of singing behaviour.

Despite the evidence that the effects of ALAN may differ among species, few studies have experimentally examined the difference in response among species in a standardised way. Here, for the first time, we studied the difference in response of sleep behaviour to ALAN in two closely related songbirds inhabiting the same study area. We experimentally provided free-living great and blue tits, sleeping in nest boxes, with artificial light to investigate whether there is a difference in their response to ALAN. In both species, we used a repeated measures design in which we looked at differences within an individual. Such a within-individual design effectively controls for the large variability in sleep behaviour among individuals and also for potential confounding factors.

In this experimental field study, we used free-living great and blue tits as model species to get more insight in possible differences in response towards ALAN. Due to the influence of the environment, there are likely differences in behaviour between free-living and captive animals (Calisi and Bentley, 2009). The laboratory is a simplified environment that fails to capture the complexity of natural conditions, which is an important aspect in behavioural and sleep studies (Aulsebrook et al., 2016). Our field experiment, that uses free-living animals, may represent a more ecologically realistic situation compared to the laboratory. We used cavity-nesting birds because we can manipulate light conditions within nest boxes thereby enabling experimentation and observations in a more natural environment compared to that in the laboratory. Our experimental light treatment is not intended to mimic a situation that could be encountered by birds roosting inside cavities or nest boxes, but with it we try to gain a more fundamental insight into possible differences in response to ALAN between closely related species.

We expected great tits to respond stronger than blue tits towards ALAN. While in a naturally dark environment great and blue tits appear to have a very similar sleep behaviour (Stuber et al., 2015), studies on singing behaviour indicate that great tits are more sensitive than blue tits to ALAN (Kempenaers et al., 2010; Da Silva et al., 2015). In both species, ALAN caused advancement of dawn song but the effect was greater in great tits than in blue tits (about a half-hour difference in response to ALAN). Thus, the disruptive effect of ALAN on sleep could be expected to be greater in great tits than in blue tits.

2. Methods

2.1. Study species and populations

The experiment was carried out during December 2015 in a study area containing a population of great and blue tits. Nest boxes of both species are situated in a semi-rural area with deciduous trees at the University of Antwerp, Wilrijk, Belgium (51°9′44″N, 4°24′15″E). They have been monitored since their installation in 1997 (e.g. Eens et al., 1999; Van Duyse et al., 2000; Janssens et al., 2001; Van Duyse et al., 2005; Rivera-Gutierrez et al., 2010, 2012; Vermeulen et al., 2016; Casasole et al., 2017; Raap et al., 2017a). The same nest boxes were used for both great and blue tits. Nest boxes were made out of plywood with a metal ceiling (120 mm × 155 mm × 250 mm) and an opening of 30 mm ø for great tits. For blue tits, nest box openings were reduced to 26 mm ø with the use of a plastic plate to prevent great tits from entering. Both species roost in nest boxes at night. Prior to the experiment, nest boxes were regularly checked throughout the year to enable us to capture and ring the birds using them. Since 2012, great and blue tits have been provided with a ring containing a passive integrated transponder (PIT) tag. This enabled us to identify the birds sleeping inside the nest boxes without physically disturbing them.

2.2. Experimental design

Approximately one week before we started with the video recordings, we checked, after sunset, for the presence of great and blue tits in nest boxes using a transponder reader (GR-250 RFID Reader, Trovan, Aalten, Netherlands). We measured light levels at the nest box by covering the entrance of the nest box with the sensor (ISO-Tech ILM 1335, Corby UK), and noise levels were measured by holding the sound meter (DVM401, Velleman Inc. Texas USA) in four places outside of the nest box: front, back, left and right (highest value of background noise amplitude; see for details: Casasole et al., 2017; Raap et al., 2017a). These light and noise levels were used to pair great and blue tits with similar light and noise exposure.

We filmed great and blue tits simultaneously to control for environmental factors that may affect sleep behaviour, such as temperature (Steinmeyer et al., 2010; Stuber et al., 2015, 2017). Video recordings were conducted for each individual bird during two consecutive nights with the first night being used as control night, while birds were exposed to artificial light the following night. Recordings were spread out over eight nights in total. When we recorded sleep behaviour, bird identity was confirmed using the transponder reader. Animals sleeping in a dark nest box do not differ in their sleep behaviour from one night to the next (Raap et al., 2015). Sleep behaviour is highly repeatable from one night to the next and little variation in sleep behaviours is to be expected in unmanipulated individuals (Stuber et al., 2017). Moreover, we used a within-individual design therefore individuals in our experiment served as their own control (as in: Raap et al., 2016b) and an additional separate control group is unnecessary in this case. Using a within-individual (observations of the same individual over subsequent nights) with a paired design (observing simultaneously great and blue tits) controls for variability in sleep behaviour and for other confounding variables (e.g. temperature; Ruxton and Colegrave, 2010). Such a design where an individual acts as its own control increases the statistical power (Seltman, 2013).

2.3. Recording sleep behaviour and light treatment

To record sleep behaviour we used an infrared camera (Pakatak PAK-MIR5). A small LED light was attached to the camera, similar to in our earlier studies on great tit sleep behaviour (15 mm × 5 mm, taken from a RANEX 6000.217 LED headlight, Gilze, Netherlands; Raap et al., 2015, 2016b). The camera and the LED were installed underneath the nest box lid. All LED lights were standardized to ensure a light intensity of 3 lux of white light at the bottom of the nest box. We used a higher light intensity than our previous studies on great tits (1.6 lux; Raap et al., 2015, 2016b) thereby increasing