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Light pollution affects activity differentially across breeding stages in an urban exploiter: An experiment in the house sparrow (*Passer domesticus*) ☆

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Highlights

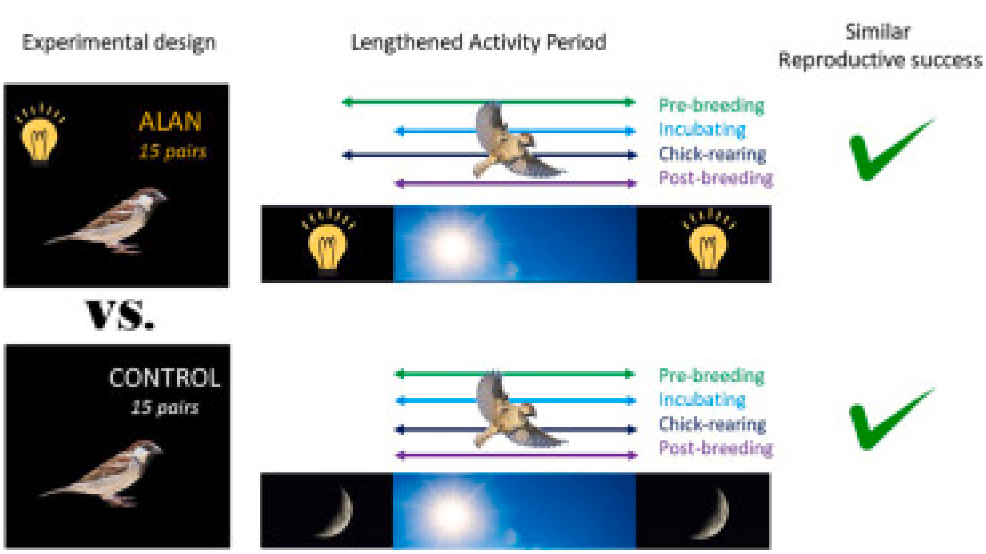
- We experimentally tested the impact of ALAN on activity rhythms in house sparrows.
- Experimental sparrows started being active earlier than controls.
- The impact of ALAN on activity is apparent during specific breeding stages only.
- Reproductive performance did not differ between experimental and control birds.

Abstract

Artificial Light At Night (ALAN) is a major urban perturbation, which can have detrimental effects on wildlife. Recent urban planning has led to an increased use of white light emission diodes (LEDs) in cities. However, little is known about the effects of this type of ALAN on wild vertebrates, especially during reproduction. We designed an experiment to test the impact of ALAN on the activity rhythms (daily time of first activity (TFA) and time of last activity (TLA)) of captive House sparrows (*Passer domesticus*) during several reproductive stages (from pre-breeding to post-breeding). We also tested the impact of ALAN on reproductive performance (laying date, clutch size, hatching and fledging success). Experimental birds were active earlier in the morning (earlier TFA) relative to controls although experimental and control birds did not differ in their TLA. The effect of ALAN on TFA

was apparent during specific stages only (pre-breeding and chick-rearing stages), suggesting that sparrows actively adjust their activity in response to ALAN only during specific periods. This impact of ALAN on activity did not persist through the whole breeding season, suggesting that sparrows may habituate to ALAN. Alternatively, they may not be able to sustain a long-term increased activity in response to ALAN because of sleep deprivation and related physiological costs. Finally, we did not find any impact of ALAN on the reproductive performance of captive house sparrows held under optimal conditions. This suggests that ALAN may not be dramatically detrimental to the reproduction of this urban exploiter, at least when food availability is not constraining.

Graphical abstract



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Introduction

Nowadays, human urban populations represent more than 50% of the world's population, and this percentage is expected to increase in the following decades (United Nations DoEaSAPopulation Division, 2018). This urban sprawl and intensification are associated with multiple types of pollution (Sepp et al., 2018), including light pollution (Dominoni & Nelson, 2018; Hölker et al., 2021; Gaston et al., 2023). Artificial Light At Night (ALAN) alters the perception of natural light cycles by organisms, with significant impacts on sleeping, reproduction, orientation, communication, or resource acquisition in vertebrates, which ultimately affect fitness (Gaston et al., 2013; de Jong et al., 2015; Dominoni et al., 2016; Sanders et al., 2021). Accordingly, ALAN is well-known to disrupt circadian rhythms (Dominoni et al., 2014; Gaston et al., 2017; Dominoni & Nelson, 2018) and for example, animals, such as diurnal reptiles or small nocturnal mammals, can shift or reduce their daily periods of activity in response to chronic light exposure in cities (e.g., Spoelstra et al., 2015). In diurnal birds, there is also strong evidence that ALAN can affect sleep duration and alter circadian and activity rhythms (Raap et al., 2015; de Jong et al., 2016; Sun et al., 2017; Grunst et al., 2023; Kumar et al., 2023) and ALAN usually results not only in an earlier activity onset but also in a later activity offset in birds (reviewed in Sanders et al., 2021). Most studies have compared the activity pattern of wild bird populations living in urban and non-urban environments (e.g., Dominoni et al., 2013; Dwyer et al., 2013; Dominoni et al., 2014; Russ et al., 2015; Da Silva & Kampenaers, 2017; Jiang et al., 2020) and additional experimental studies manipulating ALAN have supported these patterns in a few bird species (e.g., Dominoni et al., 2013; Spoelstra et al., 2015; de Jong et al., 2016; Alaasam et al., 2021; Bani Assadi & Fraser, 2021; Sur et al., 2021; McGlade et al., 2023).

Although the impact of ALAN on daily activity is likely to vary depending on the breeding status of individuals, this question has so far been overlooked. An earlier activity onset and a later activity offset can allow individuals to be active and to acquire resources during a longer daily duration (Gaston et al., 2013; Dwyer et al., 2013; Leveau, 2020; McGlade et al., 2023). This may be beneficial when individuals have to find and guard a partner or a nesting site, acquire energy to produce their eggs, and when they have to provision their chicks as frequently as possible to sustain their growth and energetic needs (e.g., Titulaer et al., 2012). In contrast, the benefits of a longer activity time window may be less obvious when individuals are less energetically and time-constrained, such as during the incubation period (when individuals have to incubate their eggs as long as possible), and the post-breeding period (when energetic needs are reduced relative to the breeding period). In addition, ALAN is known to affect physiological and molecular mechanisms that govern circadian rhythms (Taufique et al., 2019; Batra et al., 2019; Jiang et al., 2020; Alaasam et al., 2021; Dominoni et al., 2022; Liu et al., 2022; Grunst & Grunst, 2023). The role of these mechanisms in mediating activity patterns could be magnified during specific breeding stages, leading potentially to a stronger effect of ALAN on activity during these stages (Dominoni et al., 2018; Liu et al., 2022). However, to our knowledge, no study has experimentally compared the impact of ALAN on activity rhythms between contrasted reproductive stages in non-domesticated birds.

Intriguingly, the impact of ALAN on reproductive performance of diurnal vertebrates remains debated. For instance, recent studies have found a negative impact of ALAN on the growth and survival of the chicks in great tits and zebra finches (de Jong et al., 2015; Raap et al., 2016a; Jha et al., 2021). In addition, ALAN could disrupt the perception of the photoperiod and affect neuroendocrine processes leading to delayed breeding or even to the suppression of reproduction (Jha et al., 2021; Jha et al., 2024; Helm et al., 2024). In addition, ALAN could be perceived as a stressor, alter glucocorticoid secretion (Ouyang et al., 2018; Grunst et al., 2020; Dominoni et al., 2021), and as a result, induce the suppression of the reproduction (Sapolsky et al., 2000). Intriguingly, such detrimental effects are not necessarily apparent in other avian studies (de Jong et al., 2015). Indeed, a few studies even reported that ALAN may increase reproductive success in birds (Russ et al., 2017; Wang et al., 2021). There is clear evidence that ALAN could affect the timing of breeding in birds (Dominoni et al., 2013) and earlier breeding can be correlated with better breeding performance in some species, but it might also potentially lead to a mismatch between the timing of breeding and food availability (Dominoni et al., 2020a). In addition, ALAN could provide additional feeding opportunity by extending the daily activity time window (Sanders et al., 2021), leading therefore to increased food acquisition, and ultimately to better reproductive performance (Russ et al., 2017; Wang et al., 2021). Further studies in multiple species are therefore warranted to better understand the link between ALAN and breeding performance.

ALAN has been historically associated with sodium lamps in urban environments (Gaston et al., 2013). However, recently, the use of these lamps has been reduced and progressively replaced by new technologies including white Light Emitting Diodes (LEDs) (Davies et al., 2013). For example, 10% of new street lights were LEDs in 2010 but this percentage has increased to 80% in 2020. Importantly, little is known about the impacts of this new source of artificial light on urban wildlife although recent studies suggest that they can have strong impact on wildlife (e.g., de Jong et al., 2015; Ouyang et al., 2017; Ulgezen et al., 2019; Evans, 2023; Bani Assadi & Fraser, 2021; Sanders et al., 2023). Indeed, LEDs is a broad-spectrum lighting technology and it is likely to affect the ability of birds to detect light reflected by objects in an urban environment at night (Davies et al., 2013). As a consequence, switching from sodium lamps to LEDs may improve the ability of some vertebrate species to acquire resources at night in urban environments (e.g., food acquisition by great tits, Titulaer et al., 2012). However, it can also induce important costs such as sleep disruption (Raap et al., 2016a; McGlade et al., 2023), or increased predation risk (Stone et al., 2012).

In our study, we designed an outdoor captive experiment to test the impact of this source of ALAN on the activity patterns and daily rhythms of breeding House sparrows (*Passer domesticus*). House sparrows are especially relevant to study this question because they are recognized urban dwellers that can thrive in highly urbanized landscapes. They have therefore co-evolved with human activities and ALAN for decades (Anderson, 2006) and they represent therefore a relevant study species to test to what extent ALAN may affect vertebrates that are supposedly well-adapted to urban environments. Importantly, house sparrows are currently showing sharp population declines in many large European cities (e.g., Mohring et al., 2021). Although the causes of these population crashes are presumably multifactorial (disease: Dadam et al. (2019); lack of green areas: Bernat-Ponce et al. (2020); Pollution: Peach et al. (2018), etc.), they broadly coincide with the replacement of sodium vapor lamps by new lighting technologies such as LEDs for street lighting. Moreover, ALAN has been suggested to increase the susceptibility of house sparrows to some disease in urban environments (Kernbach et al., 2020).

We exposed house sparrows to either experimental night pollution (LEDs, Experimental group) or background night light (Control group) during the whole breeding season. To fully assess the potential effect of ALAN on breeding house sparrows, we monitored daily times of first activity (TFA) and times of last activity (TLA) during several reproductive stages (pre-breeding, egg-laying, incubation, chick-rearing, and post-breeding stages). In addition, we tested whether ALAN had an impact on reproductive performance of house sparrows by monitoring reproductive phenology, clutch size, hatching and fledging success. Because of the potential effect of ALAN on sleep duration and daily rhythms (reviewed in Sanders et al., 2021), we predicted that the experimental birds would (1) start being active earlier in the morning; and (2) remain active later at night. In addition, we also expected that (3) these effects may be exacerbated during demanding stages when an increased daily activity window may be beneficial to individuals (i.e., pre-breeding and chick-rearing periods when individuals have to either find and guard a mate or to provision their brood as frequently as possible). Finally, we predicted that ALAN may (4) improve reproductive performance. Indeed, ALAN may increase the daily time available to energy acquisition leading to better parental condition but also to better brood provisioning during the chick-rearing period. It may also extend the daily activity window of the birds, allowing individuals to engage earlier (seasonally and daily) into breeding activities (mating, nest building, and parental care). ALAN could also alter reproductive performance if it is associated with a state of chronic stress that suppress or delay the initiation of the reproduction. Importantly, a potential impact of ALAN on reproductive performance may be attenuated by the suboptimal captive conditions of our study (food *ad libitum*).

Section snippets

Study population and housing

The study was carried on a captive population of house sparrows (N=30 females and N=30 males), maintained in 6 outdoor aviaries of 6(length) ×4 (width) x3 (height) m at the Centre d'Etudes Biologiques de Chizé (CEBC-CNRS, 79360, Villiers en Bois, France). These birds originated from the countryside at the CEBC field station. After capture, they were then transferred to captivity where they were held in a large outdoor aviary before the experiment. The field station is composed of a few…

Time of first activity (TFA)

TFA was significantly affected by the "light treatment", the "reproductive stage" and the "light treatment x reproductive stage" interaction (Table 1A, Appendix 1). Specifically, experimental pre-breeding and chick-rearing birds started being active earlier than control birds (pre-breeding: $t=2.63$, $p=0.009$, chick-rearing: $t=5.20$, $p<0.001$; Fig. 1A), but this effect of light treatment on TFA was not apparent in incubating and post-breeding birds (all $p>0.350$, Fig. 1A). TFA was also…

Time of first and last activity

As predicted, we found that nocturnal LED ALAN significantly affects the activity of house sparrows during the reproductive period. Firstly, our results showed that irrespective of the LED treatment, TFA and TLA were logically affected by the natural photoperiod. Secondly, experimental sparrows started being active earlier than controls as previously reported in other bird species (Raap et al., 2015; de Jong et al., 2016; Sun et al., 2017; Sanders et al., 2021; Dominoni et al., 2020b; McGlade…

Ethics

All experimental procedures were performed at the Centre d'Etudes Biologiques de Chizé (CEBC) and were approved by French authorities (authorization 19917–2019031516516631 issued by the Comité d'Ethique n°804).…

Data accessibility

Data will be available upon request.…

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CRediT authorship contribution statement

Erika Beaugeard: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **François Brischoux:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Frédéric Angelier:** Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.…

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.…

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