



## Behavioural plasticity in the onset of dawn song under intermittent experimental night lighting



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The disruption of daily rhythms is one of the most studied ecological consequences of light pollution. Previous work showed that several songbird species initiated dawn song earlier in areas with light pollution. However, the mechanisms underlying this shift are still unknown. Individuals may immediately adjust their timing of singing to the presence of artificial light (behavioural plasticity), but the observed effect may also be due to phenotype-dependent habitat choice, effects of conditions during early life or micro-evolution. The main aim of this study was to experimentally investigate how males of four common passerine species respond to day-to-day variation in the presence of artificial night lighting in terms of the timing of singing. During two consecutive breeding seasons, we manipulated the presence of light throughout the night in a cyclic fashion in several naturally undisturbed forest patches. We show that individuals of all four species immediately and reversibly adjusted their onset of dawn singing in response to artificial light. The effect was strongest in the European robin, but relatively small in the blue tit, the great tit and the blackbird. The effect in the latter two species was smaller than expected from the correlational studies. This may be coincidence (small sample size of this study), but it could also indicate that there are longer-term effects of living in light-polluted urban areas on timing of dawn singing, or that birds use compensatory behaviours such as light avoidance. We found no evidence that our light treatment had carryover effects into the subsequent dark period, but robins progressively advanced their dawn singing during the light treatment.

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The singing behaviour of many songbird species is characterized by a peak of song production around sunrise, i.e. the dawn chorus, and previous work suggests that the timing of dawn song initiation may be regarded as a reliable predictor of male quality (Grava, Grava, & Otter, 2009; Murphy, Sexton, Dolan, & Redmond, 2008; Otter, Chruszcz, & Ratcliffe, 1997; Poesel, Kunc, Foerster, Johnsen, & Kempenaers, 2006). Several studies suggest that artificial night lighting advances the start of the dawn chorus in songbirds (Da Silva, Samplonius, Schlicht, Valcu, & Kempenaers, 2014; Dominoni, Carmona-Wagner, Hofmann, Kranstauber, & Partecke, 2014; Kempenaers, Borgström, Loës, Schlicht, & Valcu, 2010; Miller, 2006; Nordt & Klenke, 2013), potentially affecting their reproductive success (Kempenaers et al., 2010). However, these studies are

all correlational and the mechanisms underlying this effect remain unknown.

In general, four nonmutually exclusive mechanisms can explain the differences in timing of behaviour observed between birds living in artificially illuminated environments and those inhabiting naturally dark places (Partecke, 2014; Swaddle et al., 2015). (1) Phenotypic plasticity in the form of behavioural flexibility: this involves an immediate adjustment of the behaviour and generally facilitates adaptive responses to changes in the environment (Price, Qvarnström, & Irwin, 2003; Sih, Ferrari, & Harris, 2011). Behavioural plasticity may be particularly important for coping with anthropogenic changes (Hendry, Farrugia, & Kinnison, 2008; Sih et al., 2011). It is the most likely mechanism, because the initiation of dawn singing is strongly linked to levels of natural light (Hutchinson, 2002) and depends on the light sensitivity of the species (Berg, Brumfield, & Apanius, 2006; Thomas, Kelly, & Goodship, 2004; Thomas et al., 2002). Later start of dawn singing on cloudy mornings (Bruni, Mennill, & Foote, 2014; Da Silva et al.,

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2014; Dominoni et al., 2014; Hasan, 2010; Nordt & Klenke, 2013; York, Young, & Radford, 2014) and earlier singing on mornings with bright moonlight (Bruni et al., 2014; York et al., 2014) also suggest a plastic response to natural light levels. (2) Phenotypic plasticity in the form of developmental effects (Senner, Conklin, & Piersma, 2015): parental phenotype or environmental conditions early in life may influence the development of the trait. For instance, individuals that have been exposed early in life (e.g. in the nest) to artificial light or to early singing males may sing earlier later in life. This requires that individuals that were raised in habitats influenced by artificial night lighting will later also settle and breed there. (3) Phenotypic-based habitat choice: individuals with early chronotypes may preferentially settle in territories affected by artificial night lighting, or 'late' individuals may avoid such areas. (4) Genetic effects: micro-evolution via natural or sexual selection (Diamond, 1986) may have changed the timing of dawn singing for urban birds living in light-polluted areas. This requires limited gene flow between rural birds living in naturally darker habitats and birds living in urbanized, light-polluted environments. Previous work on great tits, *Parus major*, showed that circadian period length is highly heritable and earlier singing may thus result from micro-evolution through selection of fast circadian rhythms (Helm & Visser, 2010).

Here, we report on a study designed to test experimentally whether birds breeding in a naturally dark habitat flexibly adjust their timing of dawn singing in response to artificial night lighting. During two consecutive breeding seasons, we repeatedly exposed songbirds in naturally undisturbed forest patches to a period of artificial light at night, followed by a period of natural darkness. Every morning, we determined the onset of dawn singing of four common songbird species for which an effect of light pollution on timing of singing had been observed previously (Da Silva et al., 2014; Kempnaers et al., 2010). Because the experiment was conducted after territorial settlement, and because we compared the behaviour of individuals under artificial night lighting with that under natural conditions in the exact same location, settlement of individuals with particular chronotypes in the illuminated territories (phenotype-based habitat choice) can be excluded as a potential explanation. Furthermore, developmental and genetic effects can be excluded, because of the short timescale of the experiment. Hence, any effect of the experiment on the timing of dawn singing reflects short-term and plastic adjustments of behaviour in response to the presence or absence of artificial light at night.

The main aim of our study was to test whether artificial night lighting causes birds to start singing earlier at dawn, as suggested by the above-mentioned correlational studies. If behavioural plasticity in response to light is the main (or only) mechanism causing earlier singing, we expect experimental effect sizes that are comparable to those found in the correlational studies. If, however, experimental effect sizes are smaller or there is no effect of the experiment, other mechanisms such as phenotype-based habitat choice may explain the correlational effects. Alternatively, the correlational studies might have been confounded by effects of other causal agents that were correlated with the presence of artificial night lighting.

Environmental light pollution may also be temporary (e.g. during construction works). Hence, a secondary aim of our study was to explore whether a few days of artificial night lighting influence the timing of singing also during subsequent naturally dark nights. Such carryover effects are expected, because the avian circadian system can store information about photoperiod during the days following a transfer from a long day to a short day (and vice versa; Brandstätter, Kumar, Abraham, & Gwinner, 2000; Gwinner & Brandstätter, 2001). If the experimental light had such an effect

on the diel rhythm of individuals, we should observe a progressive return to natural times of dawn chorus initiation during consecutive dark days. Such carryover effects have been shown for the timing of emergence from the roost in female blue tits, *Cyanistes caeruleus*, that were experimentally exposed to night light (Schlicht, Valcu, Loes, Gerg, & Kempnaers, 2014). We also tested whether the light effect becomes progressively stronger after the control 'treatment' (dark phase), and for simplicity also refer to this as a 'carryover' effect.

## METHODS

### Experimental Procedure

The experiment was carried out in a woodland area with minimal light pollution in Seewiesen (southern Germany). In 2014, we selected two sites (site 1: coordinates 47.9705°N, 11.2380°E; site 2: 47.9730°N, 11.2325°E). In 2015, we repeated the experiment in the same two sites (although with a small shift for site 1: 47.9708°N, 11.2385°E) plus two additional sites (site 3: 47.97235°N, 11.2363°E; site 4: 47.97435°N, 11.23185°E). The sites were edges of predominantly coniferous forest, mixed with deciduous trees (mainly European beech, *Fagus sylvatica*) and shrubs. They were chosen such that (1) tree density was similar across sites and (2) the following four songbird species were present: European robin, *Erithacus rubecula*, common blackbird, *Turdus merula*, great tit and blue tit. This allowed a direct comparison with descriptive data on the timing of dawn song under artificial night lighting (Da Silva et al., 2014; Da Silva, Valcu, & Kempnaers, 2015; Kempnaers et al., 2010). The experimentally illuminated sites ranged from 0.3 to 0.4 ha and edges of adjacent sites were on average 180 m apart (range 160–200 m). These distances are comparable to the smallest distances between dark control sites and illuminated sites in Kempnaers et al. (2010), where no influence of artificial light on singing in the control areas was detected. Based on these results, we assumed that the singing behaviour of individuals at one site did not influence the singing behaviour of individuals at another site, even though far-carrying songs (e.g. from the robin) could be detected (at lower amplitudes) in the closest neighbouring sites.

At each site, we placed eight mobile halogen spotlights (article number TL800A, Elro, EU) in three parallel rows (two lights in one row, three lights each in two rows) such that lights were approximately 5 m apart. Each light consisted of two bulbs ( $N = 16$  bulbs per site), which provided a broad light spectrum (500 W white warm light, colour temperature 2900 Kelvin, flicker rate 50 Hz) at a high intensity (8850 lm, 100 klx at the bulb). Each bulb was directed towards the foliage of the surrounding trees (angle range 20–60°) to illuminate the entire site, from the lower branches to the canopy (and light reflection on the ground). In 2014, we measured an average light intensity of 4 lx during the night at the centre of each site (recorded with a 400 000 Light Lux Meter DT 1308, ATP Instrumentation Ltd, Ashby-de-la-Zouch, U.K., held horizontally 2 m above the ground, 5 m from the nearest light bulb). Ambient light levels during illuminated nights were therefore comparable to intensities found in the centre of large cities, where effects on timing of singing are typically strongest (Dominoni et al., 2014; Nordt & Klenke, 2013).

In 2014, the experiment took place between 1 April and 6 May and consisted of five cycles of an illuminated phase (3 nights with lights turned on from sunset to sunrise), immediately followed by a dark control phase (4 nights without artificial lighting, except for the second cycle where it lasted 5 days by mistake). Dark control phases were longer to allow males to return to their normal singing times after being disrupted by the artificial night lighting (allowing

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