**Does light pollution alter daylength?**

**A test using light loggers on free-ranging European blackbirds (Turdus merula)**

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Artificial light at night is one of the most apparent environmental changes accompanying anthropogenic habitat change. The global increase in light pollution poses new challenges to wild species, but we still have limited understanding of the temporal and spatial pattern of exposure to light at night.

In particular, it has been suggested by several studies that animals exposed to light pollution, such as songbirds, perceive a longer daylength compared with conspecifics living in natural darker areas, but direct tests of such a hypothesis are still lacking. Here, we use a combination of light loggers deployed on individual European blackbirds, as well as automated radiotelemetry, to examine whether urban birds are exposed to a longer daylength than forest counterparts. We first used activity data from forest birds to determine the level of light intensity which defines the onset and offset of daily activity in rural areas. We then used this value as threshold to calculate the subjective perceived daylength of both forest and urban blackbirds. In March, when reproductive growth occurs, urban birds were exposed on average to a 49-min longer subjective perceived daylength than forest ones, which corresponds to a 19-day difference in photoperiod at this time of the year. In the field, urban blackbirds reached reproductive maturity 19 day earlier than rural birds, suggesting that light pollution could be responsible of most of the variation in reproductive timing found between urban and rural dwellers. We conclude that light at night is the most relevant change in ambient light affecting biological rhythms in avian urban-dwellers, most likely via a modification of the perceived photoperiod.

1. Introduction

The beginning of scientific studies on ecological effects of light pollution dates back almost 80 years, when British physiologist William Rowan published a paper in *Nature* which examined the potential effects of artificial lights on the seasonal reproduction of European starlings (*Sturnus vulgaris*) [1]. Ever since, new studies on this topic have been sparse and mostly focused on immediate effects of artificial lights on mortality [2–4]. However, the past decade has seen renewed interest in this topic, pushed by a review of the research field which attracted international scientific attention [5]. Now, exactly 10 years later, this current special issue highlights and summarizes what has been achieved in the past 10 years. We see the shift from correlational data to experimental-based evidence as one of the major recent advancements of our field [6–8]. However, despite the burgeoning of studies on the ecological effects of artificial lights, there is still limited knowledge about the level of light intensity to which wild organisms are exposed, as well as the patterns of exposure and their variation over time and space. Using light loggers deployed on individual birds, we have previously shown that the average light intensity to which a bird is subjected at night is a good predictor of its daily timing of activity [9]. Nevertheless, we still have limited understanding of whether animals living in...
light-polluted environments perceive an altered daylength compared with counterparts thriving in natural ecosystems.

Why is an understanding about exposure to daylength so important? Photoperiod, i.e. the light fraction of a 24 h day, is the most predictable proximate cue that organisms use to time their daily and seasonal biology [10]. Even in tropical environments, where only small variations in daylength occur during the year, animals are still able to use this information to fine-tune their life-history events [11]. Moreover, photoperiod is the most potent synchronizer of circadian rhythms, the endogenous mechanism that most organisms have evolved to synchronize their daily and annual events to the external environment and thus maximize their fitness [10]. The relationship between daylength, circadian rhythms and daily as well as seasonal behaviour has been investigated in several species across a great range of taxa, from bacteria to humans [10]. In recent years, it has become clear that light pollution is posing new challenges to ecological systems as well as to human health and society [12–14]. When focusing on the effects of anthropogenic habitat change on the light environment, we argue that the latter can be modified in two ways. The first is by increasing light intensity during the night through artificial illumination. This is what we usually define as ‘light pollution’, the most studied alteration of the lightscape, which is thought to extend daylength and thus increase the time available on a daily basis for species to forage, mate and move. The best example is the earlier onset of dawn singing expressed by many species of songbirds, which has been hinted to confer adaptive reproductive value [15]. Second, we suggest that anthropogenic habitat change, and particularly urbanization, may alter the light environment during daytime, too, as it dramatically affects the landscape by substituting natural habitat with artificial buildings and structures. In particular, deforestation is one of the most apparent alterations of the landscape that precedes urban sprawl [16]. As light intensity inside forest patches is usually lower than in the surrounding, more open land, we hypothesize that daytime light intensity would be higher in urban areas compared with nearby forested areas. This could have important consequences in terms of both daily and seasonal organization of activities, as decreased light intensity during the day has been suggested to be interpreted by birds as a shorter daylength, independently of the actual photoperiod to which birds were exposed [17].

The goal of our study was to elucidate whether free-living birds inhabiting a city are exposed to a different ‘subjective daylength’ than forest conspecifics. We defined as subjective daylength the light fraction of a 24 h day to which an individual bird is exposed in its natural environment. This might vary considerably between individuals that live in the same area, because small differences in the microhabitat that a bird occupies, or its ability/will to escape light-polluted areas, might result in strong differences in the perceived subjective daylength. In addition, the subjective daylength may not always coincide with the observed activity patterns of an animal. For instance, in an urban area, light (at least at low intensities) may be always present, although animals can try to escape from it. The question is for how long animals are exposed to light intensities that are above the naturally occurring light intensity at night (full moonlight). If this period of time is longer than that defined by sunrise and sunset, it is plausible that urban birds are exposed to a longer daylength than forest conspecifics. To explore this possibility, we used the European blackbird (Turdus merula) as our study species, for which an extensive amount of published data are already available in the context of urbanization [18], light pollution [19] and daily [20] as well as seasonal rhythms [21]. In a recent study, we investigated the relationship between light exposure at night and daily patterns of activity, using light loggers attached to individual birds in the city of Munich, Germany, and in a nearby protected forest [9]. We present a novel analysis of the same dataset to test two specific hypotheses which we had not previously explored. First, we hypothesized that artificial lights not only increase the average nocturnal light intensity, but animals also exposed to the artificial light at night experience a longer subjective daylength compared with conspecifics living in natural habitats. To test this hypothesis, we first obtained radio-tracking data from forest birds to assess the light intensity at which these birds started their activity in the morning and ended it in the evening. We then used this information to determine the time at which light intensity passed this threshold in the morning and in the evening for both urban and rural birds. Last, we compared the amount of time between the morning and evening threshold passing, to estimate the subjective daylength to which urban and rural blackbirds were exposed. Second, we hypothesized that the amount of daytime light irradiance to which birds are exposed would be different for urban and rural individuals. Specifically, we predicted that birds thriving in the business district of metropolitan areas, where tall buildings interfere with light penetration, will be exposed to a lower daytime light intensity compared with birds breeding in large, open urban parks, but higher in comparison with forest birds. We anticipated that testing these two non-mutually exclusive hypotheses will elucidate the mechanisms by which artificial lights might affect the perception of daylength in urban-dwelling animals such as songbirds, thereby modifying their daily and seasonal rhythms.

2. Material and methods

(a) Ethical statement

All experimental procedures were conducted in accordance with the regulations of the regional animal research committee (Regierung von Oberbayern, Munich, Bavaria; permit no. 55.1-8642.3-17-2008). The data presented in this manuscript has already been analysed for a recent study of Dominoni et al. [9]. These are time-series of locomotor activity recorded through radio-telemetry (§2c) and light intensity data recorded with light loggers placed on individual birds (§2d). Because these data were normally recorded on a 2-min basis for several days, they are an incredible source of information that can be analysed in different ways to answer different questions. In the former study, we correlated time of onset and offset of activity with the average light intensity during the true night (22.00 to 03.00), excluding the twilight phases, as a measure of the nocturnal light environment in the territory of a bird. In this manuscript, our goal, however, was to estimate the subjective perceived daylength for each individual bird. We therefore use data that we had not explored in the previous analysis, that is, the twilight phases.

(b) Study populations, capture and tagging

The study populations of European blackbird were located in the city of Munich, southeast Germany (48°07' N, 11°34' E; 518 m.a.s.l.) and in a rural forest near the village of Raisting.
Birds in the city were sampled in two different habitat types: (i) ‘urban park’: large urban parks (25–30 ha) with high tree and bush cover outside the city centre (Alter Südfriedhof and Olympia Park) and (ii) ‘business district’: medium-small green areas (1–4 ha) on the edge of the old town (Alter Botanischer Garten and Maximilian Platz), with little tree cover and higher density of people. The rural population inhabited a temperate mixed deciduous forest, with alder (Alnus spp.) and spruces (Picea spp.) as dominant species.

We captured 100 blackbirds in three consecutive years (2009, 2010, 2011), by mist-netting at dawn and without using playbacks. Exact dates were: 25 March to 1 July 2009; 1 March to 15 June 2010; 22 February to 25 June 2011. Birds were tagged with a backpack containing a radio-transmitter and a light logger, and then were immediately released in their territory. We attached the backpack using a rubber band covered in cotton. We recaptured the birds whenever possible after two weeks of recording, removed the backpack and released the bird. In total, we were able to recapture 50% (n = 50) of the birds. We could retrieve data from 32 light loggers, and final sample sizes were: rural forest n = 9; urban park n = 11; business district n = 12. As a cautionary note, the total mass of the backpack was 4.8 g, which represents approximately 5% of blackbirds’ body mass (90–100 g). In the case that a very light individual was tagged, the backpack exceeded 5% of its body mass. However, we have no evidence of birds dying because of the backpack, and although we were not able to recapture all birds, we have re-sighted several of them in the following years. All had lost the backpack.

(c) Measurement of activity patterns using radio-telemetry

Radio-transmitters (Sparrow Systems, USA, in 2009 and 2010, mass = 1.8 g; Holohil Systems, Canada, in 2011, mass = 1.8 g) were used in combination with automated recording units (ARUs, Sparrow Systems, USA) to infer activity state. The ARU was placed close to the territory of a bird and connected to an H-antenna (Sparrow Systems, USA). The unit was programmed to scan every minute for the corresponding frequency of each bird and to record the strength of the transmitter’s signal. In Munich, we used four ARUs, one in each of the four locations, because these areas were relatively small and with little physical obstruction; therefore, we were able to pick up good-quality radio signals from all the birds. In the forest, we used two ARUs which we moved every two weeks from one bird’s territory to another. Because moving individuals show more variation in signal strength than non-moving (resting) ones [22], we used the change in signal strength over time to detect switches in activity status. Specifically, we applied behavioural change point analysis [23] to infer changes in activity status in the morning and in the evening, that is, the onset and end of daily activity of each single bird. We assumed that the change in signal strength comes from two different distributions, one for the active and one for the non-active state. All time points were given an Akaike information criteria (AIC) as a measure of how different the variances were for the 2 h before and the 2 h after each time point. The specific time that produced the lowest AIC value in the morning and in the evening was identified as onset/cessation of activity. We have already used this technique on the same dataset and published the results in a previous manuscript by Dominoni et al. [9], and data are publicly available (http://doi.org/10.5061/dryad.425r). Here, we used these previously published data to calculate the light intensity to which these birds were exposed when they started their activity in the morning and when they ceased to be active in the evening (see §2e) as a measure of natural ‘subjective’ daylength or photoperiod.

(d) Measurement of natural exposure to light at night on free-living birds

We calculated the light intensity to which free-ranging European blackbirds are exposed to by using micro light loggers. In 2009 and 2010, we deployed commercially available loggers (Sigma Delta Tech., Australia, mass = 3 g). In 2011, we switched to custom-made loggers produced in collaboration with the Electronics Department at the University of Konstanz (Germany, mass = 3 g). Both types of loggers used the same photodiode (TSI, 235, TAOS, USA) with spectral sensitivity ranging from 300 to 1100 nm (peak at 780 nm). Each logger was calibrated during morning twilight against a pyranometer (LI-1400 and LI-2100, LI-COR, USA), to calculate irradiance (W m$^{-2}$) from frequency values. These calibrations were done outdoors in areas where no artificial light sources were present. Loggers recorded and stored light intensity every 2 min. In this study, we used these data for two main objectives:

(1) To calculate average and total daily light intensity, we split the data into day- and night-time values based on the sunrise and sunset functions in the R package RAtmosphere [24], and then we calculated the average light intensity in these two time periods, as well as the sum of all data points to calculate total irradiance over time.

(2) We used the activity data from rural and urban birds to calculate the average light intensity at which each bird started its morning activity and ceased to be active in the evening. We calculated the average light intensity for the 5 min around the time of onset of morning activity or end of evening activity, and then calculated the average values for all rural and urban birds. We then used these averaged values for morning and evening light intensity as threshold values: we extrapolated the time at which the morning and evening thresholds were passed by the light intensity time-series, within a time window of 2 h before sunrise and 2 h after sunset. We then calculated the ‘subjective daylength’ as the time difference (in minutes) between the morning and the evening times of threshold passing. Because we were interested in whether urban birds perceive different daylength owing to artificial light at night compared with rural conspecifics which experience natural light regimes in their habitat, we focused our analysis on light intensity thresholds derived from the activity of rural birds. Nevertheless, we also present the results of the analysis conducted using rural- and urban-defined light thresholds applied to the rural and urban birds, respectively. More details on this analysis are found in the electronic supplementary material.

(e) Statistical analysis

All statistical analyses were performed using the software R v. 3.1.2 [25]. All tests were two-tailed, and significance level was set at α = 0.05.

We analysed the difference in light intensity threshold values between morning and evening using a Mann–Whitney test with light intensity as response variable and time of day (morning or evening) as explanatory variable, separately for urban and rural birds. Similarly, we tested whether urban and rural values differed between each other using the same type of test.

We used three different linear-mixed effects models (LMMs) to analyse the change in daylength, the time of threshold passing in the morning (hereafter ‘onset of day’), and the time of threshold passing in the evening (hereafter ‘end of day’) across sites. LMMs were performed using the R package lmer [26]. Site (rural forest–urban park–business district), date and their interaction were included as fixed effects, whereas individual was modelled as random effect to account for non-independency of light intensity values collected on the same individual on different days. We ran the interaction site × date, because...
Table 1. Results of the LMM analyses of the variation in the start, end and length of day across the three urban sites. The estimates were controlled for seasonal variation in natural photoperiod by including date as fixed factor. Reference for site (intercept) is the rural forest.

<table>
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previous studies have shown a seasonal change in the activity timing of songbirds: early in the breeding season birds tend to be active earlier in the morning and later in the evening than at the end of the breeding season [9,27,28]. This seasonal trend may be different for urban birds compared with rural conspecifics: for instance, urban birds advanced much more their onset of daily activity in the beginning of the breeding season compared with forest birds. Because light exposure and activity are interconnected, it is reasonable to expect not only a seasonal variation in activity, but also in light intensity, and that the slope of this seasonal trend might be different for urban and rural birds. If the interaction was found to be non-significant, we removed it from the model and we analysed only the main linear effects of site and date. Pairwise comparisons of the three different sites were run using Tukey’s post hoc tests with the R package multcomp [29]. We checked model assumptions using qplot (normality of variance) and by plotting residuals for the three study sites against each other (homogeneity of variance). These LMMs were used to estimate repeatability of day length attributes (daylength, onset of day, end of day; daylength was calculated as the time of the end of day minus the time of the onset of day, in minutes). We defined repeatability as the proportion of phenotypic variance explained by the individual [30]. As the variance in both between and within-individual onset and end of activity is generally higher for urban than for rural birds [29], we hypothesized that exposure to light intensity and therefore daylength would also show the same pattern. We used the R package rptr [31], which allows the calculation of repeatability and confidence intervals (CIs) using REML estimation in a mixed model design. We used 50 000 simulations to obtain the repeatability estimates (R). R-values were considered to be different between paired sites (rural forest versus urban parks, rural forest versus business district, urban parks versus business district) if the R of one site was not included in the CI of the other site.

LMMs were also used to analyse the variation in total and average light intensity during the day and night. Total or average day- or night-time light intensities were modelled as response variables. Like in the previous models, site, date and their interaction were included as fixed factors, whereas individual was modelled as a random factor.

3. Results

The morning and evening threshold values of light intensity calculated from forest living blackbirds did not significantly differ from each other (morning: mean ± s.d. = 0.0033 ± 0.0028 W m⁻², n = 6; evening: mean ± s.d. = 0.0041 ± 0.0057 W m⁻², n = 6; test: Mann–Whitney, W = 565.5, p = 0.728). These threshold values were significantly higher than those calculated from activity data of urban birds (morning: W = 3433, p < 0.001; evening: W = 2762.5, p < 0.001), which also did not differ from each other (morning: mean ± s.d. = 0.00035 ± 0.00028 W m⁻², n = 13; evening: mean ± s.d. = 0.00038 ± 0.00031 W m⁻², n = 11; test: Mann–Whitney, W = 7096, p = 0.751).

The model investigating the variation in subjective daylength using rural-defined light thresholds revealed a significant difference between the business district and the other two sites (p = 0.013, table 1 and figure 1c) and date (p = 0.032, table 1 and figure 2c). Post hoc tests indicated that subjective daylength was on average 49 min longer in the business district compared with the rural forest (mean ± s.e.m. = 0.35 ± 0.10, z = 0.26, p = 0.032), and 34 min longer than in the urban park (mean ± s.e.m. = 0.23 ± 0.08, z = 0.21, p = 0.079). In the urban park, subjective daylength was 14 min longer than in the rural forest, but this difference was not significant (mean ± s.e.m. = 0.12 ± 0.10, z = 0.90, p = 0.368). The differences in subjective daylength between sites were much larger in late winter, at the beginning of the breeding season, compared with the end of the reproductive phase (figure 2c).

We detected a significant effect of the interaction between business district and date (p = 0.002, table 1 and figure 1a) on the onset of the subjective day. Indeed, onset of day was...
significant earlier in the business district compared with both
the urban park (mean ± s.e.m. = −1.26 ± 0.43, z = −2.91, p = 0.010) and the rural forest (mean ± s.e.m. = −1.52 ± 0.44, 
z = −3.42, p = 0.002), but this effect was evident only in
the beginning of the breeding season (figure 2a). There was no
significant difference in the onset of day between the rural
forest and the urban park (mean ± s.e.m. = −0.26 ± 0.51, 
z = −0.50, p = 0.872). The model for the end of the subjective
day revealed a significant difference between the business
district and the other two sites (p = 0.005, table 1 and figure 1b),
but no effect of date (p = 0.170, table 1 and figure 2b). Post hoc
tests indicated a marginally significant difference between the
rural forest and the business district, with the end of day
being later in the business district (mean ± s.e.m. = 0.11 ± 0.05, 
z = 3.55, p = 0.094), but no differences either between the
urban park and the rural forest (mean ± s.e.m. = 0.06 ± 0.05, 
z = 0.23, p = 0.514), or between the two urban sites
(mean ± s.e.m. = 0.05 ± 0.04, z = 1.51, p = 0.478). The same
types of models were run using rural- and urban-defined light
thresholds on the rural or urban birds, respectively, and
showed similar results (see the electronic supplementary
material, figure S2 and table S1), but because urban-defined
thresholds were far lower than rural-defined ones (see above),
these results are less conservative than using rural-defined
thresholds on both populations.

Repeatability in subjective daylength, onset and end of day
was significant for all sites, but it was not consistently different
between sites. Repeatability in subjective daylength did not
differ between sites (rural forest: R = 0.405, CI = 0.033, 0.649;
urban park: R = 0.296, CI = 0.049, 0.526; business district: 
R = 0.292, CI = 0.094, 0.487). For the onset of the subject-
ive day, repeatability was higher in the business district
(R = 0.282, CI = 0.082, 0.480) than in the urban park (R = 0.071, CI = 0.000, 0.246), but not compared with the rural
forest (R = 0.184, CI = 0.000, 0.469). Last, repeatability in
the end of the subjective day did not differ among all three
sites (business district: R = 0.032, CI = 0.000, 0.400; urban
park: R = 0.255, CI = 0.017, 0.472; rural forest: R = 0.171, 
CI = 0.000, 0.469).

The LMM for the total light intensity during day indicated a
significant main effect of site (LMM, t = −5.86, p < 0.001,
electronic supplementary material, figure S1). Post hoc tests
revealed that daytime total light intensity was higher in the
urban park compared with both the business district (z = 5.47, p < 0.001) and the rural forest (z = −4.92, p < 0.001),
but no difference was detected between the business district

Figure 2. Seasonal variation in onset, end and length of subjective day. We retrieved data from birds tagged and recaptured in three different habitats (rural forest, circles; urban park, triangles; and business district, squares), between the end of March and the end of June, from a total of 32 birds (see figure 1 for sample sizes). Each symbol represents the mean for an individual bird, and all means are standardized to the relative sunrise (a), sunrise (b) and sunset (c). There was no significant effect of date on the onset of the subjective day (a) and the subjective daylength (c), such that early during the breeding season the onset of day was earlier and the subjective daylength longer in urban birds compared with the forest conspecifics. No significant effect of date was detected for the end of the subjective day (b). Trend lines represent data simulated from the model using the function predict in the R package lme4 [26] (dashed line, rural forest; solid black line, urban park; solid grey line, business district). Date was plotted as the midpoint between the two capture dates for each individual.
and the rural forest \((z = -1.39, p = 0.339)\). We also detected a significant effect of site on total light intensity during night (LMM, \(t = -6.80, p < 0.001\)). Specifically, total light intensity during night was higher in the urban park compared with both the business district \((z = 6.26, p < 0.001)\) and the rural forest \((z = -6.99, p < 0.001)\). In addition, we also found that total light intensity during night was higher in the business district compared with the rural forest \((z = -2.88, p = 0.010)\). Similar to total light intensity during day, we also found a significant effect of site on average light intensity during day (LMM, \(t = -6.35, p < 0.001\), electronic supplementary material, figure S1). Post hoc tests revealed that total light intensity during day was higher in the urban park compared with both the business district \((z = 5.81, p < 0.001)\) and the rural forest \((z = -5.20, p < 0.001)\), but no difference was detected between the business district and the rural forest \((z = -1.45, p = 0.305)\). Last, average light intensity during night was also significantly different between sites (LMM, \(t = -6.93, p < 0.001\)). Indeed, post hoc tests showed that average light intensity was significantly higher in the business district compared with both the urban parks and the rural forest (rural forest–urban park: \(z = 6.97, p < 0.001\); urban park–business district: \(z = 6.26, p < 0.001\); rural forest–business district: \(z = 2.87, p = 0.011\)).

4. Discussion

In this study, we use data on activity patterns of rural European blackbirds, collected by an automated telemetry system [9], to determine the average light intensity that corresponds to the onset and end of activity of free-living rural birds in their natural environment, by deploying light loggers on the same animals from which we measured activity patterns. These values (morning = 0.0031 W m\(^{-2}\), evening = 0.0040 W m\(^{-2}\)) were very similar to the highest light intensity level to which rural birds are naturally exposed at night (0.004 W m\(^{-2}\)), which could suggest that rural birds use this information as a way to measure daylength and thus time their daily rhythms of activity, although other environmental factors might also play a role, such as conspecific songs and temperature. We used these light intensities as threshold values to estimate subjective daylength of individual free-living rural and urban blackbirds, by calculating the time at which light exposure passed this threshold value in the morning and in the evening in both urban and rural birds. We show that birds living in the city centre of Munich are exposed to a subjective daylength on average 49 min longer than conspecifics breeding in a nearby rural forest. Conversely, there was no significant difference in daylength exposure between the rural forest and urban parks with intermediate level of urbanization (figure 1c). This pattern holds also when rural- and urban-defined thresholds of light intensity were used to calculate subjective daylength of rural and urban birds, respectively (see the electronic supplementary material), although this approach is less conservative as urban-defined thresholds were far lower than rural ones. The difference in subjective daylength between the rural forest and the business district is likely owing to the presence of artificial light at night. Indeed, as we have previously shown [9], the average exposure to light at night is lower in the rural forest compared with the urban parks and the business district, similar to the pattern in daylength exposure. Repeatability of subjective daylength was between 0.292 and 0.405, an average to high value if compared with that found by a recent meta-analysis of repeatability in behaviour [32]. This indicates that both urban and rural birds were consistently exposed to a certain light environment, and we suggest that the differences we found in subjective daylength reflected true characteristics of the habitat where the birds live. However, the hypothesis that consistent behavioural traits may reflect environmental conditions where they are expressed still needs to be tested directly.

The difference in subjective daylength between urban and rural birds was stronger in the beginning of the breeding season (March = 62 min, April = 17 min, May = 6 min). Interestingly, this result mirrors the seasonal variation in daily rhythms that has been suggested by several authors [9,15,27], with male songbirds normally advancing their dawn song and activity more during the first period of the breeding season, in late winter/early spring, when gonadal size and steroid hormone levels reach their peak. These differences in perceived subjective daylength between rural and urban blackbirds resemble a seasonal shift of 19 days in March, 6 days in April and 2 days in May at our urban business district. That is, our data indicate an almost three-week difference in subjective daylength between urban and rural blackbirds during March. Given that urban blackbirds have been found to develop a functional reproductive system 19 days in advance of their forest counterparts in our study populations [33], our results strongly support the hypothesis that exposure to artificial lights may explain most of the variation in reproductive timing observed in urban birds [6,15,19].

An alternative hypothesis for the observed results is that urban environmental conditions owing to different habitat structures cause an overall higher daytime light intensity than in rural areas. Daytime light intensity has been found to affect daylength perception, with lower intensities usually perceived as a shorter photoperiod than brighter levels of daytime irradiance [17,34]. The rural forest inhabited by our rural blackbird population is quite dense compared with the tree cover in the city of Munich; thus light might penetrate later in the forest and daylength appear shorter than in the city. However, we found contrasting evidence in support of this hypothesis. Namely, we found no significant difference in the light exposure during the day between the rural forest and the business district, but blackbirds in the urban park were exposed to an average and total daytime light irradiance greater than birds breeding in both the rural forest and the business district (electronic supplementary material, figure S1a,b). These results might offer an explanation for why blackbirds in the urban park, despite being exposed on average to lower light intensity at night than birds in the business district, showed very similar activity patterns [9]. It is plausible to hypothesize that increased daytime light intensity in these large open areas with little tree cover might be perceived as the same daylength as that which blackbirds in the business district, only few kilometres away, perceive, despite the latter being exposed to higher levels of light at night. Thus, this extending effect of daytime light irradiance on photoperiod in the urban parks could counteract the relatively lower light intensity at night in these areas compared with more light-polluted areas in the city centre of Munich. Eventually, the shift towards an earlier onset of activity recorded in both urban sites compared with the rural forest might be related to different habitat characteristics, namely natural daytime light.
intensity in the urban parks and artificial light at night in the business district. However, differences in light intensity during the day are also not urban-specific, but do certainly occur in many different habitat types with different vegetation structure. Such drastic effects can, for instance, happen during complete clear-cut logging [35].

In this study, we did not know the locations of the birds throughout the day and night. This is a clear limitation, as individuals could behaviourally modulate daily activity depending on their sensitivity to light and/or their preference for spending their time in bright or dark areas. In addition, birds in different populations can consistently differ in some behavioural traits that can, in turn, consistently affect their light exposure. For example, song-post height has been shown to be higher in urban habitats compared with rural areas [36], which could have biased our results. Future studies should aim at obtaining the exact position of birds at night, as this could most likely explain some of the variation in subjective daylength. Similarly, we could not control for the effect of other environmental variables that might have affected the activity of rural birds, upon which our analysis of subjective daylength has been based. For instance, although we have shown that weather conditions have little effect on the activity timing in our rural population [9], other studies have shown the opposite [27]. In addition, the onset of activity in rural birds could strongly depend on factors such as food abundance, breeding density and reproductive status, which we did not record. Obviously, other non-light-related environmental factors might affect the timing of daily activity, as we thoroughly discussed in reference [9]. However, the large body of work done in the context of circadian rhythms and photoperiodism in the past century strongly hints at daylength as the most important environmental cue regulating daily and seasonal rhythms of most living organisms, including birds [10]. Thus, we believe that our calculations on rural birds represent a true relationship between natural light intensity and daily rhythmicity. However, it is important to note that changes in the sensitivity to light might have biased our results. Indeed, the light intensity at which urban birds woke up was considerably lower compared with that which rural birds experienced at awakening. Although using these urban-defined thresholds of light intensity (instead of the rural-defined thresholds which were the core of our study) did not change the direction of the difference in daylength that we found (although it did affect the magnitude of this difference), waking up at a lower light intensity might require a shift in sensitivity to light. In addition, the effect of light at night is apparently different between the morning and evening phases. The difference in the time of threshold passing between urban and rural sites is greater in the evening than in the morning (figure 1a,b). Conversely, variation in activity patterns of the same animals revealed a greater shift in activity timing between urban and rural birds in the morning rather than in the evening [9], but no difference in light intensities between the early and the late night, in any of the sites along the urbanization gradient. Similarly, a study has indicated a greater effect of light at night on song timing in the morning than in the evening, and not only in the blackbird but also in other European songbird species, despite similar light levels in the two phases [27]. These results might point to a higher light sensitivity of songbirds in the morning. However, this hypothesis still lacks experimental support, although a few studies have suggested a phase-dependent responsiveness of the avian circadian clock to light intensity and wavelength [37,38]. Either way, to demonstrate that daylength perception is altered in urban animals by light pollution, we need to collect experimental data at the molecular/biochemical level. For example, as the response of the circadian clock to light is regulated by a transcriptional/translational feedback loop in gene expression, it is reasonable to hypothesize changes in gene expression during the night as a consequence of higher light intensity. Thus, sampling individuals at different times during the night and collecting tissue on which to perform gene expression analysis might help us understand whether daylength perception is altered under light pollution. This procedure has already been successfully deployed in the context of light pollution in rodents [39,40], where researchers have shown that rats and mice exposed to light at night have an altered pattern of clock gene expression.

Although the behavioural data previously collected on several avian species had already suggested that light pollution might affect the detection of daylength [15,27,28,41,42], here we used advances in radio-telemetry and bio-logging technology to test this hypothesis directly. Altogether, our results suggest that birds thriving in highly light-polluted areas are exposed to a light environment that could be perceived as a longer photoperiod than in other nearby, but darker, regions. Experimental work in captivity has suggested that artificial light at night can affect daily and seasonal rhythms to an extent similar to the differences observed in the field [6], but experimental data are needed also from the field if we want to discern whether a direct relationship exists between exposure to light at night and disruption of biological rhythms, as well as the relative importance of light and other environmental factors. We believe that a combination of individual-based field studies and experimental manipulations in the laboratory will help us understand the mechanisms through which light pollution affects natural populations [43].

Ethics statement. All experimental procedures were conducted in accordance with the regulations of the regional animal research committee (Regierung von Oberbayern, Munich, Bavaria; permit no. 55.1-8642.3-17-2008). See §2a.

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