

Report

Artificial Night Lighting Affects Dawn Song, Extra-Pair Siring Success, and Lay Date in Songbirds

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Summary

Associated with a continued global increase in urbanization [1], anthropogenic light pollution is an important problem [2]. However, our understanding of the ecological consequences of light pollution is limited [2–4]. We investigated effects of artificial night lighting on dawn song in five common forest-breeding songbirds. In four species, males near street lights started singing significantly earlier at dawn than males elsewhere in the forest, and this effect was stronger in naturally earlier-singing species. We compared reproductive behavior of blue tits breeding in edge territories with and without street lights to that of blue tits breeding in central territories over a 7 year period. Under the influence of street lights, females started egg laying on average 1.5 days earlier. Males occupying edge territories with street lights were twice as successful in obtaining extra-pair mates than their close neighbors or than males occupying central forest territories. Artificial night lighting affected both age classes but had a stronger effect on yearling males. Our findings indicate that light pollution has substantial effects on the timing of reproductive behavior and on individual mating patterns. It may have important evolutionary consequences by changing the information embedded in previously reliable quality-indicator traits [5, 6].

Results and Discussion

Urbanization and related anthropogenic activities have a strong impact on ecosystems [7, 8], particularly through habitat destruction and chemical, noise, and light pollution [9]. Studies in avian urban ecology have shown effects of urbanization on population dynamics and community composition [10, 11], and behavioral ecologists recently emphasized the impact of anthropogenic noise on avian communication [12–16] and species interactions [17]. In contrast to the general awareness of the consequences of noise pollution for terrestrial organisms [18, 19], the effects of artificial night lighting on natural populations have received much less attention [4], although it is becoming an emerging area of research [2, 20].

In this study, we examined the influence of light pollution on the reproductive behavior of a population of blue tits over seven breeding seasons. The study site has edges next to roads with and without street lights (see [Figure S1](#) available online). Comparing reproductive behavior of birds in edge territories with and without street lights to that of birds in

central territories allowed us to differentiate between edge effects per se and effects of artificial night lighting. We also made daily recordings of the dawn song of five common songbird species over a 19 day period in spring, comparing locations near and away from street lights ([Figure S1](#)).

Effects on Timing of Dawn Song

Males from four of the five species started singing significantly earlier in locations close to street lights than in locations away from street lights ([Figure 1](#); [Table S1](#)). A study on American robins (*Turdus migratorius*) also found that males began singing earlier in areas with high levels of artificial night lighting [21], but another study suggested that this was due to a response to daytime noise, not night lighting [14]. It is perhaps not surprising that noise can have a stronger effect on singing than light [14], because noise makes communication difficult, if not impossible. A response to daytime noise is an unlikely explanation for our results, however, because noise levels are very low throughout the study area. Furthermore, an effect of noise should be most pronounced for species in which males start singing close to the start of human activities, which is after dawn during the recording period. In fact, our results show the opposite pattern: the advance in the timing of dawn singing was stronger in species in which males generally started dawn song earlier relative to sunrise ([Figure S2](#)). This suggests that species that start singing long before dawn (e.g., the robin *Erithacus rubecula*) are more sensitive to light pollution.

In several previously studied species, including the willow tit *Poecile montanus* and the blackbird *Turdus merula*, the dawn song started earlier during peak female fertility [5, 22, 23]. For the majority of the singing individuals, we do not have information on their females' fertility, but the differences in start of dawn song between the locations with and without artificial night lighting were present over most of the recording period ([Figure 1](#)).

Effects on Timing of Reproduction

We compared the lay dates of female blue tits that bred on different territory types. Females from edge territories with street lights started egg laying on average 1.5 days earlier than females that bred either in a neighboring territory or in a central forest territory ([Figure 2A](#); [Table 1](#); [Table S2](#)). This was not simply an edge effect, because females in territories along the nonlighted edge did not start laying earlier ([Figure 2B](#); [Table 1](#); [Table S2](#)). The effect was similarly strong when lay date was plotted against the distance from the nearest street light to the nest, whereby the effect decreased exponentially, as expected from the decreasing influence of light (generalized linear mixed model [GLMM], effect of log-transformed distance on lay date: 0.77 ± 0.29 , $n = 321$, $z = 2.62$, $p = 0.009$). Although female age has a strong effect on lay date, the effect of artificial night lighting was independent of female age ([Figure 2A](#); nonsignificant female age \times territory class interaction, $z = -1.3$, $p = 0.19$), and territories near street lights were not more likely to be occupied by adult females ([Table S3](#)). Our findings are consistent with a study on captive blue tits that showed that females advanced their laying date

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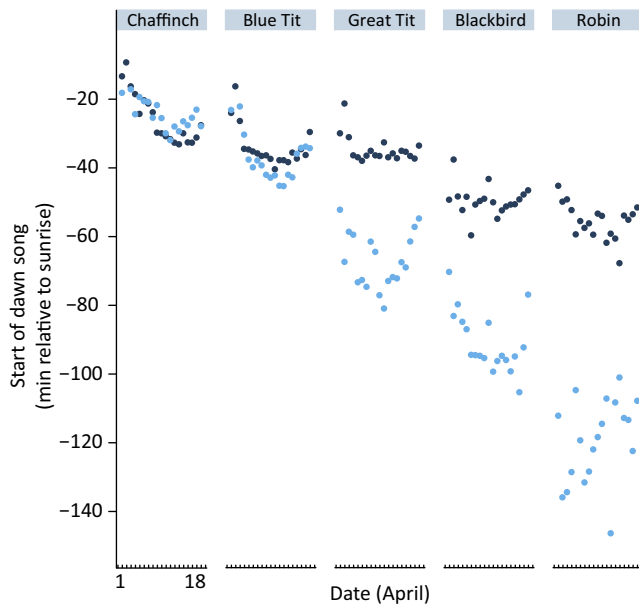


Figure 1. Effect of Artificial Night Lighting on the Start of the Dawn Chorus in Five Songbird Species

In the spring of 2009, we recorded bird song at 12 locations in the forest (see Figure S1A for details) on 19 consecutive mornings. Shown is the average start of dawn song relative to the time of sunrise on each day from March 31 until April 18 in territories affected by artificial light (light blue dots; $n = 6$) and in territories without artificial light (dark blue dots; $n = 6$). The difference between territories with and without artificial light is significant for all species except the chaffinch (chaffinch *Fringilla coelebs*: $p = 0.092$; blue tit *Cyanistes caeruleus*: $p < 0.0057$; great tit *Parus major*: $p < 0.0001$; blackbird *Turdus merula*: $p < 0.0001$; robin *Erithacus rubecula*: $p < 0.0001$; for full model details, see Table S1). We analyzed recordings using the software Audacity v. 1.3.9 (<http://audacity.sourceforge.net/>). Each sound file from each recorder on each day (approximately 2.5 hr) was cut into 30 min sections, and the exact time of the first visible and audible song of each species was recorded as “min after the start of the recording” and transformed to “min before or after sunrise.” Song from each of the five recorded species was not only audible but also visually distinct in a sonogram and easily distinguishable against the background noise. However, in some cases—most notably on mornings with rainfall—it was difficult to detect a singing bird, and on five occasions (robin: 2, chaffinch: 3) one of the species was not observed singing during the entire recording. These data (54 out of 1095 species-day-recordings, or 4.9% of data) were excluded from the analyses.

when exposed to artificially extended photoperiods [24]. Note that although clutch size generally increased with earlier laying in our population [25], females that bred on territories near street lights did not lay more eggs compared to females breeding elsewhere (Table S2), suggesting that they were not of higher quality or in better condition.

Effects on Extra-Pair Paternity

Artificial night lighting had strong effects on patterns of extra-pair paternity. Males that occupied edge territories with street lights were twice as successful in obtaining extra-pair mates (females with whom they sired at least one extra-pair offspring) than their close neighbors or males occupying central forest territories (Figure 2C; Table 1; Table S2). Again, this was not an edge effect per se, because males in nonlighted edge territories were in fact less successful than other males in the population (Figure 2D; Table 1), probably because of a lower local breeding density at the edge of the study area. Similarly, male paternity gain decreased exponentially with the distance

of the male’s territory center to the nearest street light (GLMM, effect of log-transformed distance on number of extra-pair mates: -0.50 ± 0.12 , $n = 321$, $z = -4.06$, $p < 0.0001$). As shown previously, male age also had a strong effect on paternity gain: older males were more likely to sire extra-pair offspring [26], sired more extra-pair offspring [26], and had more extra-pair partners (Table 1). Our results indicate that artificial night lighting affected males of both age classes, but it had a stronger effect on the success of yearling males (Figure 2C; factor of 2.4 for yearlings and 1.7 for adults; Table 1). Yearling males rarely sired extra-pair offspring when occupying territories that were not influenced by light. However, under the influence of artificial night lighting, they became almost as successful in obtaining extra-pair mates as adult males occupying nonlighted territories (Figure 3).

An alternative explanation for these results is that edge territories near street lights were occupied by males of higher quality. However, our analyses do not support this. First, males in street light territories did not differ in age, size, or condition from males breeding elsewhere (Table S3). Second, males in street light territories were equally likely to lose paternity in their brood as males breeding either in a neighboring territory or in a central forest territory (Figures 2E and 2F; Table S2). In general, males occupying edge territories lost less paternity than neighboring males (Figures 2E and 2F; Table 1), probably because they had fewer neighbors (local density effect). Third, females paired to males in street light territories did not lay larger clutches (though they started laying earlier) or produce more fledglings (Table S2).

We propose that the observed increase in extra-pair success is caused by the effect of light on dawn song, which in turn influences female extra-pair behavior. A previous study showed that adult male blue tits started singing earlier at dawn than yearling males [6] and that early-singing males had higher extra-pair success [6]. Our results suggest that night lighting induces males to sing earlier at dawn. Early dawn song may be a signal of male quality to which females are attracted for extra-pair copulations [27, 28]. This is supported by studies on dawn song in eastern kingbirds (*Tyrannus tyrannus*): early-singing males were larger and had longer flight feathers [29], and early-singing, large males sired most extra-pair young [30] (see also [5]). Effects of light on singing behavior could be expected to extend to neighboring males through behavioral interactions. If so, this clearly did not translate into an effect on extra-pair behavior: males in territories next to night-lighted territories were not more successful at obtaining extra-pair mates than other males in the population (Table S2).

Direct or Indirect Effects of Light

Our results suggest that under the influence of artificial night lighting, females laid eggs earlier during the season and male started dawn song earlier in the morning. Both of these effects may be a direct consequence of the exposure to night light. It is also possible that the effect on male behavior was influenced by the effect on female reproductive status, or vice versa. Night lighting may have caused earlier development of female gonads, and hence earlier laying [24]. For individual males, the start of dawn song is influenced by the reproductive status of the female, such that the earliest singing is observed on the days closest to the start of laying ([6] and unpublished data). Males influenced by night light may thus sing earlier in the morning because of a shift in the timing of dawn song with date, such that the earliest dawn song occurs earlier during

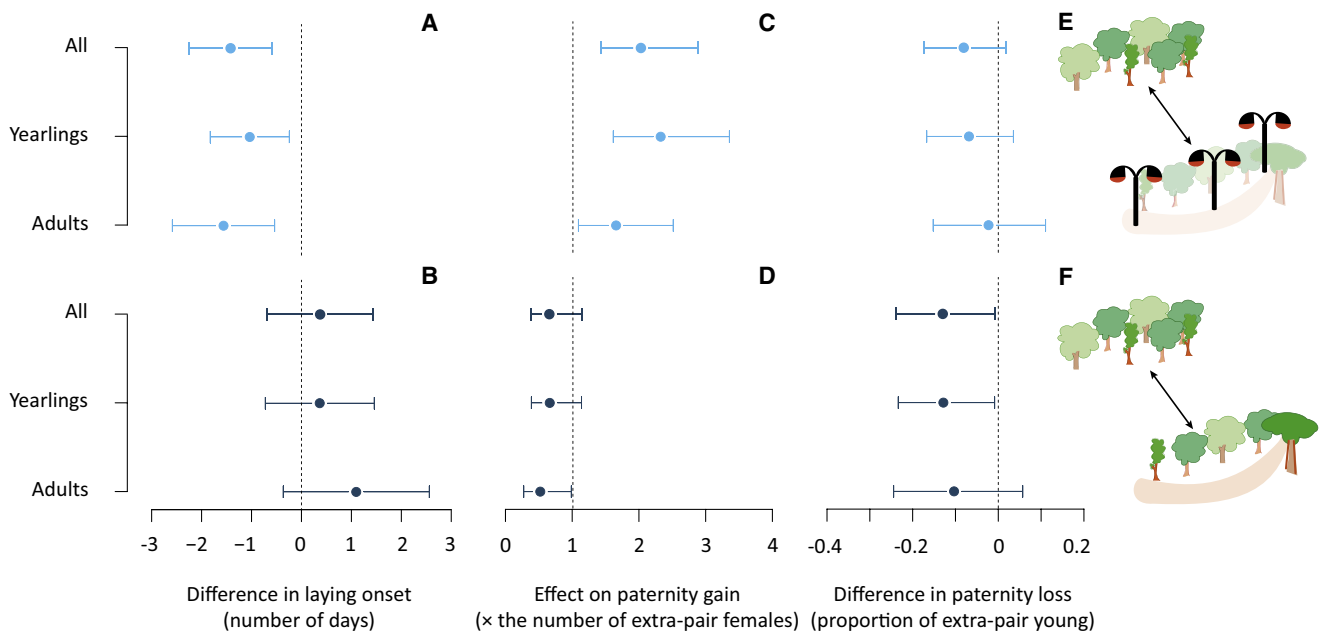


Figure 2. Effect of Artificial Night Lighting on Reproductive Parameters in the Blue Tit

(A and B) Effect on lay date.

(C and D) Effect on paternity gain.

(E and F) Effect on paternity loss.

Shown are effect sizes and 95% confidence intervals of the contrasts between edge territories and neighboring territories for street light territories (A, C, and E) and nonlighted edge territories (B, D, and F), both age classes combined, and for yearlings and adults separately. The vertical dotted line indicates no difference between the territory types. In all cases, the effect sizes are back-transformed and presented on their original scale. Effect sizes for breeding onset are from a generalized linear mixed model (GLMM) with a Gaussian error structure and an identity-link function (additive effect); effect sizes for paternity gain are from a GLMM with a Poisson error distribution and a log-link function (multiplicative effect: difference by a factor of the value indicated on the x axis); effect sizes for paternity loss are from a GLMM with a binomial error structure and a logit-link function (probability effect).

the season for these males. However, Figure 1 suggests that males in lighted territories started singing earlier over most of the recording period, and the results remain unchanged when variation in female reproductive state is partly removed by including for each day only the earliest singing male—presumably closest to the start of laying—among the six microphone locations (data not shown). Nevertheless, in future studies on the timing of male dawn song, it will be important to take the reproductive status of the female into account. An alternative scenario is that night lighting caused males to sing earlier at dawn, which in turn induced their females to lay earlier during the season. These alternative hypotheses could perhaps be tested experimentally by providing artificial night lighting to one sex but not to the other (e.g., night lighting inside the nest box with the roosting female). Finally, we note that males in lighted territories may have started performing dawn song earlier in the season, which may have influenced both their females' lay dates and their extra-pair success. Data on individual variation in the seasonal timing of dawn singing are lacking.

Conclusion

Our findings indicate that light pollution may have important long-term consequences by affecting the timing of reproductive behavior, individual mating patterns, and the information embedded in previously reliable quality-indicator traits. Artificial night lighting caused female blue tits to start egg laying earlier, which may lead to a mismatch between the time of peak food demand from the offspring in the nest and the peak in food availability [24]. Thus, artificial night lighting

potentially leads to maladaptive timing of reproduction. Artificial night lighting also caused males to sing earlier and led to an increase in their extra-pair success. Earlier observations in blue tits and other passerines showed that females leave their territory early in the morning to perform extra-pair copulations [27, 31]. Our analyses support the hypothesis that females target the earliest-singing males for extra-pair copulations, suggesting that the timing of dawn song is a quality indicator [30]. Artificial night lighting would then disrupt the link between quality and dawn song, making yearling males more attractive than they would otherwise be. Thus, light pollution potentially leads to maladaptive mate choice decisions of females with respect to extra-pair behavior, thereby altering selection pressures on mating behavior. Whether earlier singing, earlier laying, and altered extra-pair mating patterns come at a cost to the individuals involved remains to be shown, but using artificial light to experimentally manipulate these reproductive behaviors opens avenues for future research.

Experimental Procedures

General Field Procedures

We studied a population of blue tits breeding in nest boxes in Kolbeterberg, Vienna (48° 13' N, 16° 14' E) between 1998 and 2004. We checked all nest boxes at least weekly during nest building, daily just before and during laying and close to hatching, and again at least weekly during the nestling stage. We caught the feeding parents in the box when the young were 8–10 days old, banded them with a metal band and three color bands, and took measurements and a blood sample. We banded 14- to 15-day-old nestlings with a metal band and took a blood sample. Unhatched

Table 1. Effects of Artificial Night Lighting on Blue Tit Reproduction

Predictors	Effect of Artificial Night Light				Edge Effect Without Artificial Light			
	Estimate	SE	z	p Value	Estimate	SE	z	p Value
Dependent Variable: Laying Date ^a								
Intercept	7.17	1.15	–	–	6.83	1.31	–	–
Female age ^b	–1.50	0.34	–4.46	<0.0001	–0.94	0.49	–1.89	0.058
Territory class ^c	–1.13	0.40	–2.79	0.0052	0.44	0.55	0.81	0.42
Dependent Variable: Number of Extra-Pair Mates ^d								
Intercept	–1.79	0.23	–	–	–1.50	0.22	–	–
Male age ^b	1.32	0.26	4.98	<0.0001	0.93	0.24	3.86	0.0001
Territory class ^c	1.24	0.30	4.12	<0.0001	–0.49	0.26	–1.86	0.063
Male age × territory class	–0.72	0.36	–1.99	0.047	–	–	–	–
Dependent Variable: Proportion of Extra-Pair Young in the Brood ^e								
Intercept	–1.95	0.14	–	–	–2.18	0.16	–	–
Male age ^b	–0.34	0.16	–2.17	0.030	–0.09	0.18	–0.49	0.63
Territory class ^c	–0.35	0.21	–1.62	0.11	–0.56	0.24	–2.33	0.02

Fitted models are GLMMs with individual identity (male or female) and season (1998–2004) as random intercepts. Predictors were age (yearling or adult) and territory class (edge territories influenced by artificial night lighting or nonlighted edge territories compared to their respective neighboring territories; for details on territory assignment, see Figure S1). All nonsignificant age × territory class interactions (all $p > 0.18$) were removed from the models. SE denotes standard error.

^a 37% and 39% of the variance in laying date were explained by female identity (relative to variance explained by season: variance female identity + variance season = 100%).

^b Estimate is for adults ($n = 230$ females, 215 males) compared to yearlings ($n = 233$ females, 270 males).

^c Estimate is for edge territories (with artificial night lighting, $n = 101$, or without, $n = 83$) compared to the neighboring territories ($n = 220$ and 162, respectively).

^d 97% and 81% of the variance in paternity gain were explained by male identity (relative to variance explained by season).

^e In both cases, 100% of the variance in paternity loss was explained by male identity (relative to variance explained by season).

eggs and dead nestlings were collected to obtain a DNA sample. For the purpose of this study, we only included first breeding attempts in which the male identity was known. In total, we monitored 508 breeding attempts, caught 693 unique individuals (351 males and 342 females), and assigned paternity to 5165 offspring.

Position and Intensity of Street Lights

Part of our study site borders streets in a quiet suburban residential area with street lights with high-pressure sodium lamps that are turned on during the entire night (for a map with the position of all street lights, see Figure S1A). We measured the light intensity at night at ground level using a digital luminance meter (PCE-172; resolution: 0.01–100 lux, accuracy: $\pm 5\%$), starting just below the street light and at regular distances into the forest. The amount of artificial light declined exponentially and was not detectable in the forest at distances above 50 m (Figure S1B).

Territory Mapping and Assignment

To analyze the effect of artificial night lighting, we contrasted territories influenced by street lights (defined as falling within 50 m of a street light; Figure S1C) against neighboring territories under a natural light regime. Territories were estimated as Dirichlet tiles ([32–34]; for further details, see Figure S1C).

Dirichlet tile construction and both polygon-polygon and point-polygon analyses were performed using the R 2.9.0 software system [35] with the packages *sp*, *spdep*, *maptools*, and *rgdal*.

Parentage Analysis

We used five to eight polymorphic microsatellite markers to determine parentage of offspring, following standard procedures described in detail elsewhere [26, 36].

Statistical Analysis

We used GLMMs with individual and nest box as random factors. We performed all analyses with the R 2.9.0 software system [35], package *lme4* [37], and *multcomp* [38]. To investigate the effects of artificial night lighting on paternity, we used two types of GLMM: (1) for paternity loss (dependent variable is the proportion of extra-pair young within the brood), we constructed models with a binomial error structure and a logit-link function, and (2) for paternity gain (dependent variable is the number of extra-pair females with whom a male sired at least one offspring), we

constructed models with a Poisson error structure and a log-link function. For the analysis of breeding onset (lay date) and other phenotypic traits, we used GLMMs with a Gaussian error structure.

Supplemental Information

Supplemental Information includes three tables and two figures and can be found with this article online at doi:10.1016/j.cub.2010.08.028.

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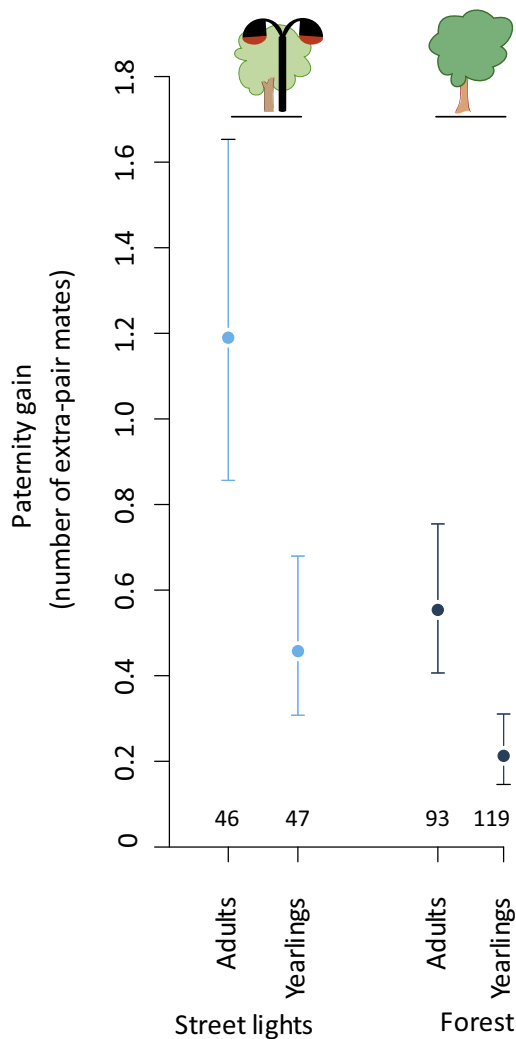


Figure 3. Effect of Artificial Night Lighting on Paternity Gain

Paternity gain is the number of extra-pair females with whom an individual sired at least one offspring. Shown are data for yearling and adult males occupying edge territories with and without influence of artificial night lighting. Data are point estimates and 95% confidence intervals from a GLMM with Poisson error distribution in which paternity gain is the dependent variable, age and territory category are fixed factors, and male identity and season are random intercepts (see Table 1 for details). Numbers refer to sample sizes.

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