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Effects of experimental light at night on extra-pair paternity in a songbird

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Abstract

Light pollution is increasing worldwide and significantly affects animal behavior. In birds, these effects include advancement of morning activity and onset of dawn song, which may affect extra-pair paternity. Advanced dawn song of males may stimulate females to engage in extra-pair copulations, and the earlier activity onset may affect the males' mate guarding behavior. Earlier work showed an effect of light at night on extra-pair behavior, but this was in an area with other anthropogenic disturbances. Here, we present a two-year experimental study on effects of light at night on extra-pair paternity of great tits (*Parus major*). Previously dark natural areas were illuminated with white, red, and green LED lamps and compared to a dark control. In 2014, the proportion of extra-pair young in broods increased with distance to the red and white lamps (i.e., at lower light intensities), but decreased with distance to the poles in the dark control. In 2013, we found no effects on the proportion of extra-pair young. The total number of offspring sired by a male was unaffected by artificial light at night in both years, suggesting that potential changes in female fidelity in pairs breeding close to white and red light did not translate into fitness benefits for the males of these pairs. Artificial light at night might disrupt the natural patterns of extra-pair paternity, possibly negates potential benefits of extra-pair copulations and thus could alter sexual selection processes in wild birds.

KEYWORDS

artificial light at night, extra-pair paternity, great tit, light color, light pollution, *Parus major*

1 | INTRODUCTION

The loss of dark nights across the world forms a biodiversity threat (Hölker, Wolter, Perkin, & Tockner, 2010), and the amount of artificial night lighting is predicted to continue to rise in the future (Cinzano, Falchi, & Elvidge, 2001; Falchi et al., 2016). We are increasingly uncovering ecological consequences of light pollution (Gaston, Visser, & Hölker, 2015; Rich & Longcore, 2006). In animals, these impacts are partly because their behavior has evolved to be synchronized with the natural light–dark cycle; photoperiod drives circannual and circadian rhythms (Dawson, King, Bentley, & Ball, 2001). Evidence of short-term effects of nocturnal illumination on animal behavior and physiology is accumulating (Swaddle et al., 2015). In birds, light at night affects daily timing of behavior. Onset of daily activity of blackbirds (*Turdus merula*) advances in urban compared to rural sites, and birds exposed to higher light intensities become active earlier in the morning (Dominoni, Carmona-Wagner, Hofmann, Kranstauber,

& Partecke, 2014). An experimental study in great tits (*Parus major*) showed that birds advance their daily rhythm when exposed to light at night in a dose-dependent manner (de Jong et al., 2016; and see also de Jong, Caro, Gienapp, Spoelstra, & Visser, 2017) and such an advancement was also shown for great tits with illumination inside their nest boxes by Raap, Pinxten, and Eens (2015). Ouyang et al. (2017b) show that, in an experimental study in the wild, great tits increase their nighttime activity when roosting in illuminated areas (but see comments on this study by Raap, Pinxten, & Eens, 2017, and the response to these comments, Ouyang et al., 2017a). Also, artificial light affects dawn song: blackbirds in urban areas sing earlier due to anthropogenic noise and light (Nordt & Klenke, 2013), and several songbird species, among which the great tit, sing earlier at dawn and in some cases, later at dusk (Da Silva, Samplonius, Schlicht, Valcu, & Kempenaers, 2014; Miller, 2006), but see the study by Da Silva et al. (2017) carried out on the same experimental sites as in this study.

The first evidence of an effect of artificial light on the extra-pair (EP) success of male songbirds was found by Kempenaers, Borgström, Loës, Schlicht, and Valcu (2010). Male blue tits that occupied illuminated forest-edge territories acquired more EP mates, compared to males breeding in nonilluminated forest and forest-edge territories. This effect may be linked to the advancement of dawn song by light, which was found in the same area for the same species. The study by Kempenaers et al. (2010) shows the potential effect of light at night on EP partner choice; however, these effects were observed around preexisting light sources along a street in a suburban residential area. Therefore, the effects may be confounded with other anthropogenic disturbances associated with light.

The onset of the dawn chorus may be a cue for male quality in some songbird species. Earlier singing blue tits (*Cyanistes caeruleus*) have more mating partners and are more likely to gain EP offspring (Poesel, Kunc, Foerster, Johnsen, & Kempenaers, 2006). Male Eastern Kingbirds (*Tyrannus tyrannus*) singing earlier sire more EP young as well (Dolan, Murphy, Redmond, Sexton, & Duffield, 2007). The onset of a male's dawn song thus may correlate with the choice of a female for EP mating partners; earlier singing males may be more attractive and hence sire more EP chicks. Additionally, an early singing male's social partner may be less eager to copulate with EP males. The presence of artificial light at night may disrupt this natural cue of attractiveness by prompting birds living in illuminated territories to sing earlier (Da Silva et al., 2014; Kempenaers et al., 2010; Nordt & Klenke, 2013), and thereby affect female mate choice and EP mating dynamics.

Another mechanism by which artificial light at night could affect EP behavior of a female is via her male's mate guarding. In great tits, the male sings near the nest box in the early morning and, once his partner emerges, subsequently copulates with her (Mace, 1987). However, females mostly engage in EP copulations at the peak of their fertility, and emerge earlier from their nest box at this time (Halfwerk et al., 2011 [in great tits]; Schlicht, Valcu, Loes, Girg, & Kempenaers, 2014 [in blue tits]). This suggests that great tit females might actively seek EP fertilizations by sneaking away before their social male becomes active. If the onset of activity of the social male is advanced by light at night (de Jong et al., 2016; Dominoni et al., 2014), the male may be more successful at guarding his female partner and preventing her from engaging in EP copulations.

In the current study, we investigate the effects of experimental light at night on the behavioral ecology of EP paternity in great tits, in the absence of other disturbances. Previously unlit areas were illuminated with white, red, and green LED lamps, and compared to a dark control (Spoelstra et al., 2015). In two consecutive years, we determined the parentage of great tit offspring and tested for an effect of light at night and distance to the light on the occurrence of EP paternity (proportion of EP young in a brood) and male reproductive success (total number of offspring sired). Following the two possible mechanisms described above, we expect females breeding in illuminated areas to have less EP copulations (and thus fewer EP offspring in their brood) and males from illuminated territories to sire more offspring (by siring more EP offspring and losing less paternity in their own brood).

2 | METHODS

2.1 | Experimental setup

We illuminated previously dark natural areas with transects of street lamps (five lamps per transect, 8.2 ± 0.3 lx at ground level) of three different colors (green, red, and white LED light) in addition to a dark control (poles without lamps). Two areas contained two sites (eight transects) and four areas one site (four transects), which gives a total of 32 transects. Light treatment was randomly assigned to transects within sites. Areas are forest-edge habitat and lights were on from sunset to sunrise at seven sites since 2012, and at one site since 2013. Nine bird nest boxes (diameter entrance hole 32 mm) were placed at each transect (a total of 288 nest boxes), following a standard pattern (distance from lamp post ranging between 1 and 94 m). For more details about the experimental setup, see Supporting Information Figure S1, and for details on the field sites and the spectral composition of the light, see de Jong et al. (2015) and Spoelstra et al. (2015). The density of nest boxes decreases with increasing distance to the lamp posts, due to the spatial pattern of the placement of nest boxes, which leads to increased occupancy rates further away from the lamp posts at all four treatment groups. All data were collected during the springs of 2013 and 2014.

2.2 | Field methods

Nest boxes were checked twice weekly from the end of March until the end of the breeding season. We only used data from first broods of great tits and there was no effect of light treatment on nest box occupancy rate, clutch size, or breeding success (for details, see de Jong et al., 2015). Samples for DNA-analysis were collected by taking blood samples from the heel vein of chicks two to four days after hatching, and by storing dead chicks and unhatched eggs. We sampled offspring and adults of 55 first broods in 2013, and of 94 first broods in 2014 (see Table 1); the number of broods in different treatments was similar (see Table 2). Adults were caught in the nest box using a spring trap (8–12 days after egg hatching), sexed, ringed with a numbered aluminum ring if unringed, and a blood sample was taken from the brachial vein. Blood samples were stored in Cell Lysis buffer (Qiagen, Redwood City, CA). For the 2014 adult samples, plasma was separated first, and red blood cells were frozen and later transferred to Cell Lysis buffer.

2.3 | Genetic analysis

Ninety-six-well genomic DNA extraction of blood and tissue samples was performed with a Favorgen kit (Favorgen Biotech Corporation, Ping-Tung, Taiwan) as described in the manufacturer's user manual. PCR was performed as described by Saladin, Bonfils, Binz, and Richner (2003) using five microsatellite DNA loci: PmaTAGAn71, PmaGAn27, PmaTGAn33, PmaC25, and PmaD105. Separation of the PCR fragments took place using an ABI 3130 Genetic Analyzer (Thermo Fisher Scientific, Waltham, MA). The capillary electrophoresis results of the ABI were analyzed with the software GeneMapper 5.0 (Thermo Fisher Scientific, Waltham, MA) that determined the sizes of the amplification products.

TABLE 1 Number of broods, adults, and offspring, for both years and in total. All caught adults were genotyped. The number of not sampled offspring was negligibly small. Number of genetic fathers identified refers to the total number of extra-pair (EP) offspring for which genetic fathers were identified

	Broods	Sampled females	Sampled social males	Sampled offspring	Genotyped offspring	Within-pair offspring	EP offspring	Genetic (EP) father identified
2013	55	50	47	403	380	326	41	9
2014	94	88	85	802	775	640	118	87
Total	149	138	132	1205	1155	966	159	96

TABLE 2 Results for the generalized linear-mixed-effects models on proportion of extra-pair (EP) chicks in a male's social brood and total genetic offspring of a male, in relation to light treatment in his territory and distance to the nearest lamp post, for both 2013 and 2014 together and separate. The model output for the treatment with distance with year interaction term is given for the analysis of both years together. For the separate years, the model output is given for the treatment with distance interaction term, treatment and distance main effects (likelihood ratio test statistics are given for the step of the backward selection before the term was taken out), and, if the interaction was significant, the effect of distance in treatment subsets was tested. The sample size (n), chi-square test statistic (χ^2), degrees of freedom (df), and significance level (P) are given for each term, and significant P -values (<0.05) are underlined

		2013 & 2014					2013				2014			
		n	χ^2	df	P		n	χ^2	df	P	n	χ^2	df	P
Proportion EP chicks per brood	Treatment: Distance: Year	149	9.00	3	<u>0.03</u>	Treatment: Distance	55	5.81	3	0.12	94	38.20	3	<u><0.001</u>
						Treatment	55	2.12	3	0.55				
						Distance	55	0.45	1	0.50				
						Distance in dark	(14)				25	4.72	1	<u>0.03</u>
						Distance in green	(13)				22	1.36	1	0.24
						Distance in red	(16)				24	5.75	1	<u>0.02</u>
Total offspring per male	Treatment: Distance: Year	132	8.49	3	<u>0.04</u>	Treatment: Distance	47	4.56	3	0.21	85	5.41	3	0.14
						Treatment	47	0.99	3	0.80	85	0.89	3	0.83
						Distance	47	0.41	1	0.53	85	1.18	1	0.28

2.4 | Paternity analysis

Paternity analyses were performed with the likelihood-statistics program Cervus version 3.0.7 (Field Genetics Ltd, London, UK; Kalinowski, Taper, & Marshall, 2007). All analyses in Cervus were performed per area and year. Allele frequencies were calculated and none of the loci deviated from Hardy–Weinberg equilibrium (one of the assumptions of Cervus). The combined exclusion probability for the microsatellite markers was 0.98 (averaged over areas) in both 2013 and 2014. Individuals were categorized as within-pair (WP) or EP offspring by comparing their genotype to that of the mother and social father. An individual was categorized as EP if one or more loci mismatched and Cervus-based analyses did not recognize the social father as the most likely father. For 3.4% of the offspring in 2013 and 2.2% in 2014, it was not possible to categorize the individual as WP or EP (see also Table 1). When offspring was EP, we compared its genotype to those of all potential fathers sampled at the same area in both years. Critical values were calculated using the following parameters in Cervus: 10,000 cycles, 98% of loci typed, and error rate 0.01%. The 2013 offspring have been sexed using Griffiths' method (Griffiths, Double,

Orr, & Dawson, 1998) and fledged males were added to the 2014 analysis in order to increase the chances of identifying the genetic fathers for the 2014 offspring. Parentage was assigned to chicks with parent combination matches of 95% confidence. The methods used for paternity analysis are described in more detail in van Oers, Drent, Dingemans, and Kempenaers (2008). We found two broods with only EP offspring, both at the same site (Voorstonden) where breeding density of great tits was very high and the proportion of EP young in nests was generally high (on average 29%).

2.5 | Statistical analysis

All statistical analyses were performed using R v. 3.1.2 (R Development Core Team 2014) with a significance level of $\alpha = 0.05$. To investigate possible effects of artificial light at night on EP behavior of great tits at our experimental study areas, we analyzed two response variables. First, we modeled the proportion of EP chicks in a brood ($cbind$ number of EP over number of WP), using a generalized linear-mixed-effects model (GLMM) with binomial error distribution and logit link

function. Then, we modeled the total number of offspring that was sired by a male (own WP offspring in social brood and EP offspring elsewhere), using a GLMM with Poisson error distribution and log link function. In both models, we fitted the interaction among light treatment (a factor with four levels: dark, green, red, and white), the distance of the nest box to the nearest lamp post, and year (a factor with two levels: 2013 and 2014). Distance to the nearest lamp post is used because the intensity decreases with distance, and thus the expected effect of light (de Jong et al., 2015). Using light intensity instead of distance is not an option because this dimension cannot be used in the dark control. We also included area (a factor with five levels in 2013 and six in 2014) as a random effect to account for between-area differences, and male identity (social father of a brood), to account for double measurements of the same males in both years. We found 19 males breeding in 2013 as well as in 2014, of which only three occupied the same nest box. Because the light with distance with year interaction was significant, we analyzed both years separately. Backward selection was used in both analyses, until only significant terms were left; the term with the highest *P*-value was taken out of the models first. If the light treatment with distance interaction was significant within a year, the effect of distance in treatment subsets was tested.

2.6 | Ethical statement

This study was carried out under license NIOO 10.07 of the Animal Experimentation Committee of the Royal Netherlands Academy of Arts and Sciences.

3 | RESULTS

We found that in one of the two years, 2014, the proportion of EP offspring in a brood was affected by the distance of the nest box to the nearest lamp post and that this effect depended on the light treatment (Table 2). The proportion of EP chicks decreased with distance to the nearest lamp post in the dark treatment (estimate = -0.02 , SE = 0.01, and $P = 0.03$), while it increased with distance in the red (estimate = 0.02, SE = 0.01, and $P = 0.02$) and white light treatments (estimate = 0.04, SE = 0.01, and $P < 0.001$; Figure 1b). The relation with distance did not differ between illumination treatments (subset 2014 broods in green, red, and white ($n = 69$): treatment with distance interaction $\chi^2 = 4.55$ and $P = 0.10$). In 2013, we found no differences between treatments in the proportion of EP young in broods (Figure 1a). We found a significant effect of the interaction between light treatment, distance, and year on the total number of offspring sired by a male (Table 2). However, in each separate year, neither treatment nor distance nor their interaction affected the total number of offspring sired (Figures 1c and 1d).

4 | DISCUSSION

Our study reveals an effect of nocturnal illumination on the proportion of EP young in broods in one out of the two study years. Only in 2014, the proportion of EP young in broods increased with distance to the red

and white lamps, while the proportion of EP young in broods in the dark control decreased with distance. We did not find an effect of distance to the light in the green transects. However, when we compared the proportion of EP young in broods only in the three illuminated treatments, the relation with distance did not differ between treatments. This indicates that the pattern in green light does not differ significantly from those in the white and red light.

Pairs nesting close to red and white light poles had a relatively low number of EP young in their broods, in one out of two studied years (2014). Egg fertilization rate in females is quite stable within species and between populations (Brommer et al., 2010), and we assume no treatment effect on fertilization rate. Thus, these lower EP proportions close to the light are most likely due to the fact that females breeding closer to the light posts were less likely to engage in EP copulations, rather than to a difference in egg fertilization rate. This potential effect of artificial light on female fidelity could originate from changes in the motivation of females to engage in EP copulations. As a first hypothesis we proposed that, through a possibly advanced onset of dawn song in illuminated areas (Da Silva et al., 2014; Kempenaers et al., 2010; Nordt & Klenke, 2013), females close to the light sources may have perceived their mate to be of high quality compared to other males, and females mated to high-quality males are more faithful (Kempenaers et al., 1992). On the other hand, females far from the light sources might have perceived their mates to be of relatively low quality, and engaged more in EP copulations. However, a study specifically looking at timing of dawn song on the same experimental sites showed no effects of light on the onset of the dawn chorus (Da Silva et al., 2017). Therefore, we think that our alternative explanation, that light at night affects the mate guarding behavior of males, is more plausible. Females spend the night in the nest box, where they are marginally affected or unaffected by the artificial light, whereas their social males may have experienced brighter conditions. A male may be more successful in mate guarding via earlier onset of activity in lighted areas (de Jong et al., 2016, 2017; Dominoni et al., 2014). However, although the dawn song may have a function for mate guarding, female great tits can vocally interact with the male by producing quiet calls and the intensity of dawn song is not related to the presence of a female (Gorissen & Eens, 2004; Slagsvold, Dale, & Saetre, 1994).

In unlit control areas, we found, also in 2014, that birds breeding close to the dark control poles had more EP young in their broods than those breeding farther away. This can be explained by the spatial pattern of our nest boxes at every transect, where the density of boxes decreases with increasing distance to the poles (de Jong et al., 2015). Great tits nesting close to the poles—and close to poles without lights at the dark control transects—potentially have the largest number of neighbors. Abundance of neighbors provides ample opportunities for females to take part in EP copulations. Breeding density, both on a large and small scale, is a predictor of EP paternity rate (Stewart, Westneat, & Ritchison, 2010; Westneat & Sherman, 1997), which may explain the higher EP proportion close to the poles in the absence of light. We note that despite the same density effect in the illuminated areas, we find differences in EP offspring in the opposite direction as predicted by the density effect.

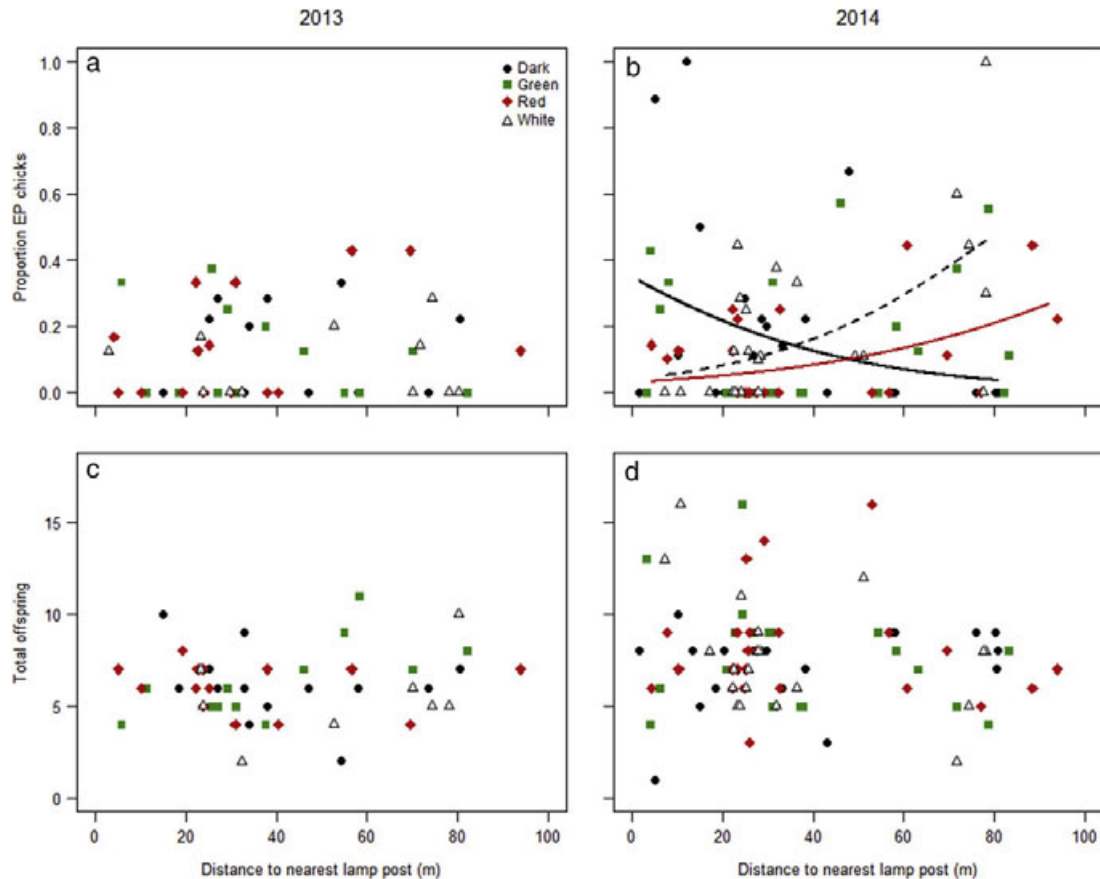


FIGURE 1 The proportion of extra-pair (EP) chicks in great tit broods, in relation to distance of the nest box to the nearest lamp post, in the four light treatments, for 2013 (a) and 2014 (b). The total number of genetic offspring of a male, in relation to distance of his social nest box to the nearest lamp post, in the four light treatments, for 2013 (c) and 2014 (d). Filled black circles are males in the dark treatment, filled green squares are males in the green treatment, filled red diamonds are males in the red treatment, and open triangles are males in the white light treatment. Plotted lines in (b) are model predictions for treatments, where distance significantly affected the proportion of EP chicks (solid black for dark treatment, solid red for red treatment, and dashed black for white light treatment) [Color figure can be viewed at wileyonlinelibrary.com]

In 2013, we found no effect of nocturnal illumination on the proportion of EP young in broods, in contrast to 2014. We may not have had enough statistical power to detect an effect of light at night in 2013, due to the lower sample size in that year ($n = 55$ in 2013 and $n = 94$ in 2014). Climatic conditions differed substantially between both breeding seasons, with 2013 being a very late and 2014 a very early spring (mean first egg laying date differed 20 days; de Jong et al., 2015). This difference is likely one of the reasons that sample sizes for 2014 were larger. In addition, in 2014, we used data from one more study area, which was not yet illuminated in 2013 and had generally high great tit breeding density and high EP paternity. However, excluding the data for this area did not change our results for proportion EP or total offspring. The decrease of EP young with distance to the dark control poles in 2014, as discussed above, was absent in 2013 (subset 2013 broods in the dark treatment: distance $\chi^2 = 0.40$ and $P = 0.53$). The nest boxes in the dark with shortest distance from the poles were not occupied in 2013 (Figure 1a), which may explain the absence of the density effect.

Following our hypotheses and the effect of light at night on proportion of EP chicks in broods, we would expect that males breeding in illuminated territories have more offspring in total, since they have

less EP offspring in their own brood and may be more attractive for EP copulations with other females. However, the total number of offspring sired by a male, those in his own nest plus the ones as EP in other nests, was not affected by artificial light at night. This demonstrates that the apparent changes in fidelity of females breeding in illuminated territories in 2014 did not translate into substantial fitness benefits for their males. This seemingly increased sexual fidelity of females breeding in illuminated areas, which may have reduced the opportunities for males to gain paternity elsewhere. For this reason, drawing conclusions on the effects of artificial light on male paternity gain would be difficult given our current findings and experimental setup. Numbers of offspring were not confounded by effects of light at night on brood size, because brood size (number of chicks that hatched) was not affected by light treatment or distance to the light (only year had a significant effect; average brood size in 2014 [8.0 chicks] was larger than in 2013 [6.9 chicks]).

Support for our hypothesis that the lower EP offspring proportions observed in broods close to the light are due to an advanced onset of activity of the social male come from a study on the circadian clock in great tits that found that EP offspring had significantly shorter free-running periods (a measure of the length of the internal circadian

rhythm) than WP offspring (Helm & Visser, 2010). Shorter free-running periods may cause birds to become active earlier in the day, and combined with the high heritability of period length (Helm & Visser, 2010), this suggests that EP fathers have a shorter free-running rhythm and thus are active earlier in the day. More EP offspring by early active males is in line with the hypothesis that the lower proportion of EP offspring in males' social broods close to light may consequently result from enhanced mate guarding, rather than higher attractiveness of the social male, which could explain why the male's total number of offspring was unaffected by light at night. Moreover, Greives et al. (2015) provided wild great tit males with continuous night-time levels of melatonin. This delayed their daily onset of activity, and nestlings of these males were more likely to be sired by an EP male.

If an earlier onset of activity of the males by artificial light indeed causes males to be more successful at mate guarding, this could explain the difference with the findings of Kempenaers et al. (2010) on blue tits. No effects were found on the proportion of EP young (paternity loss) in broods in artificial light. In blue tits, there seems to be no relationship between unfaithfulness and emergence time (Schlicht et al., 2014) and thus artificial light would not be expected to aid mate guarding in blue tits. Although blue tit females exhibit strong sexual preferences in both their EP and WP partner choice based on specific male characteristics (Kempenaers, Verheyen, & Dhondt, 1997; Poesel et al., 2006), the importance of specific male characteristics that female great tits use for EP mate selection is less clear (Kawano, Yamaguchi, Kasuya, & Yahara, 2009; Strohbach et al., 1998). This preference could explain why paternity gain in blue tits is so strongly affected by artificial light, probably by advancing the onset of dawn song (Kempenaers et al., 2010), whereas it seems not for great tits.

One of the aspects of male quality is age. Many studies in blue tits have shown a higher EP siring success of older males (Foerster, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003; Kempenaers et al., 1997; Kempenaers et al., 2010; Poesel et al., 2006), however less in great tits (Kawano et al., 2009), but see Lubjuhn, Gerken, Br un, and Schmoll (2007). In our data on great tits, for both years, adding male age (first year male or older male) in the model for total offspring did not change the results. Also, there was no difference in the total number of offspring between males that bred for the first time and males that had bred before.

We are aware of the fact that individual birds were free to choose nest boxes at different distances to the lamp posts. Hence, a nonrandom selection of the population may breed in nest-boxes under light at night. However, we have shown in an earlier study on the same populations of birds and in the same years (de Jong et al., 2015) that the breeding density did not differ between light treatments (nor was affected by the interaction of treatment with distance to the nearest lamp post), and birds that survived from 2013 to 2014 did not move to a particular light color or away from the illuminated area to the dark control. Although there is no reason to assume that males that were more attractive (and hence are mated to females that are less likely to engage in EP copulations) settled in more illuminated territories, we cannot exclude this.

We show that the relation between the proportion of EP young and distance to the light in 2014 did not significantly differ between green,

red, and white treatments. However, the distance effect was specifically present in red and white light. This was also the case in a study on stress hormone concentrations in the same experimental setup: adults nesting in white or close to red illumination had elevated corticosterone levels (Ouyang et al., 2015). Our red and white light both include larger proportions of longer wavelength radiation compared to our green light (Spoelstra et al., 2015). Long wavelength light is known to penetrate the skull more easily and has been found to be more effective at inducing a photoperiodic response (Hartwig & van Veen, 1979), stimulating gonadal development and promoting body fattening than short wavelength light (Malik, Rani, & Kumar, 2002). Our 2014 results are consistent with this pattern and suggest that EP paternity is more strongly affected by long wavelength than short wavelength light. More years of data are needed to get better insight in the EP mating dynamics under artificial light at night, particularly in the role of light spectra.

We found that artificial light at night, in absence of other anthropogenic disturbance, potentially disrupts the natural patterns of EP paternity. This disruption could lead to maladaptive mate choice decisions of females (Kempenaers et al., 2010). Great tits breeding at experimentally illuminated transects in natural habitat showed a reduced proportion of EP young in one of the two study years. Potential benefits of EP copulations (Foerster et al., 2003) may therefore be negated by nocturnal illumination. Our finding of fewer EP offspring in illuminated broods thus shows that light at night might alter sexual selection processes in wild birds. Future studies should focus on obtaining the behavioral data, which are missing so far, to further explain and better understand the patterns and underlying processes of the effects of light pollution on EP paternity patterns.

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