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„Does light pollution affect wild birds? An experiment on blue tits (*Cyanistes caeruleus*) in the Viennese Forest“

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Clara Leutgeb

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Abstract

In the last decades it has been found out that artificial light does not only bring comfort but that there might also be a toll to pay and the term "light pollution" was coined. Birds are especially vulnerable to light pollution because their whole life cycle heavily depends on a fine-tuned synchronisation with seasonal events. So far mostly correlative evidence has been gathered on how their behavior is altered under the influence of artificial light, but what we still do not know is how severe the indirect impact of light is and whether it also translates into the next generation, which is of great conservational relevance.

This study sought elucidating these pressing questions using a nest box population of the blue tit (*Cyanistes caeruleus*) in the Viennese Forest, Austria. Breeding phenology and fitness parameters are compared between birds breeding near streetlamps, experimental LED lamps or without manipulation. To our knowledge, this is the first experimental study to investigate the effects of light at night on reproductive decisions, breeding success and offspring quality at the same time.

Artificial light did neither lead to an earlier onset of egg laying nor to a reduced number of eggs, hatchlings, hatching success or fledglings. Also an invasive test (PHA-challenge) for indirect immunocompetence of offspring did not reveal significant differences. Condition, however, was significantly lower in nestlings growing under the influence of LED lamps. Although the effect is minor, this study shows that negative consequences are detectable at close inspection. Nevertheless, the blue tit is less affected by light pollution than expected, probably due to a combination of certain traits: it is a cavity-nesting bird, rather late riser in the morning, and well urbanized. These factors render the species very adaptive which is why I suggest to compare the findings with another less hemerobic bird species in order to thoroughly investigate the subtle and time-delayed effects of light pollution on breeding behavior and reproductive success.

Keywords: *Blue tit · light pollution · artificial light at night · experiment · breeding phenology · breeding success · offspring quality*

1 Introduction

Artificial light has certainly enhanced our everyday life in terms of security and comfort. Upon the introduction of street lamps in the 17th century and in line with the predominant zeitgeist, they were uncritically connected with progress and prosperity (Held et al. 2013; Hölker et al. 2010). Only in the last decades it has been found out that there might be a toll to pay: Although light is vital for our vitamine and hormonal balance, we and nearly all other living organisms on Earth have evolved under a natural rhythm of day and night, which is why light at the wrong time can have severe adverse effects in the long run (Posch et al. 2013). The relatively young discipline of chronobiology has compiled an extensive body of work on negative consequences for human health such as depression, anxiety, cancer and cardiovascular disease (e.g. Borugian et al. 2005; Ha & Park 2005; Schernhammer et al. 2001 etc.).

Concerning flora and fauna, the conservational issue has been neglected for some time. We protect ourselves by shutting the curtains at night, but how do animals and plants react (Held et al. 2013)? As the problem of light pollution is taking on a global scale, more and more researchers also study the implications for organisms other than man, but knowledge is still sparse (Navara & Nelson 2007; Longcore & Rich 2004). It is yet unclear whether animals will be able to adapt quickly and sufficiently enough to meet the challenges of rapidly changing environments. In this context, artificial lighting has even been termed "a global self-experiment with unpredictable outcomes", potentially reshaping entire ecosystems (Hölker et al. 2010). In fact, the time lag concerning animals is somewhat surprising because the stimulating effect of light has been industrially used for almost a century now: Already in 1918, it was commonly known that domestic fowl (*Gallus domesticus*) can be manipulated to lay more eggs by artificially extending day length (Shoup 1918). Similarly, juncos (*Junco hyemalis*) kept in outdoor enclosures start to show mating behavior in winter when stimulated by a few minutes of electric illumination (Rowan 1925). These early findings already suggest that artificial light may cause profound changes in an animal´s endogenous clock and endocrine balance, hence substantially altering its perception of the photoperiod. However, the knowledge of these phenomena went dormant for decades, and only in the last few years ambitions have erupted once again to illuminate the dark sides of light.

Although almost omnipresent in industrial countries, light pollution is subtle and less obvious than other anthropogenic environmental stressors such as noise, chemicals or habitat destruction. Nevertheless, it pervades nearly all aspects of life on Earth, be it influences on the endogenous clock, the circadian rhythm, physiology, behavior, immune function, energy metabolism, food web interactions or biotope connectivity (Navara & Nelson 2007). Famous examples include nocturnal insects and their positive phototaxis at night as well as marine turtle hatchlings distracted by lightings ashore (Rich & Longcore 2006). However, the maybe most prominent findings arose from birds since they constitute ideal model organisms to study the effects of light pollution. This is because they are highly sensitive to the external zeitgeber light when it comes to optimal timing of migration, reproduction or molt: There is indication that in most nontropical bird species seasonality is in general controlled by the length of the photoperiod (Dawson et al. 2001). In European blackbirds (*Turdus merula*), for instance, artificial light at night alters daily rhythmicity (Dominoni et al. 2014), affects locomoter activity and molt (Dominoni et al. 2013a), advances reproductive physiology (Dominoni et al. 2013b), reduces nocturnal melatonin release (Dominoni et al. 2013c), and even leads to different phenotypically flexible chronotypes of forest and city dwellers (Dominoni et al. 2013d; Partecke et al. 2004).

The majority of avian studies deal with the direct and more obvious impacts of light pollution. These include light-induced mortality in nocturnally migrating birds which collide with buildings or lighthouses. Often, they also become entrapped in spotlights or skybeamers and either leave disoriented or die of exhaustion (Miles et al. 2010; Le Corre et al. 2002). Another conspicuous effect is the shift of onset of singing activity in the early morning, which even leads to nocturnal singing in some species such as the American robin (*Turdus migratorius*) (Miller 2006). The indirect and long-term effects of light pollution, on the other hand, are less well studied because they are far more subtle and not seen right away. For instance, light at night could potentially alter breeding performance and reproductive success, hence it might have large-scale ecological implications for whole populations and could ultimately even lead to maladaptation (Kempenaers et al. 2010). These profound influences need to be investigated thoroughly as the light domes of the cities continuously expand and reach pristine habitats.

Until now some correlative field studies have indeed documented indirect consequences of light at night, but the exact underlying mechanisms remain unknown. So far only one experimental study examined the effect of light exposure on a species closely related to the focal species of this study, the blue tit (*Cyanistes caeruleus*). Experiments using the great tit (*Parus major*) did not show adverse impacts of artificial light on breeding phenology or nestling development as such, but it did affect parental feeding behavior. Females performed significantly more feeding trips but nestling condition did not improve. This suggests that the parents had to compensate a negative influence and invested more in a current brood than they would under natural conditions, which eventually decreases their lifetime reproductive success (Titulaer et al. 2012). Concerning the blue tit in specific, one long-term observational study showed that under artificial light, females laid eggs earlier, males started to sing earlier, and extra-pair mating preferences were altered unfavorably (Kempenaers et al. 2010).

However, these results provide correlative evidence only, and for a real proof of causality an experiment would be necessary, in which ambient light conditions are actively manipulated to control for possible confounding variables. The aim of our study was to design an experiment in which the birds cannot choose freely anymore whether they want to breed under the influence of light or not. This is essential, because by doing so we can exclude other influencing factors. To understand the role of light as a territory feature of blue tits and its influence on offspring quality we applied a binary approach. In a correlative part, birds were allowed to breed under the respective condition they preferred, but in the experimental part they were forced to breed under the influence of light. We wanted to explicitly test for potential changes in breeding phenology (i.e. seasonal timing) and reproductive success. One prediction was that an artificially prolonged photoperiod stimulates females to start laying eggs earlier. Concerning reproductive output, we had no clear predictions since scenarios in both ways were possible: either light-polluted females lay fewer eggs due to chronic stress, or they lay more eggs because light enables them to forage earlier and build up more body reserves. For nestlings, however, we expected an impaired development and immune response if light at night was a substantial environmental stressor. In conclusion, our study investigates for the first time the effects of light at night on reproductive decisions, breeding success and offspring quality at the same time. This could help to understand whether light leads to behavioral changes in adult blue tits and whether it also translates into the fitness of future generations. If this is the case, light pollution could in the long run affect evolutionary processes such as natural and/or sexual selection and has serious implications for species conservation.

2 Material and methods

2.1 General methods

The study site was located in Pressbaum (Lower Austria; 48° 18´ N, 16° 8´ E, about 320 m a.s.l.) near Vienna. The experiment was conducted in the forest around the Sacré Coeur School where a long-term monitoring project has been launched in 2009. As part of the Viennese Forest, the area consists of a typically mid-European mixed deciduous forest with beeches, ashes and some conifers interspersed. Approximately 350 nest boxes have been installed in total, and every year about 60-80 blue tits breed in the boxes. For the correlative approach, included data covers the period 2009 to 2014 (except 2013). Experiments were conducted in 2013 and 2014.

2.2 Study species

The study species has been chosen for a number of reasons: The blue tit (*Cyanistes caeruleus*) is a common European songbird that constitutes an ideal model organism. For instance, previous studies have shown that the species is a reliable bioindicator for global warming, which is why it is well-studied and provides a great amount of reference literature (Föger & Pegoraro 2004). Furthermore, blue tits are suitable to study the effects of various other man-made impacts including light pollution because (i) they are natural cavity-nesting birds and readily breed in nest boxes where they can be monitored and manipulated, (ii) the nestlings are altricial which is why developmental measurements can be taken, (iii) blue tits only produce one single clutch per season (second or replacement clutches are very rare) (Glutz von Blotzheim & Bauer 1993), which allows for precise comparisons of breeding parameters between pairs and (iv) the species is well urbanized and more or less “anthropophilic”, so it is less sensitive to human disturbance and handling.

Due to the continuation of the project it can be guaranteed that no bird suffered long-term harm. Furthermore, it has been shown that capture at nest site has no negative long-term effects on blue tits (Schlicht & Kempenaers 2015; Bub 1995). All animal procedures were approved by the institutional ethics committee and the national authority according to §26 of Law for Animal Experiments, Tierversuchsgesetz 2012 – TG 2012 (reference number: 68.205/0067-WF/II/3b/2014).

2.3 Treatment design and measurements

For the experiment, blue tits were assigned randomly to one of two groups: The control group bred under a natural light regime, whereas the experimental treatment group was exposed to unnatural photoperiodic conditions as ambient light was actively manipulated. To simulate light pollution, this group received two hours of additional light in the morning (3:30-5:30) and in the evening (21:00-23:00) over a period of about three weeks. These times of the day reflect the extended activity patterns of birds living in urbanized areas with night lighting (unpublished data, Katharina Mahr). The artificial light sources used were LED lamps (Globaltronics GmbH & Co, model GT-AL60-LED3) put up at surrounding tree branches at a distance of 1-1.5 m to the nest box and faced directly towards the entrance hole. The treatment started when the female had constructed and finished a nest and lasted until the nestlings were 10 (± 1) days old. However, during the incubation phase of 14 days light treatment was suspended because only then females are very sensitive to disturbance and could easily desert the clutch.

For the correlative approach, one group bred in nest boxes installed in the vicinity of streetlamps near to the school or houses. These birds were confronted with some sort of a "natural experiment", but they were not experimental birds in the true sense: The essential difference from experimental birds was that they were completely free to choose dark over light-polluted territories or not. Thus, light at night was a habitat feature they could in principle integrate into their territory (nest site) choice. The experimentally manipulated group in contrast was forced to breed under the influence of light because they were stimulated by light from a specific point after settling decision, specifically after completion of nest construction, when egglaying motivation was already high. This means that in the experimental group breeding pairs only experienced a short-term manipulation after territory settlement, whereas the streetlamps group faced light during the whole breeding cycle.

Territories differed depending on the habitat type in which the nest boxes were set up. They were either located in dense forest areas or on forest edges adjacent to meadows, roads or close to the school ground. These habitat types may cause qualitative differences between territories concerning food supply or intraspecific competition, which was taken into account for group selection and statistical analyses to correct for a potential edge effect (cf. Kempenaers et al. 2010).

Body measurements were taken from both adults and nestlings. The former were trapped inside the nest box when feeding the 6-day-old chicks, the latter were processed four days in a row from day 7-10 (± 1 day) post hatching. The birds were banded with standard Aluminium rings, and adults additionally received a unique combination of colored Darvic rings. Tarsus and flattened wing length were measured to the nearest 0.1 mm using digital callipers, as well as body weight to the nearest 0.1 g using a digital balance. To examine a possible effect of light pollution on blue tit reproductive success, we determined several parameters including clutch size (number of eggs laid), brood size (number of hatchlings) and hatching success (%) as the proportion of nestlings hatched from all eggs laid. Furthermore, we determined the number of fledglings, which represent all nestlings that survived until the last day of nestling measurements (day 10, a developmental stage when they could potentially fledge). To assess nestling condition, we calculated the residual body weight (g) not explained by tarsus length (mm) (as a predictor for body size). The same procedure was applied to determine the condition of parents. For adults, additionally tail length (mm), sex (depending on the presence or absence of a brood patch), and age (depending on molt characteristics, as one year or older birds), were recorded. Finally, an immune challenge using PHA (phytohemagglutinin) was performed on 9-day-old (± 1 day) nestlings. This substance is a mitogen used to measure T-cell mediated indirect immunocompetence. It was injected subcutaneously into the patagium of the left wing and PBS (phosphate-buffered saline) as reference into the patagium of the right wing. The treatment causes measurable tissue swelling at the site of injection, which can be quantified 24 hours later with a pressure sensitive micrometer. The larger the ratio between the two swellings, henceforth termed PHA-response (mm), the stronger the immune response is (Tella et al. 2008). Although the technique has been criticized by some in the past, it has been successfully employed in a number of previous avian studies (Thompson et al. 2014; Butler et al. 2010; Martín-Vivaldi et al. 2006) and is considered appropriate today.

2.4 Statistical analysis

All statistical analyses were performed with the IBM SPSS Statistics version 22 software package. The data were tested for normal distribution and homoscedasticity, statistical tests were used as appropriate. All tests were two-tailed and significance was accepted at $\alpha < 0.05$. Sample size of subsets (n) may vary (e.g. between number of eggs and number of hatchlings) because some clutches were either predated, displaced by physically superior species or deserted for some other unknown reason.

Results are reported as mean ± standard error of the mean (SEM). Mann-Whitney U-test and Kruskal-Wallis H-test were applied for not normally distributed dependent variables. Additionally, the effect size estimates are reported by Pearson´s correlation coefficient r. For "start of egg laying", we excluded annual effects by defining every year as day 1 the date when the first egg was layed by any of the females. For "condition" and "PHA-response", univariate General Linear Models (GLMs) were constructed via one-way independent ANOVA. To account for the influence of year, variables of interest were z-standardized. The initial models contained the respective dependent variable of interest, and group, habitat and year as fixed factors as well as number of hatchlings per nest as covariate. These models also included interactions between the variables. Step by step, nonsignificant terms (starting with interactions followed by explanatory variables) were sequentially deleted in order of decreasing significance until the final model contained only terms with $p < 0.05$.

To account for the study design, results are presented in two separate parts. In the first section, control pairs are compared with birds from the streetlamps group over five years (2009–2014 except 2013, during which no blue tits bred next to streetlamps). The aim here was to see whether blue tits may pay any attention towards artificial light as a territory feature and whether effects on reproductive success can be detected. Since the streetlamps group was always breeding in edge habitats (streetlamps are per se situated at borders), only control pairs breeding at edges were selected to achieve comparability. This section provides long-term correlative data since the years are almost consecutive. Secondly, in order to address a possible causal effect of artificial light on blue tit offspring, control birds are compared from two years (2013–2014) with experimental birds manipulated by LED lamps from the same time period. Here the main focus was to detect possible effects on offspring quality.

3 Results

3.1 Breeding near streetlamps: correlative approach

3.1.1 Start of egg laying

In blue tits start of laying within a season can vary for about 20 days. The earliest observation of an egg laid was 24 March 2014 and the last was 12 May 2010.

We could not find a difference in the onset of egg laying between the two groups experiencing different light regimes (*U* = 437.50, *p* = 0.367; *r* = -0.100) (see fig. 1).

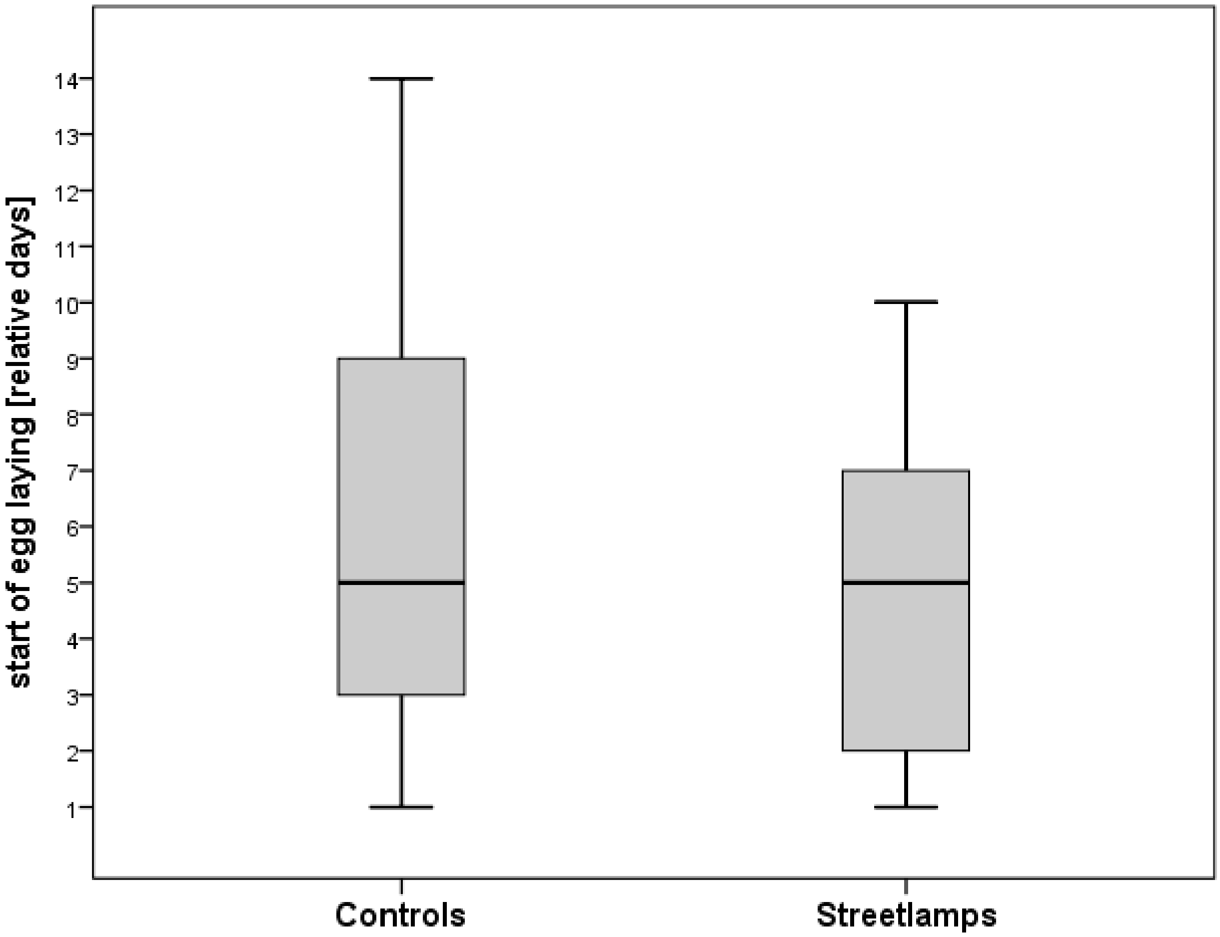

Figure 1: There is no premature egg laying in the streetlamps group (n=16) in comparison to the control group (n=64). Box-whisker-plots depict the interquartile range including median as well as minimum and maximum of all of the data.

However, except for the year 2009, females of the streetlamps group always started laying eggs somewhat earlier than the control group (see fig. 2). The former showed an overall start of laying at day 97.75±2.14 (after Julian calendar), and the latter at day 99.53±1.00.

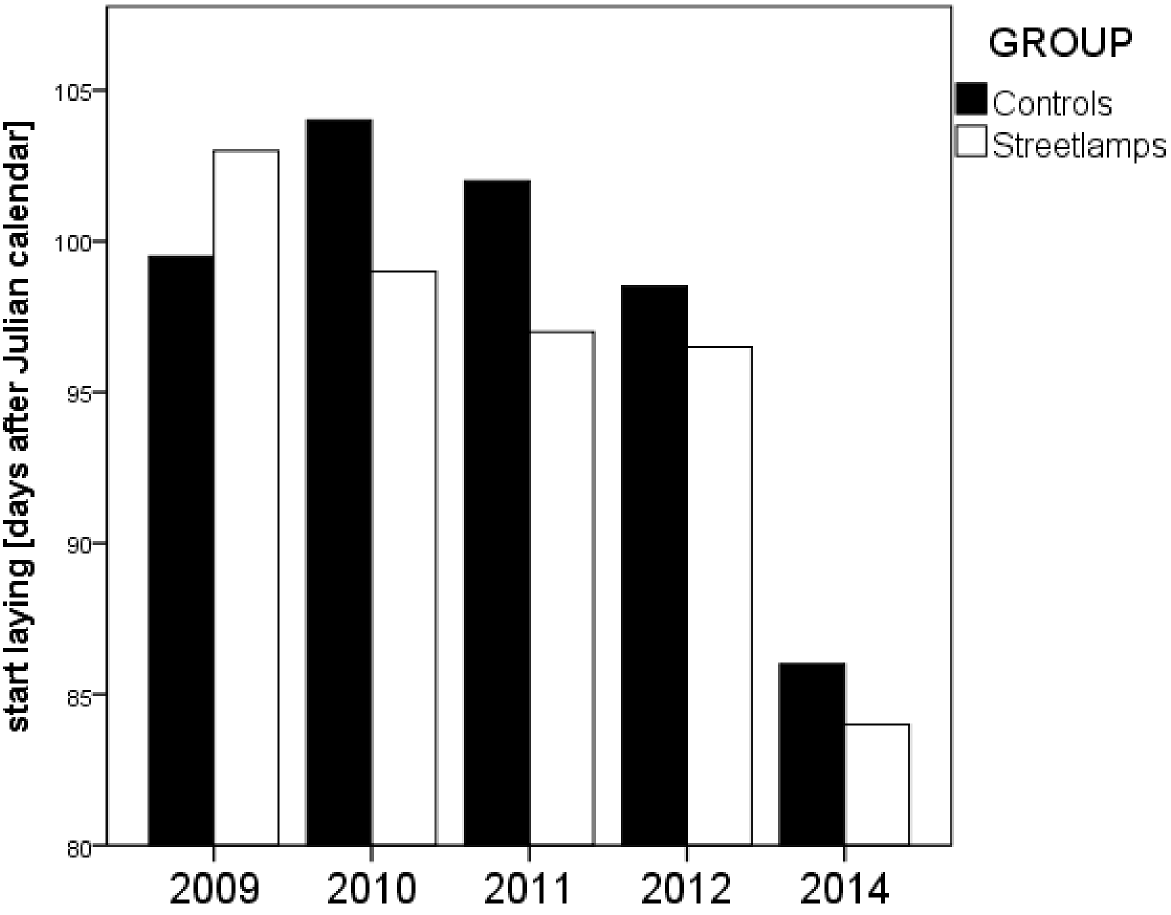

Figure 2: Apart from the pronounced annual variation, this graph demonstrates that in four out of five years females breeding next to streetlamps started laying eggs a little bit earlier than control females. The bars represent median values.

3.1.2 Number of eggs

In contrast to start of egg laying, there were no obvious differences between years concerning clutch size (*H*(5) = 4.631, *p* = 0.463). Also in relation to light conditions, variation in number of eggs did not differ consistently between the groups (*U* = 469.50, *p* = 0.736; *r* = -0.038). On average, females of control pairs (n=62) laid 9.95±0.23 eggs and streetlamp females (n=16) laid 10.31±0.25 eggs.

3.1.3 Number of hatchlings and hatching success

Similarly, the number of hatchlings did not differ between controls and streetlamps group (*U* = 538.00, *p* = 0.945; *r* = -0.007). Averages were almost identical with control pairs (n=68) having 8.99±0.26, and streetlamp pairs (n=16) having 9.00±0.47 hatchlings per nest. Again, years differed significantly from each other (*H*(5) = 14.549, *p* = 0.012).

Also hatching success did not differ between the two groups (*U* = 356.50, *p* = 0.730; *r* = -0.042). In control birds hatching success was on average 89.2±2.0% (n=54) and in streetlamp birds 86.2±4.8% (n=14). Even between years, no differences could be found (*H*(5) = 8.005, *p* = 0.156).

3.1.4 Number of fledglings

The number of fledglings did not vary between control (7.05±0.45, n=56) and streetlamp birds (7.73±0.64, n=11) (*U* = 296.00, *p* = 0.838; *r* = -0.025). Years differed significantly from each other (*H*(5) = 28.195, *p* < 0.001).

3.1.5 Condition

Taking the number of hatchlings per nest and year into account, there was no difference in the condition of nestlings originating from control or streetlamp nest boxes (*F*(1,60) = 1.068, *p* = 0.306; eta^2 = 0.018). Control nestlings had a slightly but not significantly higher condition (average residual body mass: 0.08±0.14, n=50) than streetlamp nestlings (average residual body mass: -0.33±0.26, n=12). Quality (i.e. condition) of adults does not constitute a potential confounding variable because male and female quality was comparable between the two groups (for females: *U* = 34.00, *p* = 0.143; *r* = -0.293; for males: *U* = 29.50, *p* = 0.386; *r* = -0.189).

3.2 Breeding under manipulated light conditions: experimental approach

3.2.1 Number of eggs

Control (n=16) and experimental (n=11) pairs laid on average the same number of eggs (U = 75.00, p = 0.544; r = -0.125), namely 11.56±0.41 or 10.91±0.90 eggs respectively. Clutch size was also not influenced by year (n(2013) = 19, n(2014) = 8; U = 55.50, p = 0.283) or habitat (n(edges) = 10, n(forests) = 17; U= 63.00, p = 0.286).

3.2.2 Hatching success

The same situation was found for hatching success: Controls (n=16) and experimentals (n=10) did not differ in this parameter (U = 72.00, p = 0.698; r = -0.085) as 88.5±3.4% or 86.7±4.8% of eggs per clutch hatched successfully. Again, there was no difference between years (n(2013) = 18, n(2014) = 8; U = 45.50, p = 0.144) or habitats (n(edges) = 9, n(forests) = 17; U = 64.00, p = 0.525).

3.2.3 Condition

However, nestling condition of control and experimental pairs differed significantly from each other (F(1,45) = 4.700, $p < 0.05$; eta^2 = 0.101) (see fig. 3). On average, nestlings raised in a natural environment were in better condition (0.2889±0.1082, n=28 clutches) than nestlings raised under the influence of artificial light (-0.0574±0.1686, n=17 clutches). The mean group difference is 0.3463, which corresponds to 6.03% poorer condition in experimental offspring.

The model also includes the number of hatchlings per nest entered as covariate in order to correct for its influence on condition. To control for differences between years, data were z-standardized for 2013 and 2014. A potential edge effect can be ruled out because the groups were approximately evenly spread across habitat types (n(edge controls) = 14, n(forest controls) = 14; n(edge experimentals) = 8, n(forest experimentals) = 9). Also the quality of adults cannot account for the difference in nestling condition since condition between control and experimental adults did not differ at all (for females: *U* = 17.00, *p* = 0.327; *r* = -0.253; for males: *U* = 37.00, *p* = 0.804; *r* = -0.054).

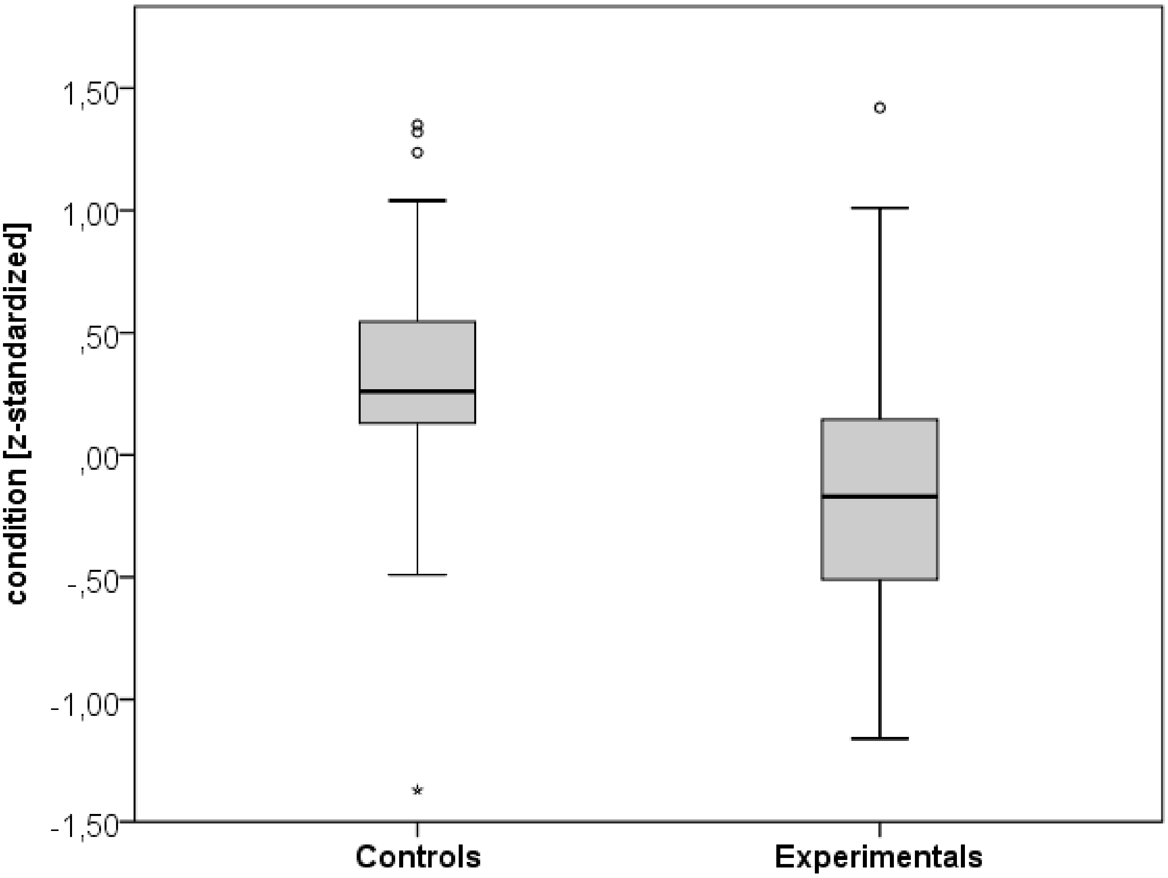

Figure 3: Control and experimental nestlings show a difference in condition of about 6%. Boxes represent the interquartile range including median, whiskers extend to a maximum of 1.5 x IQR beyond the box. Outliers are depicted as circles (if greater than 1.5 x IQR) or asterisks (if greater than 3 x IQR).

3.2.4 Nestling immune response

The immune response in terms of PHA-reaction was affected by the number of nestlings in a clutch as well as by year and habitat, but it was not influenced by exposure to artificial light (see tab. 1, fig. 4).

Table 1: Determinants of PHA-response (n(controls)=18, n(experimentals)=11) (variables entering the final model are in bold).

	df	*F*	*Mean±SE*	*p*	*partial eta²*
treatment (group)	1,29	0.580	1.62±0.092	0.455	0.028
hatchlings per nest		**8.656**	**9.66±0.489**	**0.007**	**0.265**
year		**25.911**		**< 0.001**	**0.519**
habitat		**4.697**		**0.040**	**0.164**

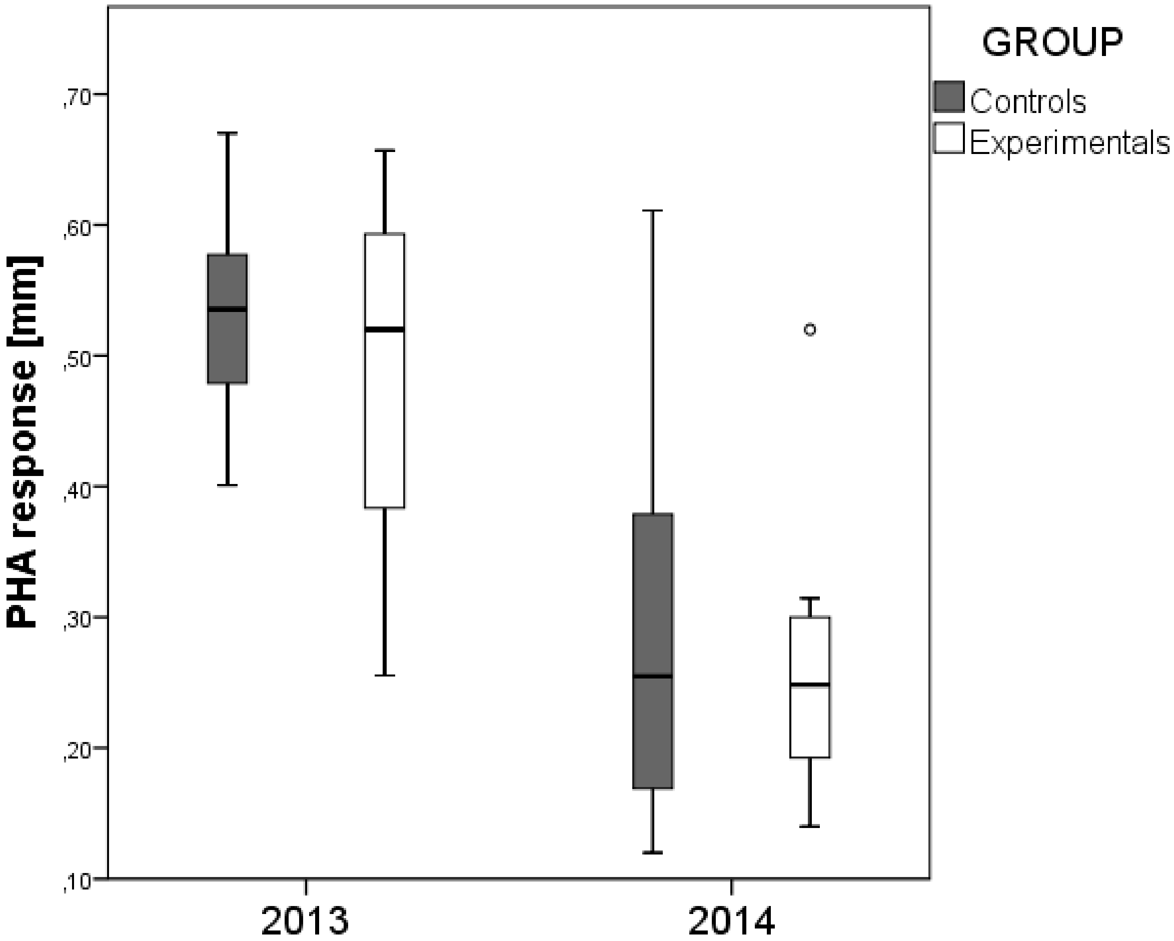

Figure 4: This graph demonstrates how PHA-response differs between the years, but it is not affected by treatment with artificial light. Box-whisker-plots are organized as in figure 3.

4 Discussion

In blue tits, start of egg laying seems to be a sensitive measure influenced by different environmental factors such as weather and fluctuating caterpillar abundance, which have a huge impact on their reproduction timing, reflected in their synchronization between peak of food availability and maximum food demand by offspring (Lambrechts et al. 1997). Therefore we already expected a significant difference in the onset of egg laying between years. In 2014, for instance, birds started to lay eggs earlier than usual in this long-term monitoring population, probably due to the mild winter and/or an extreme gradation of caterpillars. In this context, it is surprising that our data regarding timing of reproduction have not been influenced by artificial light in the natural experiment of streetlamps (see Kempenaers et al. 2010). Though not significant our data at least indicate an effect on start of egg laying. For instance, apart from 2009, in which the first nest boxes for the long-term project were just being installed, the streetlamps group always showed a trend to lay earlier or belong to the "early birds" in comparison to naturally breeding control birds. Furthermore, although Kempenaers et al. (2010) found a significant influence of light, effect size was rather small (1.5 days of an earlier onset of egg laying over a 7 year period). Thus, with a higher sample size our results may have reached statistical significance. Finally, there are a number of additional factors apart from photoperiod that may camouflage the potentially minor role of light for the breeding onset in blue tits, such as ambient temperature, vegetation development and social interactions (Caro et al. 2013). Birds may also rely on these cues for optimally timing reproduction.

Concerning experimental birds, we could not compare laydate in the same way as we did with control and streetlamp birds, because experimental females were exposed to light only in a very late phase of breeding preparations (at the final nest status) when the motivation to lay eggs was already high. In contrast to females breeding under the constant and "freely chosen" influence of light from streetlamps, experimental females were already biased in their decision making from the point in time onwards when we started to manipulate their environment and "forced" them to breed under these conditions. Therefore, we did not make conclusions about their start of egg laying as our focus was on the causal relationship between artificial light and reproductive success. Here we see the potential for future studies to experimentally manipulate females, which are yet unbiased in their decisions, on a long-term basis (i.e. during the whole reproductive cycle).

Regarding parameters of reproductive success such as number of eggs and hatchlings, hatching success and number of fledglings, we did not find a significant influence of artificial light from streetlamps or LED lamps. The experimental study of Titulaer et al. (2012) on great tits showed no effects of light at night on breeding phenology and nestling development as well. They rather propose altered parental feeding behavior, which is also possible in our case but we did not have the capacities to record it. Thus, behavioral observations of adults and their onset of feeding, feeding frequency and quality of food provided would be an interesting addition to future studies. By doing so, we could get a more complete picture of how deep the influence of artificial light runs.

However, for one main developmental nestling parameter, we did find a significant effect: condition was significantly reduced in light-polluted offspring growing under LED lamps. We showed that at least in birds breeding next to streetlamps there seems to be no mismatch between start of egg laying and optimal breeding time with highest amount of food available. The effect can also not be due to changes in clutch size or clutch viability as was explained in the previous paragraph. Finally, female and male quality can be excluded as explaining variables because adults of the two groups were in comparable shape. By eliminating these possibilities, we propose another conceivable factor of influence for impaired nestling condition, namely female behavior: In blue tits, only the female spends the night in the nest box, which is why her presence has an impact on nestling development by heating up the small air volume of the box. The offspring is growing up in a rather dark and protected environment and are more cut off from the external world than is their mother, who frequently comes under the influence of artificial light right in front of her nesting site. It is possible that light-polluted females go to rest later and/or get up earlier. This reduced period of rest does probably not result in a prolonged timespan of nestling provision because the blue tit is a very specialized forager (Föger & Pegoraro 2004) collecting caterpillars high up in the canopy where in the evening it is already, and in the morning it is still too dark to forage efficiently. Thus, the females warm their nestlings less during the night, they cool down and have a higher energy expenditure which could potentially manifest itself in an impaired condition. Nevertheless, we want to underline that this is merely hypothetical and we cannot ground the idea on hard data with statistical analysis whatsoever. We only did some anecdotal testing of this assumption with iButtons (thermologgers recording temperature curves – i.e. the female´s presence or absence – over time), which did not reveal obvious differences between females´ behavior. However, this technique is known to depend on a high number of different factors other than the experimental one, all influencing the resulting temperature curve (time of year, female´s individual daily rhythm, ...). Therefore, for a thorough and statistically relevant testing more data (e.g. including webcams installed within the nest boxes for detailed behavioral analyses) would be necessary to add another valuable piece of information to the mosaic.

Another question arising is why we did not find a difference in body condition between control and streetlamp birds. It has been proposed by others that light-polluted territories around streetlamps could depict artificially constructed niches which can be exploited in a beneficial way by light-polluted parents (Longcore & Rich 2004). These areas are affected by light at night in a less localized or spot-like way as is the case for LED lamps in the dark forest, attracting more prey such as insects and rendering the territory more valuable. Comparable to several urban generalist bird species exploiting an assemblage of trapped insects at a glass building (cf. Robertson et al. 2010), individual blue tits could pursue adaptive settlement strategies and specialize on this new niche. Secondly, blue tit pairs breeding under the influence of streetlamps supposedly lived longer and voluntarily in this condition, so their situation might be different from a forced-upon short-term manipulation as was the case for our experiment.

This demonstrates how ambivalent light pollution can be and that unexpected outcomes are thinkable. Nevertheless, it leaves us with altered predator-prey interactions and competition dynamics on the population level, making the issue more complex than it might seem at first glance. We simply do not know yet, whether a – though only slightly – reduced condition can last into adulthood and create a negative runaway effect accumulating over generations or even lead into an ecological trap as suggested by Titulaer et al. (2012). Therefore, to study the issue comprehensively, as a next step it would be necessary to investigate whether there is really a decreased local recruitment of impaired nestlings into the next breeding generation.

Concerning immunocompetence of nestlings, we could not find a negative influence of light from LED lamps. However, the PHA-challenge is a technique which mainly mimicks acute stressors but light pollution is an environmental stressor of chronic nature. It is possible that the treatment was not long enough to manifest itself in an impaired immune response.

From the sum of these results, we conclude that blue tits are indeed affected by light at night, so we have indication that the problem does translate into the reproductive output of light-polluted parents and might even lead to negative fitness consequences, *but* the effect is minor, almost negligible as some might say. There may be several reasons for this outcome, and especially for this species: Firstly, blue tits are cave-dwelling birds, which could constitute some sort of protection against all-day-all-night light in comparison to birds nesting on the ground or elsewhere unprotected. Additionally, the blue tit is a more or less synanthropic species, thus it might be less affected than other more sensitive and secluded living birds of deep forests. Kempenaers et al. (2010) also found that bird species, which naturally rise earliest, are the most affected by light, e.g. the European robin (*Erithacus rubecula*) is frequently stimulated by light at night to sing nocturnally. Blue tits do not belong to the earliest rising birds but rather to the medial section, rising by dawn under natural conditions. Another point to mention is that blue tits are well urbanized, so they might be very efficient in adapting quickly to new circumstances, even if they are inconvenient. Taken together, these buffers could effectively protect blue tits from being negatively influenced by artificial light all too much. Therefore, it would be of great interest to compare our findings with other less hemerobic, purely forest dwelling or ground nesting birds which are less adaptive. By doing so, we could narrow down the exact impact of artificial light on the breeding biology of more vulnerable species as well. We must not forget that light pollution is subtle and could slowly but steadily undermine the delicate balance of entire ecosystems. To keep potential adverse effects at bay, we have to continue our research effort and deduct strategies of artificial light use which are also compatible with nature.

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Appendix

Zusammenfassung

Erst in den letzten Jahrzehnten hat sich herausgestellt, dass uns künstliche Beleuchtung nicht nur mehr Komfort und Sicherheit beschert, sondern dass es auch eine dunkle Seite des allgegenwärtigen Lichtes gibt – der Begriff der „Lichtverschmutzung“ war geboren. Was die Tierwelt angeht wurde dieses Problem längere Zeit standhaft ignoriert, was verwundert, denn eine industrielle Nutzung derselben ist schon seit dem 19. Jahrhundert etabliert. So kann man etwa Haushühner (*Gallus domesticus*) durch Bestrahlung mit wenigen Minuten künstlichen Lichtes zu erhöhter Eiproduktion stimulieren. Allmählich richtete sich der wissenschaftliche Fokus auf direkte, unmittelbare Auswirkungen wie etwa desorientiere Zugvögel, die mit nächtlich beleuchteten Gebäuden kollidieren oder auch Singvögel, die nächtens unter Straßenlaternen zu singen beginnen. Überhaupt sind Vögel eine besonders stark von Lichtverschmutzung betroffenen Organismengruppe, da ihr Leben oft einer ausgeprägten Rhythmizität bzw. Synchronisierung mit der Außenwelt und dem zeitlichen Jahresverlauf unterworfen ist. Nun wendet sich der Blick also auf die indirekten weniger auffälligen, doch gleich bedeutsamen Auswirkungen, die die Brutbiologie und potentiell künftige Populationen betreffen. Wie schwerwiegend ist der Einfluss von künstlichem Licht und kann man ihn in den Nachkommen tatsächlich nachweisen?

In der vorliegenden Masterarbeit wird diesen, für den Artenschutz bedeutenden Fragen auf den Grund gegangen. Die Studie wurde im Wienerwald an einer mehrjährig bestehenden Nistkastenpopulation von Blaumeisen (*Cyanistes caeruleus*) bei Pressbaum (Niederösterreich) durchgeführt. Es wurden Parameter der Brutphänologie sowie der Fitness zwischen drei verschiedenen Gruppen verglichen: Als „natürlich“ stattfindendes Experiment galten Vögel, die in der unmittelbaren Nähe von Straßenlaternen ihr Brutgeschäft tätigten. Eine weitere Gruppe wurde experimentell mit LED-Lampen bei Dämmerung und im Morgengrauen künstlich beleuchtet, die dritte Gruppe wurde von nicht manipulierten, natürlich brütenden Kontrollvögeln gebildet. Nach meinem Wissensstand ist dies die erste experimentelle Studie, welche gleichzeitig die Effekte von Nachtlicht auf Fortpflanzungsverhalten, Bruterfolg und Qualität der Nachkommenschaft untersuchte.

Künstliches Licht führte weder zu einer verfrühten Eiablage, noch zu einer geringeren Anzahl an Eiern, Schlüpflingen, Ästlingen oder zu reduziertem Schlupferfolg. Auch ein invasiver Test (PHA-Test) zur Ermittlung der indirekten Immunkompetenz der Nestlinge zeigte keine Unterschiede zwischen den Gruppen. Der Entwicklungsparameter „Kondition“ hingegen war bei den Nachkommen der Experimentalgruppe signifikant geringer als bei den Nachkommen der Kontrollgruppe. Zwar ist der Effekt schwach, jedoch beweist es, dass sich Lichtverschmutzung sehr wohl in den Nestlingen und damit dem Bruterfolg manifestieren kann. Inwieweit sich dies dann bei der Eingliederung der Nachkommenschaft in die folgende reproduzierende Generation auswirkt, muss noch genauer erforscht werden. Offensichtlich sind Blaumeisen für Lichtverschmutzung weniger anfällig, und eine Reihe verschiedener Gründe dafür sind möglich: Erstens brütet die Art in Höhlen, was per se als Schutzfaktor vor Licht gesehen werden kann. Außerdem liegt der Aktivitätsbeginn im späteren Morgen, wodurch der Einfluss auch abgeschwächt werden könnte. Blaumeisen zeigen des Weiteren geringe Scheu vor Menschen, sind sehr anpassungsfähig und können durchaus auch im Stadtbereich vorkommen. Diese Faktoren können in ihrer Gesamtheit dazu führen, dass die Art von keinen drastischen Folgen durch Lichtverschmutzung betroffen ist. Nichtsdestotrotz

müssen wir den Gegenbeweis an etwa einer scheuen Waldvogelart erst antreten, um die subtilen weil zeitversetzten Auswirkungen von künstlichem Licht auf Brutverhalten und Reproduktionserfolg gründlich zu untersuchen.

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