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Effects of nocturnal illumination on life-history decisions and fitness in two wild songbird species

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The effects of artificial night lighting on animal behaviour and fitness are largely unknown. Most studies report short-term consequences in locations that are also exposed to other anthropogenic disturbance. We know little about how the effects of nocturnal illumination vary with different light colour compositions. This is increasingly relevant as the use of LED lights becomes more common, and LED light colour composition can be easily adjusted. We experimentally illuminated previously dark natural habitat with white, green and red light, and measured the effects on life-history decisions and fitness in two free-living songbird species, the great tit (*Parus major*) and pied flycatcher (*Ficedula hypoleuca*) in two consecutive years. In 2013, but not in 2014, we found an effect of light treatment on lay date, and of the interaction of treatment and distance to the nearest lamp post on chick mass in great tits but not in pied flycatchers. We did not find an effect in either species of light treatment on breeding densities, clutch size, probability of brood failure, number of fledglings and adult survival. The finding that light colour may have differential effects opens up the possibility to mitigate negative ecological effects of nocturnal illumination by using different light spectra.

1. Introduction

Light pollution has shown a worldwide increase in the past century, especially in the past six decades [1], and artificial lighting of urbanized and rural areas continues to increase. Nineteen per cent of the Earth's surface experiences nocturnal illumination from artificial sources and one-fifth of the world's population lives in areas where the Milky Way cannot be seen with the naked eye [2]. Light pollution is considered a problem for many organisms, including humans; evidence for short-term negative effects of artificial light on several species is accumulating [3]. Modern light-emitting diode (LED) outdoor lighting allows for custom-built spectra, and adaptation of the light spectrum could be one of the options to reduce the effects of night-time light pollution on ecosystems [4].

One reason why light pollution has such a profound effect on organismal function may be that organisms have evolved under a natural light–dark cycle with high levels of light in daytime and very low levels of light at night. In birds, photoperiod is one of the most important factors determining daily activity patterns as well as seasonal timing. Their internal circadian and circannual clocks are entrained by light stimulation of photoreceptors to time physiological activities to the appropriate time of the day and year [5]. Artificial night lighting is hypothesized to affect the perceived photoperiod, and thereby change the natural and temporal behaviour of birds, which in turn might affect their fitness [6].

Research has only recently focused on changing light conditions at night, and the understanding of the ecological consequences of light pollution is still limited. A well-known response of birds is attraction to artificial light, which causes high mortality of seabird fledglings owing to fatal collisions and higher predation [7], and of songbird nocturnal migrants owing to exhaustion at light sources [8]. Other studies on bird populations in the wild have shown that the presence of street lights may cause several species to sing earlier at dawn [9,10] and in the year [11], female blue tits (*Cyanistes caeruleus*) to advance egg laying [12] and female great tits (*Parus major*) to increase chick feeding rates [13]. In an experimental study in a controlled environment, nocturnal illumination advanced the reproductive physiology of blackbirds (*Turdus merula*) on a short-term basis [14], but suppressed reproductive activity in the long run [15]. An experimental study in a wild godwit (*Limosa limosa*) population revealed that early arriving godwits chose nest sites at greater distance from road lighting than late arriving birds [16]. This relatively small set of studies all demonstrate rather short-term effects of light pollution on the behaviour of birds. Experimental studies on the effect of light on life-history traits and fitness components in a field situation with no other anthropogenic disturbance are lacking [17].

The role of spectral composition in the impact of nocturnal illumination on avian behaviour is poorly studied [18], although the omission of specific colours could mitigate possible negative effects [17]. Gonadal growth, a measure of reproductive readiness, is dependent on the wavelength of the light to which birds are exposed; longer wavelengths (red light) advance growth [19]. Nocturnally migrating birds are disoriented by illuminated spots, especially with overcast skies, and removing red light from the spectrum makes this effect less pronounced [20,21]. A possible mechanism is that cryptochrome receptor molecules are dependent on short-wavelength light, which aligns with the wavelength dependency of magnetoreception observed in behavioural tests (the avian radical pair mechanism hypothesis) [22,23].

In order to gain more knowledge on the effects of artificial night lighting on life-history decisions and fitness components of wild individuals of passerine birds, we studied their response to light at night during the breeding season. We make use of a unique, large-scale, experimental set-up in The Netherlands, where we assess the effects of three different colours of street lighting on several species groups [24]. At our eight study sites, previously dark, natural habitat is experimentally illuminated with white, green or red light, in addition to a dark control. As a result of the altered perception of photoperiod owing to the light at night, we expect birds that are breeding in illuminated territories to start laying eggs earlier compared with those in the dark. For light colour, we expect the strongest effect for white light, then red light (which is known to affect the reproductive system [19]), followed by green light. Although light at night may increase male fitness [12], we have no clear expectations for effects towards different colours of nocturnal illumination on fitness components. If light attracts insects at night, resulting in higher insect density in illuminated areas in daytime, the fitness of insectivorous bird species may increase. However, light at night may adversely impact daily rhythms and reproductive physiology, and thereby decrease fitness. The experimental nature of our set-up gives the possibility to test the effects of nocturnal illumination independently of other anthropogenic disturbances normally associated with light at night.

2. Methods

(a) Experimental set-up

At eight sites in The Netherlands [24], we illuminate previously dark natural areas with street lamps (intensity 8.2 ± 0.3 lux, measured directly under the lamp at ground level), from sunset until sunrise. Each site has four transects with five lamp posts with LED lights, each transect with one light colour treatment: Fortimo white, ClearSky green and ClearField red light (Philips, Amsterdam, The Netherlands) and a dark control (poles without lamps). Within each site, each transect was randomly assigned a light treatment. All three lamp types emit full spectrum light; however, green lamps have an increased blue and reduced red, and red lamps have an increased red and reduced blue emission (for details on the spectral power of the light, see Spoelstra *et al*. [24]). The intensity of the light at ground level at all transects is standardized for human vision (in lux), such that the light of the three different colours is perceived by humans as equally intense. The sensitivity spectrum of birds differs from that of humans; most birds perceive colours through four single cone types [25]. The intensities of the treatments are therefore different for birds. The ability of birds to see UV light [26] does not contribute to this difference as the UV emission of our lights is negligible. We chose to standardize the intensity at all transects in lux, because the street lamps we have placed at our study sites are eventually intended for road lighting for human purposes.

Sites consist of coniferous, deciduous or mixed forest edge habitat where four transects, each consisting of five lamp posts, were placed perpendicular to the forest edge in 2012, and at one of the sites in 2013 (figure 1 and [24]). A large variety of species groups are monitored yearly at these sites, see also Spoelstra *et al*. [24]. In order to study the breeding ecology of cavity-breeding passerines, at each site 36 bird nest-boxes (diameter entrance hole 32 mm) were placed in the forest in the year the lamp posts were set up (288 in total). Our sites have few natural cavities. The placement of nest-boxes follows a standardized pattern, in order to test the effects of light on individuals nesting at different distances from the lamp posts (figure 1).

All data were collected during the springs of 2013 and 2014. The nest-boxes were occupied by breeding pairs of four species; great tit, 96 broods in 2013 and 151 broods in 2014, pied flycatcher (*Ficedula hypoleuca*), 47 and 66 broods, respectively, blue tit, nine and 24 broods, and coal tit (*Periparus ater*), three broods in 2013 and one in 2014. Here, we report on the life-history traits and fitness components for the great tit, a small, 18 g resident songbird, and the pied flycatcher, a 12 g trans-Sahara migrant songbird (sample sizes for blue tits and coal tits were too small to conduct meaningful statistical analysis).

(b) Field methods

Nest-boxes were checked twice weekly from the end of March until the end of the breeding season (end of June/early July) in 2013 and 2014. We recorded nest stage, number of eggs and species. In this study, we used data only from first broods for both species; both replacement broods and second broods were excluded. All clutches that started more than 30 days for great tits, or 22 days for pied flycatchers, after the first clutch in that site and year were considered to be replacement clutches. First egg laying dates were calculated on the assumption that one egg is laid per day. The number of eggs after clutch completion (clutch size) and exact egg hatching dates were recorded. During the nestling
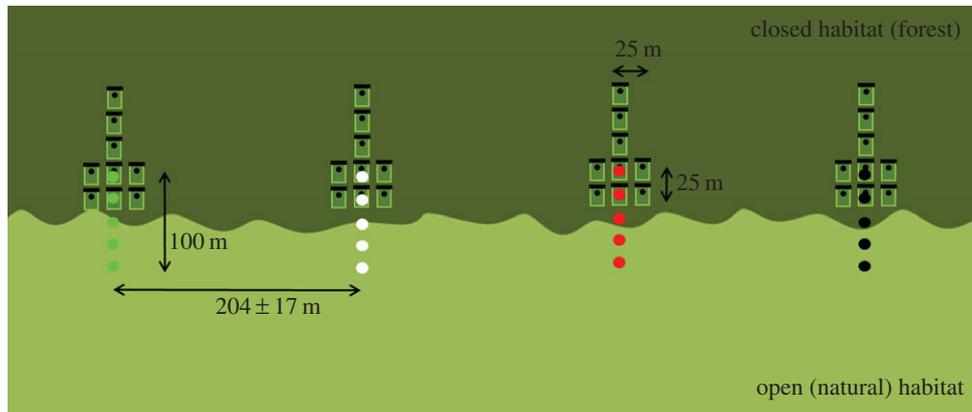
Downloaded from http://rstb.royalsocietypublishing.org/ on March 16, 2015

closed habitat (forest)
25 m
25 m
100 m
204 ± 17 m
open (natural) habitat

Figure 1. Schematic overview of the set-up of one study site, which is replicated eight times. Five lamp posts are placed in transects perpendicular to the forest edge. Within a site, orientation of transects is constant. Distance between transects is variable and depends on the local situation. Each transect was randomly assigned to one of the four light treatments, here green, white, red and dark, respectively. In each transect, nine nest-boxes were attached to trees at 1.6 m height and at approximately 25 m distance from each other (dependent on the nearest tree). Orientation of the nest-box opening was always towards the forest edge.

stage, chicks were ringed with a numbered aluminium ring (8 days after hatching in great tits, 6 days after hatching in pied flycatchers). The mass of the chicks, a measure of fledgling quality [27], was recorded using a digital scale (nearest 0.1 g, 15 and 13 days after hatching in great tits and pied flycatchers, respectively). Adults were caught in the nest-box using a spring trap and ringed with a numbered aluminium ring (great tits: 8–9 days (2013) and 10–12 days (2014) after hatching; pied flycatchers: 6–7 days (2013) and 9–11 days (2014) after chick hatching). Nests were checked after the chicks fledged, and the number of fledglings is the number of chicks that left the nest.

(c) Statistical methods

In all models, we fitted the interaction between light treatment (a factor with four levels: dark, green, red and white) with the distance of the nest-box to the nearest lamp post, because we expected the effect of light to decrease with light intensity (see electronic supplementary material, figure S1 for the relation between light intensity at nest-box level and distance to the nearest lamp post). We also included site (a factor with seven levels in 2013 and eight in 2014) as a random effect to account for between-site differences. Additionally, in the models for fledgling mass, we added brood size (the number of chicks that hatched) as an explanatory variable and nest-box as a second random effect, to account for common environment effects of chicks raised in the same brood. Sex was used as explanatory variable in the models for adult survival. We analysed the data for both species and both years separately.

Data on settlement of the breeding pairs were analysed using a generalized linear-mixed-effects model (GLMM) with binomial error structure and occupancy of the nest-box (0, not occupied; 1, occupied) as response variable. Egg laying dates (first egg; in April date, May 1 = April 31) and clutch sizes (number of eggs) were analysed using linear-mixed-effects models (LMMs). Fledging success was computed in two steps as the distribution of the number of fledged chicks for the great tits was strongly zero-inflated. First, we analysed the probability of brood failure (0, at least one chick fledged; 1, no chicks fledged) in a GLMM with binomial errors. Second, we analysed the number of chicks fledged excluding brood failures in an LMM, following Reed *et al.* [28]. Pied flycatchers had very few nests that failed (10 of 108); therefore we analysed only the number of chicks that fledged excluding brood failures (LMM). Fledgling mass was analysed using an LMM and adult survival using a GLMM with binomial errors (0, found breeding in 2013, but not in 2014; 1, found breeding in 2013 and 2014). All statistical analyses were done using R v. 3.1.1 [29] with a significance level of $\alpha = 0.05$.

3. Results

Our light treatment had no effect on the probability of nest-box occupancy by great tits or pied flycatchers. In great tits, nest-boxes closer to the lamp posts were occupied less often in both 2013 and 2014; this effect was the same in the dark control transects (table 1).

In 2013, there was a significant effect of light treatment on laying date of great tits: birds in green and white illuminated transects laid their eggs on average earlier than those in the dark control (figure 2*a* and table 1). In 2014, however, there was no effect of light treatment on laying date. In pied flycatchers, we found no effect of light treatment on lay date in either year (figure 2*b* and table 1). Clutch size in both great tits and pied flycatchers was not affected by light treatment, but in 2013, great tits laid larger clutches further away from the poles, independent of treatment (table 1).

Light treatment did not affect the probability of brood failure (no chicks fledged) or the number of chicks fledged (if at least one chick fledged) in great tits in either year (figure 3*a* and table 1). In 2014, great tits breeding further away from the poles fledged fewer offspring, again independent of treatment. In the pied flycatcher, the number of chicks fledged was also not affected by light treatment (figure 3*b* and table 1).

In 2013, but not in 2014, fledgling mass in great tit broods was explained by the interaction between treatment and distance to the nearest lamp post, in combination with brood size (see table 1 for estimates). For pied flycatchers, there was no treatment effect on fledgling mass in either year (table 1).

The probability of survival from breeding season 2013 to breeding season 2014 did not differ between light treatments in both great tits and pied flycatchers (table 1). Some of the surviving females and males moved from one light treatment to another between years, but without any clear pattern (out of 18 surviving female great tits eight moved; out of 12 surviving great tit males one moved; out of six surviving female pied flycatchers one moved; out of 12 surviving male pied flycatchers eight moved).

Table 1. Results of the generalized linear-mixed-effects models (GLMM) and linear-mixed-effects models (LMM) on seven response variables, for great tits and pied flycatchers, in 2013 and 2014. For each term, the numerator and denominator degrees of freedom (d.f.), the F-test statistic (F) and the significance level (p) are given.

	great tit						pied flycatcher					
	2013			**2014**			**2013**			**2014**		
	d.f.	F	p^a	d.f.	F	p^a	d.f.	F	p^a	d.f.	F	p^a
occupancy												
GLMM (random: site)	($n = 252$)			($n = 288$)			($n = 252$)			($n = 288$)		
treatment	[b]		0.61	[b]		0.98	[b]		0.90	[b]		1.00
distance to lamp post			*0.02 (0.02)*			*0.02 (0.02)*			0.94			0.47
treatment : distance to lamp post			0.17			0.32			0.91			0.80
lay date												
LMM (random: site)	($n = 75$)			($n = 111$)			($n = 45$)			($n = 63$)		
treatment	3, 68.04	2.84	*0.04*[c]	3, 103.95	0.17	0.92	3, 37.52	1.10	0.36	3, 55.14	0.36	0.79
distance to lamp post	1, 69.81	0.34	0.56	1, 105.47	1.56	0.22	1, 39.92	0.01	0.94	1, 59.43	0.31	0.58
treatment : distance to lamp post	3, 63.81	0.46	0.71	3, 100.42	0.40	0.75	3, 35.36	0.73	0.54	3, 53.87	0.08	0.97
clutch size												
LMM (random: site)	($n = 66$)			($n = 104$)			($n = 44$)			($n = 63$)		
treatment	3, 59.39	0.37	0.77	3, 96.13	0.44	0.72	3, 41.90	0.14	0.71	3, 56.01	1.20	0.32
distance to lamp post	1, 63.44	4.32	*0.04 (0.02)*	1, 97.32	0.06	0.83	1, 38.94	0.05	0.82	1, 56.64	0.03	0.86
treatment : distance to lamp post	3, 54.86	1.31	0.28	3, 91.45	0.30	0.83	3, 34.25	0.43	0.74	3, 53.87	0.81	0.50
probability of brood failure												
GLMM (random: site)	($n = 75$)			($n = 111$)								
treatment	[b]		0.71	[b]		0.71	[d]			[d]		
distance to lamp post			0.53			0.45						
treatment : distance to lamp post			0.07			0.42						
no. fledglings (if ≥ 1)												
LMM (random: site)	($n = 41$)			($n = 84$)			($n = 39$)			($n = 59$)		
treatment	3, 35.59	0.97	0.42	3, 73.60	0.71	0.55	3, 30.92	2.03	0.13	3, 52.55	0.20	0.89
distance to lamp post	1, 33.70	0.02	0.89	1, 79.13	4.16	*0.04 (-0.01)*	1, 31.16	0.07	0.79	1, 53.88	0.00	0.96
treatment : distance to lamp post	3, 32.03	0.45	0.72	3, 70.05	1.11	0.35	3, 27.74	0.72	0.55	3, 49.67	2.10	0.11

(Continued.)

Table 1. (*Continued.*)

	great tit						pied flycatcher					
	2013			**2014**			**2013**			**2014**		
	d.f.	*F*	*p*[a]	d.f.	*F*	*p*[a]	d.f.	*F*	*p*[a]	d.f.	*F*	*p*[a]
chick mass												
LMM (random: site and nest-box)	(*n* = 214)			(*n* = 535)			(*n* = 199)			(*n* = 281)		
treatment	[e]			3, 72.30	0.09	0.97	3, 29.97	1.33	0.28	3, 46.98	0.65	0.59
distance to lamp post				1, 79.35	0.01	0.93	1, 28.75	0.27	0.61	1, 49.26	0.08	0.78
brood size	1, 32.64	21.57	*<0.001 (-0.55)*	1, 86.46	0.76	0.38	1, 31.64	4.11	0.05	1, 53.07	0.36	0.55
treatment : distance to lamp post	3, 29.79	3.28	*0.03*[f]	3, 69.96	0.43	0.73	3, 24.40	0.29	0.83	3, 44.13	1.00	0.40
adult survival												
GLMM (random: site)	(*n* = 99)						(*n* = 80)					
treatment	[b]		0.27	[g]			[b]		0.90	[g]		
distance to lamp post			0.67						0.38			
sex			0.28						0.18			
treatment : distance to lamp post			0.27						0.36			

[a]*p*-values are in italics when considered significant (<0.05). For the significant terms the estimate is given behind the *p*-value, between brackets.

[b]For comparisons of LMM an *F*-test was calculated according to the approach of Kenward and Roger, GLMM were compared using parametric bootstrap methods where a number of simulations of the Likelihood Ratio Test statistic are generated [30]. Therefore, no degrees of freedom or *F*-test statistic are given for the GLMM.

[c]Estimates for lay date for each treatment: dark 33.3, green 29.0, red 33.2 and white 29.5.

[d]Pied flycatchers had very few nests that failed; therefore we only analysed the number of chicks that fledged excluding brood failures.

[e]Because we found a significant interaction effect of treatment by distance to the nearest lamp post on mass of great tit chicks in 2013, we did not calculate *p*-values for the individual fixed effects.

[f]Estimates for chick mass for each treatment: in dark chick mass = $21.0 - 0.022 \times$ distance, in green $18.6 - 0.004 \times$ distance, in red $18.1 + 0.024$ and in white $16.6 + 0.056 \times$ distance.

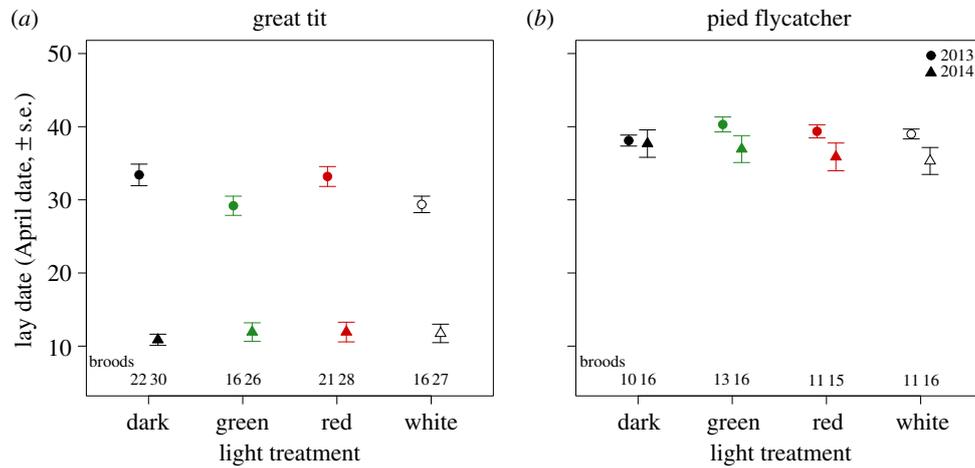[g]Adult survival to the next breeding season could only be calculated for birds breeding in 2013.

Figure 2. Average first egg laying dates (April date) for each light treatment for great tits (*a*) and pied flycatchers (*b*) (see also table 1). Circles are 2013, triangles are 2014 data and error bars show $\pm$ 1 s.e. Sample sizes (number of broods) are indicated above the *x*-axis for each treatment in each year (2013, 2014). Average first egg laying date in 2013 was 31.6 for great tits and 39.3 for pied flycatchers, and in 2014, 11.6 and 36.5, respectively.
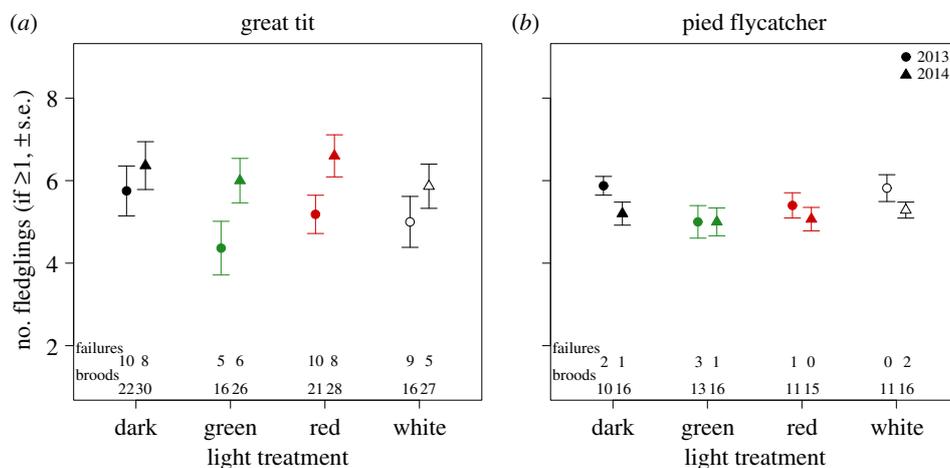

Figure 3. Average number of fledglings of broods that fledged at least one chick, for each light treatment for great tits (*a*) and pied flycatchers (*b*) (see also table 1). Circles are 2013, triangles are 2014 data and error bars show $\pm$ 1 s.e. Number of failed broods (zero fledglings, failures) and sample sizes (number of broods) are indicated above the *x*-axis for each treatment in each year (2013, 2014).

4. Discussion

We assessed the effects of light at night with different spectral composition on the breeding biology and fitness components of two wild songbird species. The effect of light treatment on timing of egg laying, one of the life-history traits, was not consistent across species and years. Fledgling production, an important component of fitness, was not affected by light at night in both species; fledgling mass was, but only for one species in 1 year. Thus, we did not show clear, unidirectional effects of experimental nocturnal illumination on fitness.

Settlement of our birds at the study sites was not affected by light treatment, but occupancy rates for great tits were higher further away from the lamp posts, also in the control treatment. Owing to the spatial pattern of our nest-boxes, the density of nest-boxes decreases with increasing distance to the lamps. Great tits usually defend territories larger than 25 m radius (the distance between our nest-boxes) during the breeding season [31], and thus each territory will contain more than one nest-box, leading to the observed pattern of increased occupancy rates further away from the lamp posts at all four treatment groups. In contrast, pied flycatchers defend just the area directly around their nest-box [32], which may explain the absence of an effect of distance on occupancy rate observed

in this species. We found no effect of artificial light at night on clutch size in either species.

Our findings on seasonal timing of great tits in 2013 are in line with the advancement in lay date of blue tits in illuminated territories reported by Kempenaers *et al.* [12]. However, the effect of artificial light on lay date was not consistent in our study. One key difference between the study by Kempenaers *et al.* and ours is that our study is experimental and thus treatments differ only in the level of light at night, whereas in Kempenaers *et al.*, differences in light levels may be correlated with other anthropogenic factors (e.g. lighted territories were also closer to human habitation).

Day length is a strong cue in timing of the start of egg laying [33] and light at night could lead to birds perceiving a longer photoperiod. In 2013, light treatment had a significant effect on the start of breeding of great tits. In 2014, when spring was warmer and birds laid much earlier, there was no effect of light at night. An explanation for this difference could be that in cold years with a late season, such as 2013, photoperiod may play a more pronounced role in the onset of egg laying than in warm years with an early season [34], such that artificial night lighting would only affect laying date in the former. Obviously, 2013 and 2014 differed in more than just their

mean spring temperature, but it is well known that temperature and photoperiod are the most important environmental variables affecting lay date. We could not identify clear differences between individual light colours, but the overall effect of light treatment may be mainly caused by the advancement of lay date in white and green light. If this is indeed the case, this effect is contradictory to our expectation that red but not green light advances breeding. However, the effects of red light [19] were reported for gonadal growth, whereas the timing of actual egg laying may be affected in a different way. Data from more years are needed to reveal an interactive effect of light at night and spring temperatures. Laying date of pied flycatchers was not affected by nocturnal illumination, which may be related to their timing of migration; they arrive at their breeding grounds a few days before the first eggs are laid, and so exposure to the light at night might not be long enough to affect timing of egg laying. In addition, different spectra may have differential effects on different species because of species specific spectral sensitivity [35].

Artificial night lighting did not significantly affect reproductive success in either species. In pied flycatchers, fledgling mass was not affected by artificial light at night; however, in great tits chick mass depended on treatment in relation to distance to lamp posts in 2013, but not in 2014. There are thus no strong indications that fledgling production or fledgling quality is affected by artificial night lighting. Nocturnal illumination did not influence the survival rates from breeding season 2013 to 2014 in either species, but the amount of data on adult survival is limited.

Fitness effects of nocturnal illumination in birds have, as far as we know, never been studied experimentally in the field. We present the first results on this here, which suggest that the effects of artificial night lighting on breeding success are absent or small. This study is one of the first to document no, or very little, effect of artificial light at night on individual organisms (see Gaston *et al.* [36]). Although we have data from 288 nest-boxes over 2 years, the dataset we present is still relatively small, so that only relatively strong effects would have been detected. Clearly, more data are needed to draw conclusions on fitness effects and ultimately contribute to evidence-based advice on nature friendly outdoor lighting.

Our study is experimental in the sense that we started illuminating a formerly dark forest and kept part of it dark. We placed the same number of nest-boxes in all transects using the same pattern. However, it was not possible to control for settlement differences, because individual birds were free to choose whether or not to start breeding near the lamp posts. This choice opens the possibility that a non-random selection of the population breeds in nest-boxes under light at night. However, we did show that the breeding density of birds did not differ between light treatments, and birds that survived from 2013 to 2014 did not move to a particular light colour or away from the illuminated area to the dark control.

Because the light intensity quickly decreases with increasing distance from the lamp posts, there are ample dark places relatively close to our nest-boxes. The nest-boxes furthest away from the lamps are not different from those in the dark transects in terms of light intensity. Birds breeding in the illuminated nest-boxes thus have the opportunity to escape the direct effect of light by moving away from it or by being inside the nest-box. This behavioural modulation could also explain the absence of strong effects on breeding success. We are currently doing measurements to determine

how much light adult birds actually perceive at our experimental field sites. Chicks in nest-boxes receive very low light levels (typically below 0.05 lux), even if these boxes are directly under the lamps. We want to stress, however, that the light levels used in our set-up are representative for outdoor lighting of, for example, roads.

Apart from direct effects of nocturnal illumination, for instance changing the perception of day length which relates to seasonal timing, there can also be indirect effects. Nocturnal illumination can, for example, affect insect abundance [37] which is the major food source for our birds during the breeding season. In our experimental set-up, it is not possible to separate these direct from indirect effects, and additional experiments in a controlled environment are necessary to identify causal relationships.

In this study, we show that experimental nocturnal artificial light in the field can affect timing of egg laying and fledgling mass, a predictor of recruitment, but only in one species and in 1 year. For most life-history variables and fitness components, we found no effects. Given the widespread use of artificial light at night, many breeding birds are exposed to light levels similar to those in our study. The non-consistent effects that we found indicate the need for long-term studies. Furthermore, if the magnitude and direction of possible effects depend on the spectral composition of the light, that could open up the possibility to mitigate specific ecological consequences with the use of coloured nocturnal illumination.

Light pollution is considered a global biodiversity threat [1]. Evidence of a wide variety of effects on behaviour of birds is accumulating, but many important questions remain to be answered: does light at night matter on a larger scale, are terrestrial breeding bird populations doing poorly in areas with more night-time illumination? The experimental design described here creates the opportunity to answer these questions; to do so we will continue to record data on nest-box breeding birds as well as all other birds present at our sites (as described in Spoelstra *et al.* [24]) during the coming years.

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