Effects of experimental night lighting on the daily timing of winter foraging in common European songbirds

Arnaud Da Silva, David Diez-Méndez and Bart Kempenaers

A. Da Silva (http://orcid.org/0000-0001-6035-2428) (arnaud.dasilva@cent.uw.edu.pl) and B. Kempenaers, Max Planck Inst. for Ornithology, Dept of Behavioural Ecology and Evolutionary Genetics, Seewiesen, Germany. Present address of ADS: Univ. of Warsaw, Centre of New Technologies, Wild Urban Evolution and Ecology Lab, Warsaw, Poland. – D. Diez-Méndez, National Museum of Natural Sciences, Dept of Evolutionary Ecology, Madrid, Spain.

The ecological effects of light pollution are becoming better understood, especially in birds. Recent studies have shown that several bird species can use street lighting to extend activity into the night during the breeding season. However, most of these studies are correlational and little is known about the effects of artificial night lighting on the timing of activities outside the breeding season. During winter, low temperatures and short days may limit foraging opportunities and can negatively affect survival of resident birds. However, night lighting may allow them to expand the time niche available for foraging. Here, we report on a study where we repeatedly manipulated the amount of night lighting during early winter at automated feeding stations in a natural forest. We used video-recordings at the feeders to determine the time of the first (at dawn) and last (at dusk) foraging visits for six songbird species. We predicted that all species, and in particular the naturally early-foraging species, would advance their daily onset of foraging during the mornings with night lighting, but would show minimal or no delays in their daily cessation of foraging during the lighted evenings. We found that two early-foraging species, the blue tit and the great tit, started foraging earlier during the experimentally lighted mornings. However, in great tits, this effect was weak and restricted to nights with inclement weather. The light treatment did not have any effect on the start of foraging in the willow/marsh tit, the nuthatch, the European jay, and the blackbird. Artificial night lighting did not cause later foraging at dusk in any of the six species. Overall, our results suggest that artificial light during winter has only small effects on timing of foraging. We discuss these findings and the importance of temperature and winter weather in shaping the observed foraging patterns.

Urbanisation is increasing at an unprecedented pace. Nowadays, more than half of the human worldwide population lives in cities and the global land area is expected to triple from 2000 to 2030 (Grimm et al. 2008, Seto et al. 2012). The impact of urbanisation on ecosystems and wildlife has sparked the interest of the scientific community over the last decades (Klausnitzer 1993, Sukopp 1998, Lepczyk and Warren 2012, Marzluff et al. 2012, Gil and Brumm 2013). On one hand, urbanisation poses important challenges to organisms, through the degradation and loss of natural habitats, and through anthropogenic nuisances such as chemical or noise pollution. On the other hand, cities offer shelter to many animals, birds in particular (Luniak 2004, Gaston et al. 2005), which probably benefit from higher temperatures (‘urban heat island’; Oke 1973), and from additional food dispensed at garden feeders (Amrhein 2014). The increasing rate of urbanisation goes hand in hand with the growing use of artificial night lighting (Hölker et al. 2010a), but the extent to which light pollution impacts birds remains unclear. Millions of nocturnally migrating birds flying over cities or illuminated shores are attracted by brightly-lit buildings and die from collision or exhaustion (Poot et al. 2008, Hölker et al. 2010b). However, more subtle effects of artificial night lighting on timing of singing (Miller 2006, Kempenaers et al. 2010, Nordt and Klenke 2013, Da Silva et al. 2014, 2015, 2016) or reproduction (Kempenaers et al. 2010, Dominoni et al. 2013) have been shown, although it remains unclear how they influence survival and reproductive success (Kempenaers et al. 2010, de Jong et al. 2015).

The impact of light pollution on the timing of maintenance behaviour has been studied even less, even though behaviours such as foraging are crucial for survival. Anecdotal reports of diurnal birds feeding close to artificial light sources at unusual times of the night are numerous and concern various taxa (King 1966, Felton 1969, Blackett 1970, Brooke 1973, Bakken and Bakken 1977, Lebbin et al. 2007, Pugh and Pawson 2016), but more systematic studies of this behaviour are scarce. During the breeding season, common blackbirds Turdus merula and northern mockingbirds Mimus...
polygлотtoс have been shown to prolong foraging and chick provisioning (respectively) shortly after dusk in areas with artificial night lighting (Stacey et al. 2014, Russ et al. 2015). Also, a field experiment in which the outside of nest boxes was illuminated, showed that female great tits Parus major increased chick provisioning rate, but only during the second half of the nesting period, and without effects on the onset or cessation of provisioning (Titulaer et al. 2012). During winter, common redshanks Tringa totanus spent a greater proportion of time foraging at night in artificially-lit estuaries (Dwyer et al. 2012). Finally, in Norway, several resident species of diurnal songbirds were observed foraging several hours before sunrise throughout the winter, possibly using street lights (Byrkjedal et al. 2012). Most of these studies were correlational, i.e. other factors such as food abundance and temperature may have affected the results. Nevertheless, altogether, they suggest that light pollution can potentially alter temporal patterns of foraging, especially during winter.

Harsh winter conditions reduce the survival prospects of birds, due to increased overnight weight loss and unpredictable foraging success during the day (Haftorn 1989, Cresswell 1998, Thomas and Cuthill 2002). Birds show adaptations to these conditions, including a peak in body mass in mid-winter (Lehikoinen 1987, Haftorn 1989, Cresswell 1998, Gosler 2002, Chamberlain et al. 2005, MacLeod et al. 2005a, b), as well as altered foraging rhythms. During winter, songbirds generally delay roosting (Steinmeyer et al. 2010, Stuber et al. 2015), and increase foraging effort throughout the morning (Bednekoff and Houston 1994, Cresswell 1998, MacLeod et al. 2005a), as predicted by models of optimal foraging (McNamara and Houston 1990, McNamara et al. 1994). Artificial night lighting may therefore offer a great opportunity for wintering birds to extend their foraging period into the night, and thereby increase food intake. This may be particularly true in urban habitats, where food is predictably dispensed at garden feeders and where competition for feeding can be high.

The use of feeders in cities generally allows birds to accumulate enough fat to survive overnight (Grubb Jr and Cimprich 1990). By increasing feeder visitation during mid-winter (Chamberlain et al. 2005), birds can improve survival (Egan andBrittingham 1994, but see Becker et al. (2015) for increased pathogen transmission), with possible positive (Robb et al. 2008) or negative (Harrison et al. 2010, Plummer et al. 2013) carry-over effects into the next breeding season. During winter, birds visiting feeders build up reserves later in the morning, and feed at a more constant rate throughout the day than unsupplemented birds (Koivula et al. 2002, Lillienahl 2002, Bonter et al. 2013), in line with risk-spreading models (Houston et al. 1993). Moreover, birds start visiting feeding stations later in the morning in urban areas than in rural areas (Ockendon et al. 2009a), probably due to the higher temperatures and the reliable presence of sufficient food in the city. However, urban birds also start foraging later in the morning at garden feeders in areas with more artificial lights (Clewley et al. 2015), which seems counterintuitive considering the effects of light pollution on daily rhythms previously described. This result may again be explained by other factors that covary with light intensity, e.g. consistent higher food availability or higher perceived predation risks in lighted urban areas.

Here, we report on a study that aimed to experimentally test whether artificial night lighting causes diurnal songbirds to extend foraging into the night during winter, while excluding the confounding effects of other anthropogenic disturbances. Each day, during early winter, we provided free-living forest birds with food at automated feeding stations around dawn and dusk, and we repeatedly exposed the feeder area to experimental night lighting for a few days at a time. Based on video-recordings at each feeder, we determined the daily onset of foraging relative to sunrise and the daily cessation of foraging relative to sunset for the six songbird species that most often visited the feeders. We expected experimental night lighting to 1) advance the onset of foraging at dusk but not (or to a lesser extent) delay cessation of foraging at dusk, because most species naturally start searching for food and gaining mass before sunrise but do not continue after sunset (Lima 1988, Macleod et al. 2005a, Bonter et al. 2013). We further predicted that the experiment would alter the daily timing of foraging more strongly 2) in the more light-sensitive birds, i.e. those which generally forage at relatively low natural light levels (Thomas et al. 2002, Ockendon et al. 2009a, b, Clewley et al. 2015), 3) during periods with lower temperatures or with otherwise inclement weather during the night (Gosler 1996, 2002, Chamberlain et al. 2005, Macleod et al. 2005a, Hatchwell et al. 2009, Clewley et al. 2015) and 4) during the first half of the experimental period, i.e. when days were shortest. The latter follows from the extended feeding times found in tits during the shortest winter days at lower latitudes (Haftorn 1989, Steinmeyer et al. 2010, Stuber et al. 2015), and the strong effects of street lighting on timing of foraging during the long winter nights at higher latitudes (Byrkjedal et al. 2012). Lastly, irrespective of the light treatment, we also expected 5) that low temperatures and inclement weather would advance onset of foraging and delay its cessation due to increased overnight weight loss (Gosler 2002, Thomas and Cuthill 2002).

Methods

Experimental design

The experiment was conducted in 2015 in a woodland area with minimal light pollution in Seewiesen (southern Germany). In December 2014, we selected four sites (site 1: coordinates 47.96928°N, 11.2357°E; site 2: 47.9708°N, 11.2385°E; site 3: 47.97235°N, 11.2363°E; site 4: 47.9730°N, 11.2325°E) which were edges of coniferous forest, mixed with shrubs and deciduous trees (mainly European beech Fagus sylvatica). Adjacent sites were on average 180 m apart. The four sites were exposed to similar levels of noise pollution (although one site was exposed to more people passing by) and had comparable temperatures both at sunrise (ANOVA, F3,135 = 0.3, p = 0.9) and at sunset (F3,135 = 0.6, p = 0.6).

Figure 1 shows a schematic overview of the experimental setup (see Supplementary material Appendix 1 Fig. A1 for photos). At each site, we placed a single handmade, wooden feeder, consisting of a 50 × 50 cm feeding platform standing 1 m above the ground, and protected by a 72 × 72 cm roof
board 22.5 cm above the platform. The feeding platform included a food chamber (11 × 7.5 cm, height = 2.5 cm), topped with a shutter which could be opened and closed automatically via a digital time switch (EG103, EG103B, Hager, Germany). The switch was placed underneath the feeding platform and activated a small infrared-sensitive, full HD video camera (Mini 0801 Car DVR HD1080P, www.combi.org.uk/products). The camera was kept in a waterproof box fixed underneath the protective roof board. One infrared-emitting LED light was placed on the opposite end of the camera to film in dark conditions. The field of view of the camera was covering most of the feeding platform and the food chamber, as well as the vegetation around the feeder.

At each site, we also placed five mobile halogen spotlights (TL800A, Elro, EU; Da Silva et al. 2016), equidistant (∼ 5 m) around the feeder. Each spotlight consisted of two bulbs, which provided a broad light spectrum (500 W white warm light) at a high intensity (100 kilolux at the bulb). One lamp was indirectly illuminating the area of the feeder, whereas the other lamps were pointed upwards and illuminated the lower and upper strata of the surrounding forest. The height of the lamps (1–2 m above the ground) was adjusted to obtain the best illumination of the surroundings. Light intensities were high within an area of roughly 0.1 ha around the feeders (average ambient light intensity: 4 lux; recorded with a 400 000 Light Lux Meter DT 1308, ATP Instrumentation, Ashby-de-la-Zouch, UK, held horizontally 2 m above the ground, 5 m away from the nearest light bulb). All electronic equipment was powered via an electric box located outside each site.

Experimental procedure

The experiment started on the evening of 5 January and continued until the morning of 10 February; it consisted of six cycles of a lighted phase (3 nights with the lights manually turned on from an hour before sunset until an hour after sunrise), followed by a dark control phase (3 nights with the lights turned off). This is typically the coldest period of the year at intermediate latitudes (Gosler 2002, Luterbacher et al. 2004), with a relatively small increase in day length (across the experimental period sunrise became 35 min earlier, and sunset 51 min later). To control for potentially confounding effects of season and weather, we arranged the order of the treatments such that when sites 1 and 3 were lighted, sites 2 and 4 were kept dark (and vice versa). To check that the lighting worked we placed a HOBO® temperature/light sensor (Onset, Bourne, MA, USA) a few decimetres in front of one of the ten bulbs at each site and recorded light intensity every minute. Another HOBO sensor was placed on a branch outside the lighted area at each site and recorded air temperature every minute.

Food chambers and video cameras were preprogrammed to dispense food and to record from 3 h before to 1 h after sunrise and from 1 h before to 2 h after sunset. By limiting food access, we created a predictable but brief daily food supply, driving birds to prioritise the dawn and dusk periods to visit the feeders. We habituated birds to the equipment and to the schedule by putting out the feeders with dummy cameras at each site one month before the start of the experiment. We provided food ad libitum throughout the first ten days, and then, we gradually limited food access during the day, until it eventually matched the experimental schedule on 5 January. Food consisted of a mixture of oatmeal, raisins, animal fat, and peanuts (<www.welzhofer.eu/>, and was replaced every day.

Data extraction

Each day, after the morning recordings, we collected and merged the 1 min-long video clips saved onto the memory card of each camera. Next, two of us extracted the data manually using VLC media player 1.1.5. This could not be done blind to the treatment, simply because the experimental lights were visible in the videos. On each day and for each site, we scored the time of the first (at dawn) and last (at dusk) foraging event (in absolute local time, later converted in minutes relative to local sunrise/sunset), for every species recorded on the feeding platform. A bird was considered foraging whenever it was filmed grabbing a piece of food in its beak. We excluded non-foraging events such as birds perching on the feeder and preening, or being involved in aggressive interactions, but these were rare
relative to foraging events. We limited data analysis to the six passerine species most commonly observed at the feeders, i.e. the great tit (N_{dawn} = 130 feeder days with at least one individual foraging at dawn, N_{dusk} = 120), the blue tit Cyanistes caeruleus (N_{dawn} = 121, N_{dusk} = 114), the common blackbird (N_{dawn} = 72, N_{dusk} = 50), the nuthatch Sitta europaea (N_{dawn} = 39, N_{dusk} = 27), the jay Garrulus glandarius (N_{dawn} = 45, N_{dusk} = 1), and the marsh/willow tit Poecile palustris/montanus (N_{dawn} = 39, N_{dusk} = 37). The blackbird is a partial migrant in southern Germany, whereas all other species are resident. Note that we did not discriminate between marsh and willow tit (Poecile sp. thereafter) because species identification was sometimes too difficult. Although we did not mark individual birds in our experiment, it was possible to identify certain individuals on the videos for the great and blue tits because some individuals were banded with a metal ring or colour bands, and some had distinct plumage characteristics (such as a small head patch without feathers). These ‘known’ individuals were rarely observed at different feeders, suggesting that each feeder provided independent data. Great and blue tits were typically foraging in flocks, such that up to 7 individual great tits and up to 5 individual blue tits were recorded simultaneously at a specific feeder. For blackbirds, only males were observed at the feeders (two in site 2, one in site 3). Jays, nuthatches and Poecile sp. were often observed foraging in pairs, on a quasi-daily basis at one feeder (site 2 for the jay, site 3 for the nuthatch and Poecile sp.), but less regularly at another site (site 3 for the jay, site 2 for the other two species). For these three species, we cannot exclude that the same individuals were recorded foraging on different days at sites 2 and 3. We note that site 1 was seldom visited during the training period and the first half of the experiment.

Statistical analyses

We conducted the statistical analyses using the R software ver. 3.1.1. (R Development Core Team). For each species and each period (dusk/dawn) separately, we used linear mixed-effects models (LMMs fit by ML, ‘nlme’ package; Pinheiro et al. 2013) with ‘site’ as a random effect and with ‘onset of foraging’ (in min relative to sunrise) and ‘cessation of foraging’ (in min relative to sunset) as the dependent variables. We included the explanatory variables ‘treatment’ (light/control), ‘date’ (intercept = 5 January), morning/evening ‘weather’ (element/inclement with inclement = snowfall and/or strong wind, as scored in the morning/evening videos), and daily ‘temperature’ at sunrise/sunset (in degrees Celsius). We used the residuals of a linear regression of temperature against date (with ‘site’ as a random effect) in the models because temperature and date were strongly negatively correlated at dawn (Spearman correlation, r_s = -0.72, n = 36, p < 0.001) and dusk (r_s = -0.74, n = 36, p < 0.001). Days with inclement weather were on average 3.3° (at dawn) and 1.9° (at dusk) warmer than days with element weather, although this difference was only significant at dawn (Mann–Whitney U test, dawn: U = 228.5, N_{element} = 20, N_{inclement} = 16, p = 0.03, dusk: U = 66, N_{element} = 25, N_{inclement} = 11, p = 0.5). We corrected for temporal autocorrelation by using the correlation structure corARMA (Box et al. 2013). The fit of the models was assessed by visual inspection of the residuals.

To test our initial predictions, for each species, we compared several candidate models that included 1) the interaction between ‘treatment’ and ‘temperature at sunrise/sunset’ (prediction 3), 2) the interaction between ‘treatment’ and ‘weather’ (prediction 3), 3) the interaction between ‘treatment’ and ‘date’ (prediction 4), 4) all three two-way interactions, and 5) no interactions. We selected the most informative model based on the Akaike information criterion (AIC) following Burnham and Anderson (2002).

Data for blackbirds and great tits included several outliers. To assess their effect on the conclusions, we ran the same analyses as described before, but excluding three outliers after sunrise for the blackbird (Fig. 2), and including only observations between 40 min before and 40 min after sunrise for the great tit, which excludes 5 outliers > 40 min before sunrise (all at the same site) and 2 outliers > 40 min after sunrise (at another site; see Fig. 2). Statistical analyses were two-tailed, and p-values lower than 0.05 were considered significant. We report means and their standard errors.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.7k525> (Da Silva et al. 2017)

Results

Effects of experimental night lighting on the onset of foraging

Blue tits and great tits started foraging earlier relative to sunrise on the experimentally lighted mornings than on the dark control mornings (Table 1, Fig. 2; for model selection see Supplementary material Appendix 1 Table A1). Blue tits started foraging on average 4.2 min earlier on lighted than on control days. For great tits, the effect depended on the weather: during lighted nights with inclement weather they started foraging 9 min earlier on average compared to during control nights with more favourable weather. The start of foraging in the other four species was not significantly affected by the artificial night lighting, although the light effects were all in the expected direction (−5.4 to −1.5 min; Table 1, Fig. 2).

Our results are not particularly robust. When we excluded three late outliers (see Methods), blackbirds started foraging significantly earlier on the lighted mornings (same final model as in Table 1, estimate: −5.0 ± 2.1 min, n = 69, t = −2.4, p = 0.02). Similarly, when we excluded 7 outliers in the great tit dataset, the ‘treatment × weather’ interaction was no longer significant (effect: −0.5 ± 0.3 min, n = 123, t = −1.5, p = 0.1), and instead we found an unexpected, small but significant delaying main effect of the night lighting (treatment effect: 0.7 ± 0.2 min, t = 2.8, p = 0.006).

None of the six study species showed a significant change in the onset of foraging relative to sunrise across the experimental period, although jays tended to start foraging later with advancing date (Table 1).
Effects of experimental night lighting on the cessation of foraging

Experimental night lighting did not affect the cessation of foraging relative to sunset in any of the six study species (Table 2, Fig. 3; for model selection see Supplementary material Appendix 1, Table A2). Poecile sp. tended to stop foraging earlier relative to sunset as the experimental period progressed (Table 2), but date did not have an effect either alone or in interaction with treatment in any of the other species.

Effects of temperature and weather on foraging times

During nights with inclement weather, blue tits and great tits tended to start foraging later in the morning (Table 1), and also stopped foraging later in the evening (significant in the blue tit, 7 min; Table 2). In blackbirds there was a non-significant trend to stop foraging earlier during bad weather (Table 2). Blackbirds, blue tits, and great tits started foraging earlier on colder mornings (0.5–1.5 min earlier per°C; Table 1), but temperature had no effect on cessation of foraging in any of the species (Table 2).

Discussion

In line with our first two predictions, we found that experimental night lighting caused two early foragers, i.e. the blue tit and the great tit, to advance their onset of foraging relative to sunrise by a few minutes in response to the presence of artificial night lighting. Blackbirds – the earliest natural forager – also tended to forage earlier on lighted mornings, but this was not significant. The other three species were not affected by the light. Artificial night lighting did not delay cessation of foraging at dusk in any of the six species. We found limited evidence for our third prediction that the light effect was conditional upon weather: only in the great tit earlier foraging at dawn was seen on mornings with inclement weather. We found no support for our fourth prediction: the light effect did not change over the season. Finally, our fifth prediction was partly supported: we found significantly earlier onset of foraging on colder mornings in the blackbird, the blue tit, and the great tit, and later foraging on evenings with inclement weather in the blue tit. Overall, effects of artificial night lighting on the timing of foraging were small.
set (Fig 3). Generally, foraging ends at higher light levels at dusk than when it starts at dawn. Thus, cessation of foraging may depend more on internal factors such as the energetic state of the bird before roosting, rather than on light levels (Cullen 1954, Lima 1988, Russ et al. 2015). Indeed, smaller birds such as blue tits and Poecile sp., which generally have higher metabolic demands than larger birds (Martin 1987, Haftorn 1989), were the last species to leave the feeders at dusk, and were visiting them regularly. In contrast, larger species stopped foraging early (blackbird) or did not feed at all in the evening (jay).

These daily differences in natural patterns of foraging onset and end are good predictors of the effects of experimental night lighting. Because most species finished foraging before sunset when natural light levels were still high, additional light should not have an effect and this is indeed what we found (Fig. 3, Table 2). However, we cannot exclude that blackbirds, which were frequently recorded foraging on the ground, extended ground feeding during the lighted evenings, as found in previous studies (Dominoni and Partecke 2015, Russ et al. 2015). The blue tit was the only species regularly foraging at the feeder after sunset, yet, it did not take advantage of the artificial light to extend its foraging time. At dawn, only the blue tit and the great tit (and possibly the blackbird; see Table 1 and analysis without outliers) advanced foraging into the night, in line with Byrkjedal et al. (2012). The absence of a light effect in the other species may be explained by their naturally late foraging times at dawn, even though low sample sizes may also have limited our ability to detect small light effects (negative effect sizes, Table 1).

The shift to earlier foraging observed at dawn in response to the light treatment in blue and great tits was weak and may have been mediated by external factors such as perceived predation risk or weather conditions, in conjunction with internal drivers such as energetic state. For example, in the great tit, the onset of foraging was earliest on the lighted mornings with inclement weather. However, when we removed the few outliers for this species (Fig. 2), this effect disappeared, suggesting that the relationship was driven by a few exceptionally early feeding events (at one site). Extreme meteorological conditions are generally reducing the chances

| Species      | Predictors² | Estimate b | SE c | t² | p   |
|--------------|-------------|------------|------|----|-----|
| Blackbird    | intercept   | −10.2      | 11.3 |    |     |
|              | light       | −3.0       | 2.5  | −1.2| 0.2 |
|              | date        | −0.2       | 0.2  | −1.3| 0.2 |
|              | weather     | −1.4       | 2.8  | −0.5| 0.6 |
|              | temperature | 1.5        | 0.4  | 3.5 | <0.001 |
| Blue tit     | intercept   | −9.8       | 5.2  |    |     |
|              | light       | −4.2       | 1.2  | −3.5| <0.001 |
|              | date        | −0.1       | 0.1  | −1.3| 0.2 |
|              | weather     | 1.9        | 1.1  | 1.8 | 0.08 |
|              | temperature | 0.5        | 0.2  | 2.7 | 0.008 |
| Great tit    | intercept   | −7.7       | 7.4  |    |     |
|              | light       | −2.2       | 2.3  | −1.0| 0.3 |
|              | date        | −0.1       | 0.2  | −0.7| 0.5 |
|              | weather     | 3.6        | 2.4  | 1.5 | 0.1 |
|              | temperature | 0.6        | 0.3  | 2.0 | 0.047 |
| Nuthatch     | light x weather² | −9.0     | 3.3  | −2.7| <0.008 |
| Jay          | intercept   | −14.2      | 12.8 |    |     |
|              | light       | −1.5       | 3.8  | −0.4| 0.7 |
|              | date        | 0.8        | 0.4  | 1.7 | 0.1 |
|              | weather     | 2.5        | 4.4  | 0.6 | 0.6 |
|              | temperature | 0.4        | 0.6  | 0.7 | 0.5 |
| Poecile sp.  | intercept   | 15.1       | 10.2 |    |     |
|              | light       | −5.4       | 4.6  | −1.2| 0.2 |
|              | date        | −0.2       | 0.3  | −0.6| 0.5 |
|              | weather     | −1.1       | 4.9  | −0.2| 0.8 |
|              | temperature | 0.6        | 0.7  | 0.8 | 0.4 |

²Variance explained by site: 71.1% (blackbird), 59.2% (blue tit), 42.7% (great tit), 33.6% (Poecile sp.), and 0% (nuthatch, jay).
³Minutes relative to sunrise.
⁴SE = standard error.
⁵Degrees of freedom: blackbird = 106, blue tit = 113, great tit = 121, nuthatch = 33, jay = 39, Poecile sp. = 33.
⁶Lighted days are compared to control days.
⁷Days with inclement weather are compared to days with clement weather.
⁸Lighted days with inclement weather are compared to control days with clement weather.

Foraging on the ground, extended ground feeding during the lighted evenings, as found in previous studies (Dominoni and Partecke 2015, Russ et al. 2015). The blue tit was the only species regularly foraging at the feeder after sunset, yet, it did not take advantage of the artificial light to extend its foraging time. At dawn, only the blue tit and the great tit (and possibly the blackbird; see Table 1 and analysis without outliers) advanced foraging into the night, in line with Byrkjedal et al. (2012). The absence of a light effect in the other species may be explained by their naturally late foraging times at dawn, even though low sample sizes may also have limited our ability to detect small light effects (negative effect sizes, Table 1).

The shift to earlier foraging observed at dawn in response to the light treatment in blue and great tits was weak and may have been mediated by external factors such as perceived predation risk or weather conditions, in conjunction with internal drivers such as energetic state. For example, in the great tit, the onset of foraging was earliest on the lighted mornings with inclement weather. However, when we removed the few outliers for this species (Fig. 2), this effect disappeared, suggesting that the relationship was driven by a few exceptionally early feeding events (at one site). Extreme meteorological conditions are generally reducing the chances
of finding food (Elkins 2010). Great tits exposed to inclement weather during the night may therefore anticipate a lower foraging success later during the day and compensate by foraging earlier at dawn with artificial light, but it is unclear why this would not be so for the smaller blue tit or Poecile sp. Birds in poorer condition or subordinates may particularly benefit from foraging at night, because in this way they might avoid the dominant individuals. Accordingly, female great tits, which are subordinate to males in this species (Gosler and Carruthers 1999), and which seemed to arrive at the feeders later than males at dawn, were observed feeding earliest during the exceptionally early feeding events on the experimentally lighted nights, but this may just be coincidence. Artificial night lighting thus has the potential to modify social structures, and to reduce aggression in some species (Kurvers and Hölker 2014). Finally, the weather-dependent light effect observed in great tits may have other explanations, unrelated to energetic state or dominance, including earlier awakening of roosting birds on windy days, or amplification of the light glow by a denser cloud cover (Kyba et al. 2011).

Unlike weather and temperature, date had no effect on the timing of feeding, irrespective of the light treatment, which suggests that weather conditions are more important than photoperiod at this time of the year. This finding is consistent with several studies that identified temperature as the prime factor behind winter fattening in passerines (Lehikoinen 1987, Cresswell 1998, Gosler 2002), but not with another study (Haftorn 1989), which identified short photoperiods as the main driver of mass gain in tits wintering at higher latitudes. Short winter days were also responsible for earlier (at dawn) and later (at dusk) feeding times (Haftorn 1989, Steinmeyer et al. 2010, Stuber et al. 2015) but our study shows that light pollution does not further extend these times on shorter days. We found that residual temperature had strong effects on the timing of morning foraging but not on evening foraging. The three early foraging species advanced foraging when temperatures were colder than normal, most likely because they suffered higher mass loss on colder nights (Lima 1988, Gosler 1996, 2002, Chamberlain et al. 2005, Macleod et al. 2005a, Hatchwell et al. 2009, Clewley et al. 2015). Bird densities at feeders also increase with colder winter temperatures, which may lead to some individuals starting foraging earlier to secure more food (Chamberlain et al. 2005). Additionally, when the weather was inclement in the morning, blue and great tits tended to start foraging later, irrespective of light, perhaps because such mornings were warmer than the mornings with clement weather. At dusk however, weather did not covary with temperature and these two species stopped foraging later (only significant in the blue tit) when the weather was inclement, suggesting that weather cues may be used to evaluate how much fat is still needed before going to roost (Gosler 2002).

The limited effects of artificial night lighting observed in our study may be generally true, but may also be due to our experimental set-up. First, the sample size was low, so idiosyncratic differences between the sites or between individuals of the same species feeding at each site (e.g. one exceptionally early individual) could have a large influence.

Figure 3. Cessation of foraging relative to sunset for experimentally lighted and dark control days for five songbird species. Numbers at the bottom indicate sample size (number of evenings the species was observed foraging at a feeder). The dotted horizontal line indicates sunset.
on the results. Thus, it would be worthwhile to repeat the experiment, preferably with more independent sites. Furthermore, it would be interesting to compare foraging times of known (marked) individuals under lighted and control conditions. It might also be insightful to use a modified approach whereby some sites are constantly illuminated at night. Indeed, effect sizes may have been relatively small because three early mornings and late evenings of exposure to artificial light may not have been enough to elicit a strong shift in timing. This is supported by two recent studies showing that light effects on onset of dawn singing or on activity increased with days of light stimulation (Da Silva et al. 2016, de Jong et al. 2016). Birds may even require more time to adjust to the new light conditions during winter than during the breeding season, due to seasonal differences in photosensitivity and hormone levels. Moreover, birds may also learn to actively exploit the night light niche to forage, and this process may be facilitated by a more permanent exposure to light, as found in cities. A larger area of light exposure may also elicit stronger effects, by increasing the probability that sleeping birds are directly exposed to artificial light during the night and hence wake up earlier, rather than being solely attracted to the lighted areas after having woken up under naturally dark conditions.

Second, the threat of predation may have prevented the birds in our study from extending foraging into the night (Lima 1988). Aerial predators (e.g. tawny owl Strix aluco and Eurasian sparrowhawk Accipiter nisus) are common at the study sites, and they may also be able to use artificial light to hunt at night (Negro et al. 2000, DeCandido and Allen 2006).

Finally, we cannot exclude the possibility that birds in our study prolonged their foraging period under artificial night lighting, but not at the feeders. The birds may have started foraging elsewhere in the lighted part of the forest before coming to the place with reliable access to food (i.e. the feeder). This scenario is particularly relevant for urban areas where food is often provided reliably and all day long, which may counteract any advancing effect of artificial light and lead to a later onset of foraging, as argued by Ockendon et al. (2009a) and Clewley et al. (2015). The effect of artificial night lighting – if it exists – may then only appear during nights with the highest energy demands, i.e. either during the long winter nights at high latitudes (Byrkjedal et al. 2012), or during extremely cold or windy nights at lower latitudes. Naturally-early foragers may be the only species exploiting the night light niche, as shown in our study and in Byrkjedal et al. (2012), which may lead to higher winter survival relative to less flexible species, and, in the long run, to the homogenization of urban bird communities (Davies et al. 2013, Galbraith et al. 2015).

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Supplementary material (Appendix JAV-01232 at <www.avianbiology.org/appendix/jav-01232>). Appendix 1.