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BirdLife NORWAY

Effects of artificial light and latitude on the dawn foraging activity of Great Tits *Parus major* during winter in northern Europe

Karoline Aasen Skryten*, Ronny Steen & Svein Dale

Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway
* Correspondance, e-mail: karolineskryten@gmail.com

Cite this article
Skryten KA, Steen R & Dale S. 2024. Effects of artificial light and latitude on the dawn foraging activity of Great Tits *Parus major* during winter in northern Europe *Ornis Norvegica* **47**: 1–12.
DOI: 10.15845/on.v47.3626

Keywords
artificial light at night
diurnal activity
feeding experiment
onset of foraging

Received 14 March 2022
Accepted 7 November 2023
Published 25 February 2024

Abstract
Recently, there has been increasing interest in the ecological consequences of artificial light on wildlife. At northern latitudes, winter is characterized by short days and low temperatures. Under these conditions, resident birds need to consume more food in a shorter time to sustain their metabolism and maintain body temperature. Access to artificial light may prolong foraging opportunities for resident birds during winter. Here, we used a field experiment to test whether Great Tits *Parus major* benefit from artificial light to start foraging before sunrise. Further, we conducted a meta-analysis to test if onset of foraging was correlated with latitude in the Great Tit. A feeding station with artificial light was placed in a forest area in Ås, SE Norway, at nearly 60° north. A camera was placed in front of the feeding station to record daily activity of the Great Tit in December and February. In December, Great Tits started foraging earlier relative to sunrise when artificial light was available. In February, Great Tits were not stimulated by artificial light to start foraging before sunrise. The onset of foraging in Great Tits was also correlated with latitude. At the northernmost location, Great Tits started foraging several hours before sunrise, whereas at the southernmost location, Great Tits started foraging only a few minutes before sunrise. The results suggest that resident Great Tits may utilize artificial light to prolong their foraging activity during midwinter, and that onset of foraging is advanced relative to sunrise with decreasing daylength further north. Our findings contribute to the understanding of how short days during northern winters can limit foraging activity in resident birds.

INTRODUCTION

Over the last decades, there has been an increasing interest in the ecological consequences of artificial lighting on wildlife (Kotler 1984, Rydell 1992, Salmon et al. 1995, Rand et al. 1997, Byrkjedal et al. 2012, Bird & Parker 2014, Van Doren et al. 2017). The increase in artificial light is strongly correlated with human urbanization, and as urbanization is predicted to expand, so are the impacts of artificial light (Hölker et al. 2010, Gaston et al. 2015). The ecological consequences of artificial light are starting to be explored, but more research is needed to determine effects on behavior, demography and other aspects. Light installations across cities and shores attract nocturnal migrating birds and lead to disorientation, which in many cases have fatal consequences (Poot et al. 2008, Rodriguez et al. 2014, Van Doren et al. 2017). Other effects include alterations in hormonal cycles (Zhang et al. 2014), habitat selection and reproductive success (Russ et al. 2017) and timing of singing (Kempenaers et al. 2010, Da Silva et al. 2014).

The majority of studies on the effects of artificial light on birds focus on how it affects birds during the breeding season. However, for most birds the breeding season only lasts for short periods of their life cycle, in particular for birds breeding in cold climates at northern latitudes (Wyndham 1986). While behaviors such as breeding, singing and predation have been widely studied, foraging behavior, which is crucial for survival, has been less explored in relation to artificial light. This knowledge gap emphasizes the need for more research regarding this topic, particularly since the majority of birds´ life span take place outside the breeding season.

Previous studies have documented that diurnal animals from a range of taxa exploit modified environments and feed close to artificially lighted areas (Heiling 1999, Minnaar et al. 2015, Bolton et al. 2017, Frank et al. 2019). Several studies have reported birds utilizing artificial light when foraging (Blackett 1970, Brooke 1973, Bakken 1977, Lebbin et al. 2007, Santos et al. 2010, Russ et al. 2015, Foley & Wszola 2017). Most of the studies of diurnal birds utilizing artificial light were conducted during relatively favorable and mild environmental conditions. On the other hand, there are relatively few studies of foraging activity during more demanding and inclement conditions. During winter, Common Redshanks *Tringa totanus* increased visually-based foraging in areas with artificial light, rather than tactile foraging behavior (Dwyer et al. 2013). Likewise, in Norway, a range of resident species of diurnal passerines (Passeriformes) were observed to be active and sometimes foraging, near artificial light several hours before sunrise in winter (Byrkjedal et al. 2012).

At northern latitudes, winter is characterized by short days and low temperatures. For resident birds, the combination makes it more challenging to find enough food. Short days imply less time to forage whereas low temperatures demand a higher food intake to sustain metabolism through long and cold nights (Nice 1938, Newton 1969, King & Mewaldt 1981). During short days, artificial light may have a greater impact on birds because daylight is already a limiting resource. Smaller birds may be more exposed to low temperatures because they have a large surface to volume ratio, and thus, are at risk of losing more heat (Kendeigh 1970). Hence, artificial light may enhance foraging opportunities and positively affect winter survival of resident birds, in particular those species with small body sizes.

Challenging winter conditions also reduce survival in resident birds due to overnight weight loss and unpredictable foraging opportunities (Källander 1981, Haftorn 1989, Cresswell 1998). Resident birds peak in body mass during midwinter, as an adaptation to the weather conditions and short days (Källander 1981, Haftorn 1989, Gosler 2002). Foraging activity tends to be highest in the morning and before roosting in the evening (Lawrence 1958, Beer 1961, McNamara et al. 1994). Furthermore, resident birds tend to increase foraging effort in the morning with decreasing temperature and daylength (Baldwin & Kendeigh 1938, Van Balen 1967, Cresswell 1998, Gosler 2002). Thus, artificial light may provide an opportunity for resident birds to increase food intake by foraging earlier in the morning or by continuing after sunset.

In urban areas, the use of feeders allows birds in general to consume enough food to survive overnight during winter (Grubb & Cimprich 1990, Doherty & Grubb 2002). However, supplemental feeding has given conflicting outcomes in bird responses, where some species commence foraging earlier, and others later in the morning (Koivula et al. 2002, Bonter et al. 2013, Clewley et al. 2016). Variable responses are likely due to other factors that may affect foraging activity, such as increased predation risk (Lima 1986, Sims et al. 2008, Seress et al. 2011), social dominance hierarchies (Ekman & Lilliendahl 1993, Gosler 1996, Lahti 1998, Gosler & Carruthers 1999), and interspecific differences in feeding strategies (Lilliendahl 2002).

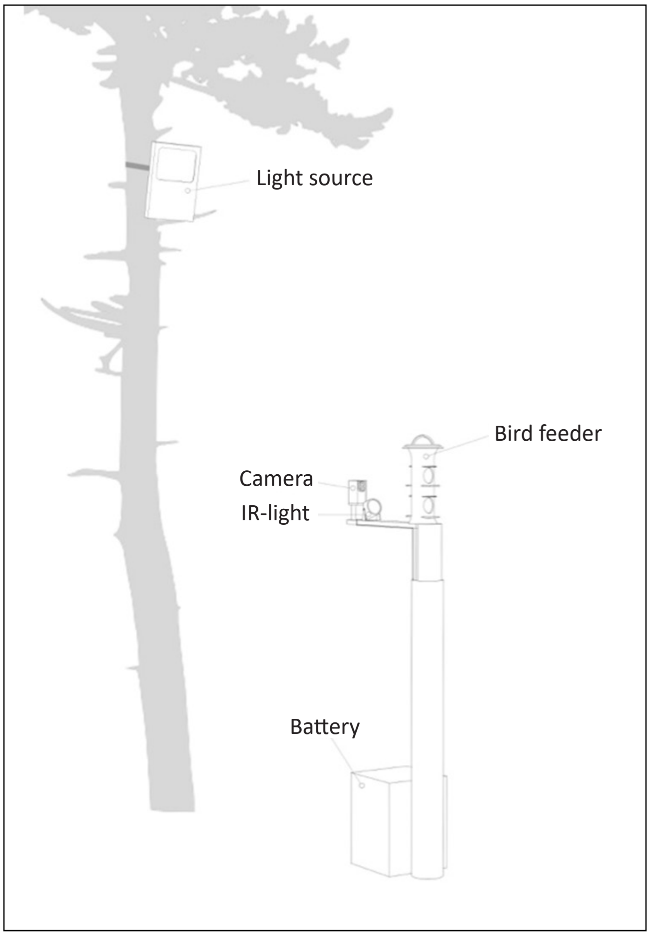

Figure 1. Schematic sketch of the experimental set up.

Clewley et al. (2016) and Da Silva et al. (2017) studied the effects of artificial light on the foraging activity of resident passerines, but found only small differences in the onset of foraging in areas with more or less artificial light. However, both studies were conducted in Central Europe (49-60 degrees north and 48 degrees north, respectively). Daylength decreases with increasing latitude in winter, and conducting a similar study further north might show increased effects of artificial light on foraging activity. Hence, northern latitudes may force passerines to start foraging earlier relative to sunrise to optimize fat storage, and prevent starvation and hypothermia. In contrast to daylength, the duration of morning civil twilight (hereafter 'twilight') increases with increasing latitude (List 1949). Thus, the low light levels during twilight might be adequate for foraging, and could therefore represent a potential clue for the onset of foraging. Moreover, artificial lighting may enable an even earlier start of foraging.

We hypothesized that both artificial light and latitude could affect foraging activity during winter in resident Great Tits *Parus major*. We conducted a field experiment with artificial light in southern Norway, and tested four predictions. If daylight and temperature are limiting factors, we predicted that resident Great Tits should start foraging earlier relative to sunrise (1) when artificial light is present, and (2) when environmental temperatures are lower. Moreover, we predicted that (3) artificial light will have less effect on the onset of foraging in Great Tits with increases in daylength and ambient temperature. Last, we predicted that (4) foraging in Great Tit should start earlier relative to sunrise with increasing latitude under natural conditions in the absence of artificial light. The latter prediction was tested by combining own field data with published information from the literature.

METHODS

Study site

The study area was located in Ås, a village in Viken county, Norway. The field experiment was conducted in December 2018 and February–March 2019 in a forest patch at Eldor, Ås. The area is a coniferous forest dominated by Norway spruce *Picea abies* which were mostly planted, and mixed with shrubs. Originally two feeding sites were established as replicates to enable a paired experimental setup, but one of the sites was omitted from the analyses due to low bird activity.

At the site selected (59° 38’ 40.2” N, 10° 48’ 13.5” E), the distances to the closest road with low traffic and settlements where other feeders potentially could be were > 100 m.

Experimental design

A Supa feast wild bird feeder with four food chambers (two on each side of the feeder) was placed 1.5 m above ground (Figure 1). The feeder was filled with whole sunflower seeds and was refilled every day after sunrise. Only the food chambers facing the camera were open.

A time-lapse camera, Brinno TLC200 Pro (Brinno Inc., Taiwan), was placed 0.5 m away from the feeder. The camera was protected with a water-resistant housing (Brinno ATH120) for weatherproofing. To power the camera, we used 4x AA Energizer® Ultimate LithiumTM batteries (Energizer Holdings, Inc., USA), which were changed every day. All videos were stored onto SanDisk class 4 SDHC Memory Cards (SanDisk Corp., USA). The time-lapse camera was set with a time interval of 1 sec and 2 frames per sec. The field of view of the camera covered the part of the feeder with open chambers and some of the vegetation around the feeder. An auto-controlled infrared-emitting light (IR) was placed right in front the camera to work when light conditions were lower than ~10 lux. The IR-light was powered by a 12V 80Ah deep cycle battery placed next to the feeder. A LED outdoor floodlight (70W, IP65 and 6500K, Gelia, Ahlsell AB, Sweden) was placed in a tree (4.9 m in direct line from the feeder and 4.5 m above the ground) to illuminate the area of the feeder and to simulate the footprint of a street light. The floodlight had one bulb which emitted white, warm light, it was connected via multiple 50 m extension cords to be powered from the closest house.

Experimental procedure

To perform a paired setup, the feeder was illuminated during periods of exposure (treatment) which were alternated with periods without illumination (control). The first field experiment took place during 8–31 December. The site had a control phase from 8–17 December, followed by an illumination phase from 20–31 December. The second field experiment was conducted during 9 February–10 March. The site had illumination phases from 9–15 February and 25 February–3 March. Control phases lasted from 17–23 February and 4–10 March. The light was switched on manually 2h after sunrise the day before an illumination phase started, and remained on constantly until it was turned off manually 2 h after sunset on the last day of the treatment phase. The feeders were supplied with food for 2–3 days before the experiments started to accustom the birds to the availability of food.

The daily timing of sunrise and sunset at Ås was extracted from www.timeanddate.no and the daily temperature at sunrise was extracted from www.yr.no. The nearest meteorological station was located ~2 km from the feeding station. There were few days with particularly inclement weather including strong winds, heavy rain or snowfall, and the days with inclement weather were evenly distributed between illumination and control phase. A thin snow cover was present during some parts of the study period.

Light conditions

Two types of measurements were conducted in the field to quantify the availability of artificial light. One measurement was to obtain a trend of the changes in light conditions during sunrise and sunset. Another measurement was of the glares from the artificial light after sunset to describe the intensity of the glare omitted from the light source at increasing distances from the feeder. The illuminance in the area of the feeder was measured by using a light meter FLUS model MT-906 (Shenzhen Flus Technology Co, Ltd, China).

In both December and February, the changes in light conditions were measured during sunrise and the measurements were started 2 h before daily sunrise and lasted until the sun had risen. Light levels were measured every 20 min for a total of seven measurements per day on two consecutive days during each phase. Light conditions were measured in lux and the light meter was placed next to and at the same level as the camera during measurements. Due to fluctuations in the lux

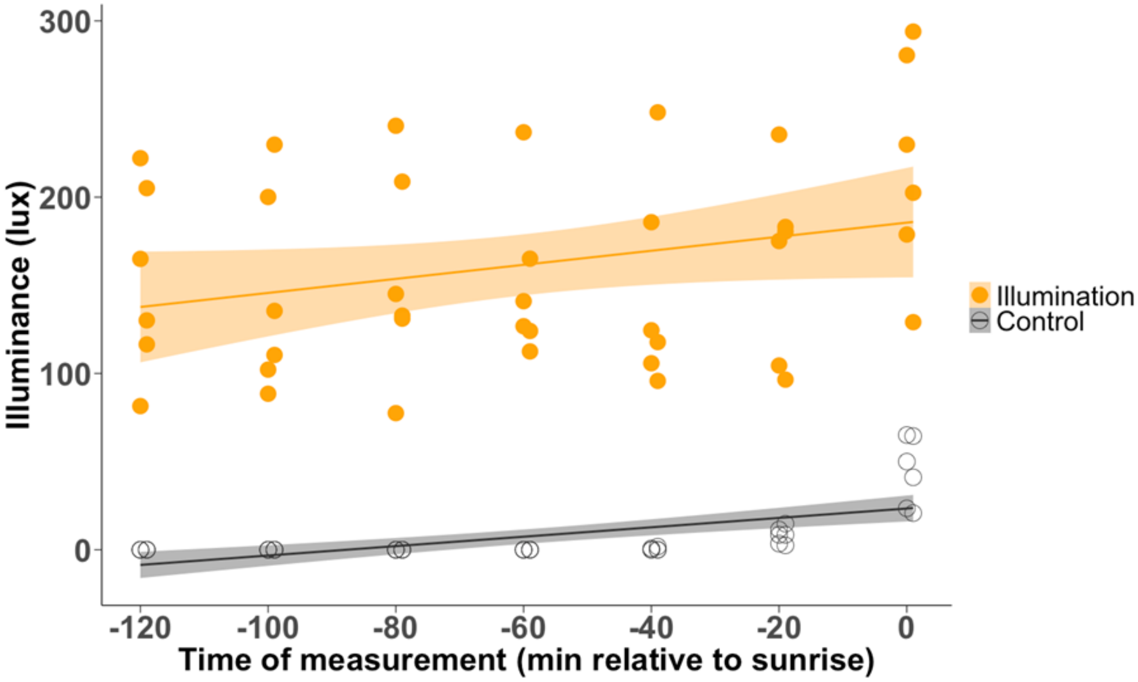

Figure 2. Change in light conditions (lux) close to the feeder during 2 hours before sunrise. The yellow (illumination) and grey (control) horizontal lines indicate the mean lux value (individual datapoints indicate median values of three measurements each day). The yellow and grey areas around the horizontal lines indicate the 95% confidence intervals. On the x-axis, 0 is the time of sunrise.

measurements, lux was measured every first, fifth and tenth second at every 20 min. The median value of the three measurements (first, fifth and tenth second) for each day was used.

In February, the level of glare (in lux) was measured after sunset in the area around the feeder as an additional measurement. Using the feeder as center, level of glare was measured in each cardinal direction at 0, 5, 10, 15, 25 and 30 m away from the feeder. Measurements at 0 m were next to the camera and had the same location as the measurements of light conditions. During these measurements, the light meter and the person doing the measurements were facing the feeder so that no shadows would interfere with the outcome of the light meter. The light meter was held at chest height during the measurements. Level of glare was measured during both illumination phases with two measurements in each cardinal direction for each distance from the feeder.

Overall, the mean lux value across individual days during illumination phase at the position close to the feeder (Figure 2) was an order of magnitude higher than that for normal street lights where light levels at the road surface vary from 7.5–50 lux (Statens vegvesen 2019). Even so, the lux level decreased drastically only a few meters from the feeder and the mean lux value was below the level for normal streetlights between the 5 m and 10 m distance from the feeder (Figure 3).

Data extraction

Videos were collected each day after recordings. All videos were saved on an external hard disk. The data were extracted manually by using VLC media player 2.2.5.1. For each day, the timing of all visits by Great Tits were recorded from 2 h before sunrise until 1 h after sunrise during the total duration of the recording. Afterwards, for each day of the field experiment, the daily timing of the three first visits were converted into min and sec relative to local sunrise. Birds were considered to be foraging whenever they were recorded taking a sunflower seed in its beak. Most visits were of birds foraging and only 2% of all visits were classified as not foraging. Still, there were occasions were individual birds visited the feeders without taking any seeds. We had no method to distinguish among different individuals of Great Tits, and it is highly likely that the same individuals visited the feeder several times. On some days there were no visits of Great Tits before sunrise. Thus, sample sizes were 19, 18, and 18 for the first, second and third visit in December, respectively, and 13, 10, and 8 for the first, second and third visit in February.

Meta-analyses

For the meta-analyses, we searched through a range of literature to find studies with relevant data. We searched for literature using Web of Science and Google Scholar with the key words “winter foraging + sunrise”, “resident passerines + foraging”, “winter ecology + bird”, “winter foraging + bird”, “winter feeding + bird”, “winter activity + bird”. Additionally, we searched through the reference lists of relevant articles for more relevant literature. The data for the meta-analyses were extracted from the result tables and texts of four studies

(Table 3) with six different locations and latitudes (von Haartman 1975, Pulliainen 1980, Haftorn 1994, Da Silva et al. 2017), and were supplemented with our own field data. Only data from December and January were used, since these months are the coldest and have the least daylight. The mean time of onset of foraging at sunrise was extracted from each study. For the studies that did not state the mean onset of foraging, it was calculated using data from the texts and tables that contained information on the onset of foraging in individual Great Tits. The data were extracted from Table 1 in Da Silva et al. (2017), Table 1 in Haftorn (1994), and the text of the Results in Pulliainen (1980) and Table 1 in von Haartman (1975). The local time for sunrise and start of twilight at each location were obtained from www.timeanddate.no. For the northernmost location in Svanvik, Norway (Haftorn 1994), there was no timing for sunrise because the site was located north of the polar circle and had conditions of polar night during midwinter. For this reason, "sunrise" in Svanvik was defined as when the sun passes the location of the local meridian at midday.

Statistical analyses

All statistical analyses were conducted by using RStudio, the R software version 3.5.2 (Rstudio Team, 2016). We used the stats package (R Core Team, 2018) for the analyses and tests were considered significant at $\alpha \leq 0.05$. Figures were made using the package ggplot2 (Wickham, 2016) and the graphics package (R Core Team, 2018).

The appearance of Great Tits at sunrise in relation to illumination was analyzed using unpaired two-sample Wilcoxon tests, with separate tests for the first, second and third visit. Onset of foraging relative to sunrise (determined by the first visit) was the response variable whereas experimental treatment (illumination/control phases) was the explanatory variable. Both two-

Table 1. Effects of illumination and temperature on the onset of foraging at sunrise in Great Tit *Parus major* at Ås, Norway in December 2018. Results from multiple linear regression models for first visit (n = 19), second visit (n = 18) and third visit (n = 18). Significant variables are highlighted in bold.

Visit no.[a]	Predictors	Estimate[b]	SE	t	P
1	intercept	-11.11	3.46	-3.22	0.005
	illumination	-19.36	3.99	-4.85	< 0.001
	temperature	1.18	0.58	2.03	0.059
2	intercept	-9.05	3.79	-2.39	0.031
	illumination	-21.10	4.44	-4.75	< 0.001
	temperature	0.95	0.68	1.40	0.18
3	intercept	-7.57	3.77	-2.01	0.063
	illumination	-20.05	4.42	-4.54	< 0.001
	temperature	1.05	0.68	1.56	0.14

[a] First, second and third visit relative to sunrise.
[b] Min relative to sunrise.

Table 2. Effect of illumination and temperature on the onset of foraging at sunrise in Great Tit (*Parus major*) at Ås, Norway in February and March 2019. Results from multiple linear regression models for first visit (n = 13), second visit (n = 10) and third visit (n = 8).

Visit no.[a]	Predictors	Estimate[b]	SE	t	P
1	intercept	34.43	5.12	7.73	< 0.001
	illumination	-7.25	7.57	-0.96	0.36
	temperature	2.11	1.87	1.13	0.29
2	intercept	34.74	6.95	5.00	0.002
	illumination	-2.53	8.45	-0.30	0.77
	temperature	0.83	2.74	0.30	0.77
3	intercept	37.03	8.90	5.78	0.009
	illumination	-5.63	10.92	-0.52	0.63
	temperature	1.33	3.58	0.37	0.73

[a] First, second and third visit relative to sunrise.
[b] Min relative to sunrise.

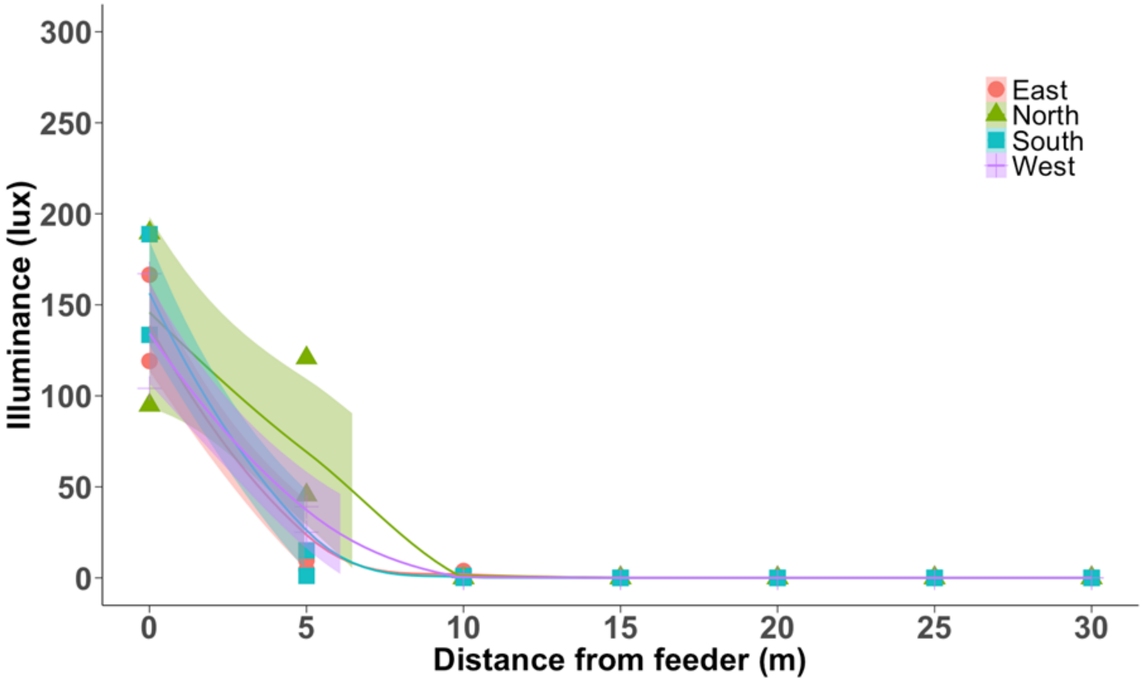

Figure 3. Level of glare (lux) measured at sunset in February and March, in each of the four cardinal directions. The values of the x-axis indicate distance from the feeder; 0 m is at the feeder. The red (east), green (north), blue (south), and purple (west) lines indicate the mean value of glare in each cardinal direction; the similarly colored areas around the lines indicate the 95% confidence intervals.

tailed and one-tailed Wilcoxon tests were calculated. One-tailed tests were relevant because we predicted that Great Tits would start foraging earlier when the site was illuminated. Thus, p-values are stated for one-tailed tests in addition to the two-tailed tests. Additionally, unpaired two-sample Wilcoxon test was used to analyze the onset of foraging in December compared to the onset of foraging in February for the illumination and control phases. Onset of foraging relative to sunrise was the response variable and month of the field experiment (December/February) was the explanatory variable.

We used multiple linear regression models (lm) to analyze the relationships between foraging activity, illumination and temperature. Onset of foraging relative to sunrise was the response variable, whereas experimental treatment (illumination/control phases) and temperature were the explanatory variables.

The meta-analyses were conducted using Spearman´s rank correlation coefficient. The relationship between onset of foraging relative to sunrise and twilight were analyzed in relation to latitude (degrees north). Analyses were done both with and without Svanvik because there is no sunrise at sites north of the arctic circle during midwinter.

RESULTS

Foraging in December

In December, Great Tits started foraging significantly earlier relative to sunrise during the illumination phase compared to the control phase (two-tailed p = 0.002, one-tailed p = 0.001, n = 19; Figure 4). During the illumination phase, Great Tits started foraging on average 34.22 min before sunrise. During the control phase, Great Tits started foraging on average 13.98 min before sunrise. Foraging started significantly earlier during the illumination phase also when taking temperature into account (p < 0.001; Table 1). There was a non-significant trend (p = 0.059) that onset of foraging was affected by temperature in the first visit, but not in the second and third visits (Table 1).

Foraging in February

In February, illumination did not affect onset of foraging in Great Tits (two-tailed p = 0.61, one-tailed p = 0.30, n = 13; Figure 5). During the illumination phase, Great Tits started foraging on average 30.55 min after sunrise. During the control phase, Great Tits started foraging on average 36.80 min after sunrise. Temperature did not have an effect on onset of foraging (Table 2). Great Tits started foraging significantly earlier relative to sunrise in December compared to February, both during the illumination (p < 0.001) and control phases (p < 0.001).

Foraging in relation to latitude

The onset of foraging in Great Tits in relation to sunrise was negatively correlated with latitude (r_S = -1.00, n = 7, p = 0.014; Figure 6, Table 3). Even without Svanvik, onset of foraging in relation to sunrise was still negatively correlated with latitude (r_S = -1.00, n = 6, p = 0.025) With increasing latitude, Great Tits started foraging earlier relative to sunrise. In Great Tits, onset of foraging in relation to twilight was not significantly correlated with latitude (r_S = -0.61, n = 7, p = 0.14;

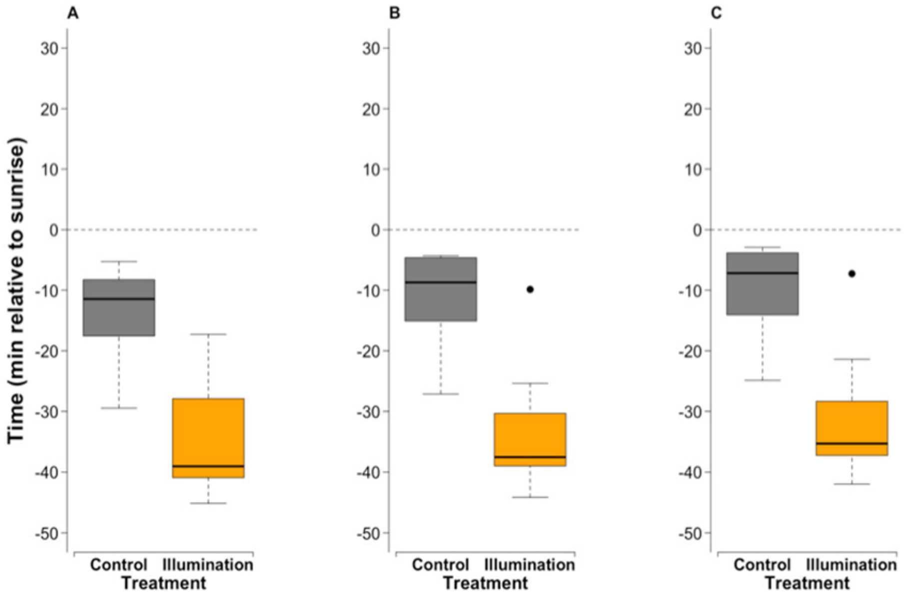

Figure 4. Onset of foraging relative to sunrise in Great Tit *Parus major* at Ås, Norway in December 2018. A–C represent first, second and third visits, respectively. Box plots indicate medians (bold horizontal lines), upper and lower quartiles (whole horizontal lines) and extending to the smallest/largest values within 1.5*inter-quartile range (vertical dashed lines). Black dots indicate outliers. Sample sizes for A–C were 12, 11 and 11 for illumination phase (yellow box plots), respectively, and 7, 7 and 7 for control phase (grey box plots), respectively. Negative values indicate time before sunrise and positive values indicate time after sunrise. The dashed horizontal line indicates sunrise.

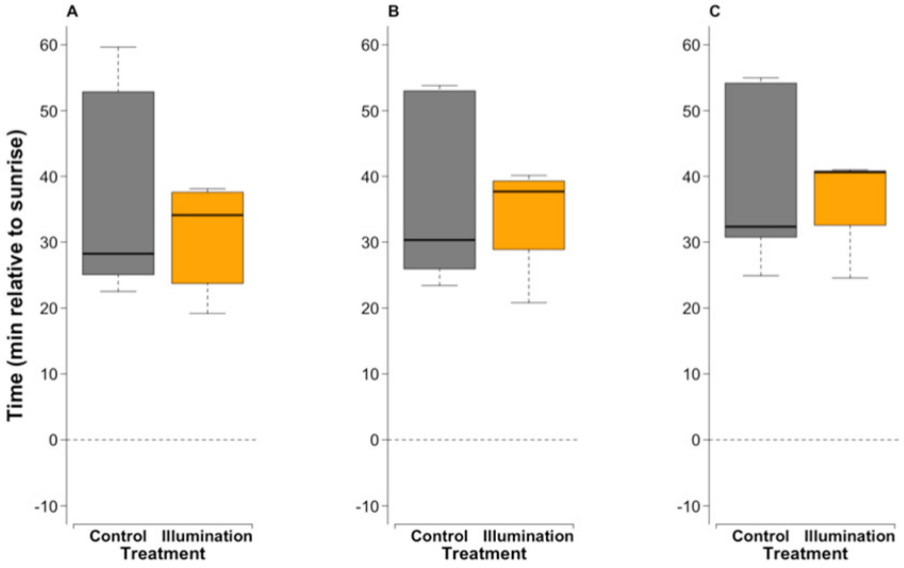

Figure 5. Onset of foraging relative to sunrise in Great Tit *Parus major* at Ås, Norway in February and March 2019. A–C represent first, second and third visits, respectively. Box plots indicate medians (bold horizontal lines), upper and lower quartiles (whole horizontal lines) extending to the smallest/largest values within 1.5*inter-quartile range (vertical dashed lines). Sample sizes for A–C were 5, 4 and 3 for illumination phase (yellow box plots), respectively, and 8, 6 and 5 for control phase (grey box plots), respectively. Negative values indicate time before sunrise and positive values indicate time after sunrise. The dashed horizontal line indicates sunrise.

Figure 7), although at the northernmost site (Svanvik), Great Tits started foraging well before twilight. There were no changed effects when removing Svanvik from the analyses ($r_S = -0.37$, $n = 6$, $p = 0.41$).

DISCUSSION

In line with our first prediction that daylight is a limiting factor, Great Tits started foraging earlier at sunrise during the illumination phase than the control phase in December. The first visit, as well as second and third visit, were significantly affected by artificial light. Our artificial light created light levels similar to the light level after sunrise (Figure 2) so that foraging should have been possible without daylight present. There was weak evidence for our second prediction that foraging activity is dependent on temperature. The first visit at sunrise by Great Tits showed that onset of foraging tended to be affected by temperature. The onset of the

Table 3. Mean onset of foraging in Great Tit *Parus major* relative to sunrise and onset of morning civil twilight in relation to latitude and study site. Negative values indicate min before sunrise and onset of morning civil twilight. Positive values indicate min after sunrise and onset of morning civil twilight.

Area	**Latitude (°N)**	**Min relative to sunrise**	**Min relative to onset of twilight**	**Source**
Seewiesen, Germany	47.97	-9	25	Da Silva et al. (2017)
Ås, Norway	59.66	-14	42	Present study
Drammen, Norway	59.74	-21	35	Haftorn (1994)
Lemsjöholm, Finland	60.48	-37	21	von Haartman (1975)
Klæbu, Norway	63.30	-80	-3	Haftorn (1994)
Värriö, Finland	67.74	-91	30	Pulliainen (1980)
Svanvik, Norway	69.45	-200	-57	Haftorn (1994)

second and third visit in relation to temperature showed similar trends, but were not significant. The lowest temperature recorded during the field experiments in December was -9°C and the highest was 2°C. The mean temperature was -2°C. The mean onset of foraging was earlier on days with temperatures below freezing. In agreement with our third prediction that artificial light would have less benefit when days became longer, Great Tits did not start foraging earlier relative to sunrise in February compared to the onset of foraging in December. Great Tits started foraging earlier during both the illumination and control phases in December, compared to the onset of foraging in February. In line with our fourth prediction that birds should start foraging earlier at high latitudes, Great Tits´ onset of foraging in relation to sunrise was significantly correlated with latitude. At the northernmost location, Great Tits started foraging several hours before sunrise, while at the southernmost location Great Tits started foraging only minutes before sunrise. Onset of foraging in relation to twilight was not significantly correlated with latitude. Thus, light conditions during twilight may represent the minimum conditions needed to start foraging.

Foraging in Great Tit during winter

The earlier onset of foraging by Great Tits in December is similar to the previous findings of Byrkjedal et al. (2012) and McNamara et al. (1994). Passerines were observed to be active several hours before sunrise, including some European Robins *Erithacus rubecula* feeding close to artificial light (Byrkjedal et al. 2012). There are numerous examples of birds and animals from other taxa utilizing artificial light for foraging. Our findings might be expected since feeding is more crucial during winter, and small passerines, such as Great Tits, need a high food intake to prevent hypothermia (King & Farner 1966, Chaplin 1974). However, the results from our field study showed different patterns than previous work (Clewley et al. 2016, Da Silva et al. 2017). For instance, Clewley et al. (2016) did not find any differences in onset of foraging in urban birds, compared to rural birds, which indicates that artificial light did not have an effect on foraging activity. However, the studies by Clewley et al. (2016) and Da Silva et al. (2017) were conducted at lower latitudes in Great Britain and Germany, compared to our study site in Norway. Moreover, previous research has shown that resident birds at higher latitude have higher fat storage than at lower latitudes (Blem 1975, Nolan & Ketterson 1983). Hence, our results suggest that artificial light may have greater benefits for foraging in resident birds at northern latitudes in winter.

The difference in onset of foraging in December and February was consistent with previous research. Resident tits gained considerably less body mass and delayed foraging to later parts of the day when the daylength was longer, compared to shorter days (Fitzpatrick 1997, Polo et al. 2007). Moreover, when days were shorter, resident birds increased body mass and started foraging earlier at low temperatures (Baldwin & Kendeigh 1938, Rogers & Reed 2003, but see Fitzpatrick 1997). Additionally, feeding rates measured as weight gain per hour were higher during midwinter (Haftorn 1989). In December, there was a trend that onset of foraging in Great Tits was related to temperature. The effects of temperature corresponded to previous findings, which show that resident birds increase fat reserves during the coldest months (Helms & Drury 1960, King & Farner 1966, Evans 1969, Newton 1969, Senar et al. 1992). Birds may adjust foraging activity in relation to an upcoming period with low temperatures (Evans 1969). The findings indicate that foraging and high food intake is more crucial during midwinter when temperature and daylength is at a minimum. Several studies have highlighted temperature as the main factor determining winter fattening and foraging (King & Farner 1966, Evans 1969, Lehikoinen 1987, Cresswell 1998, Gosler 2002). Therefore, temperature may also play an important role for the onset of foraging. Other factors, such as food availability and snow cover, may also play an

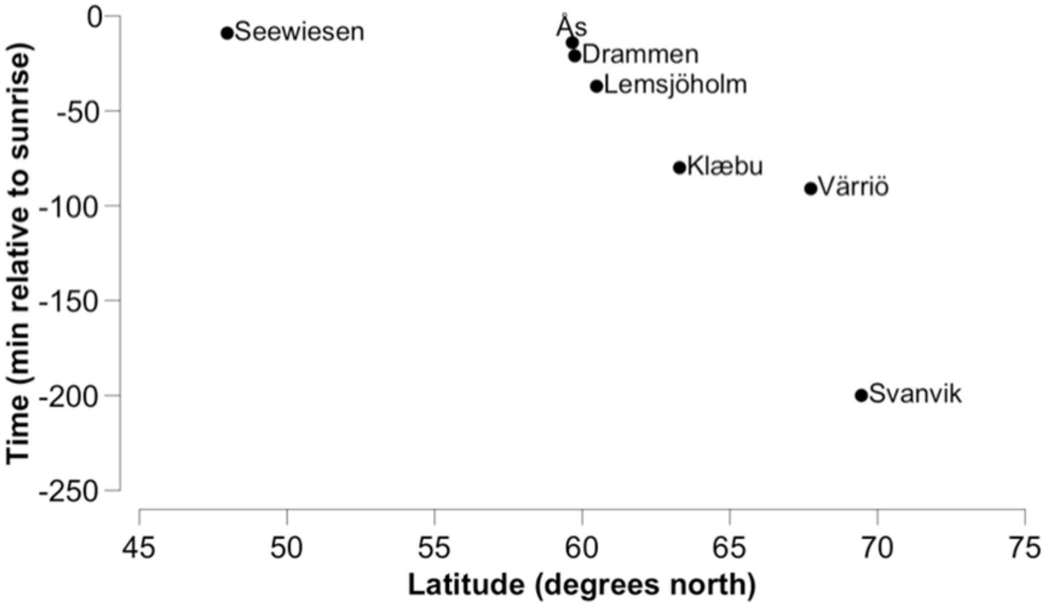

Figure 6. Onset of foraging relative to sunrise in Great Tits (Parus major), in relation to latitude (°N) during midwinter. The datapoints were extracted from studies with different locations and latitudes, including our own data (n = 7; see main text for detailed citations). On the y-axis, 0 is the time of sunrise.

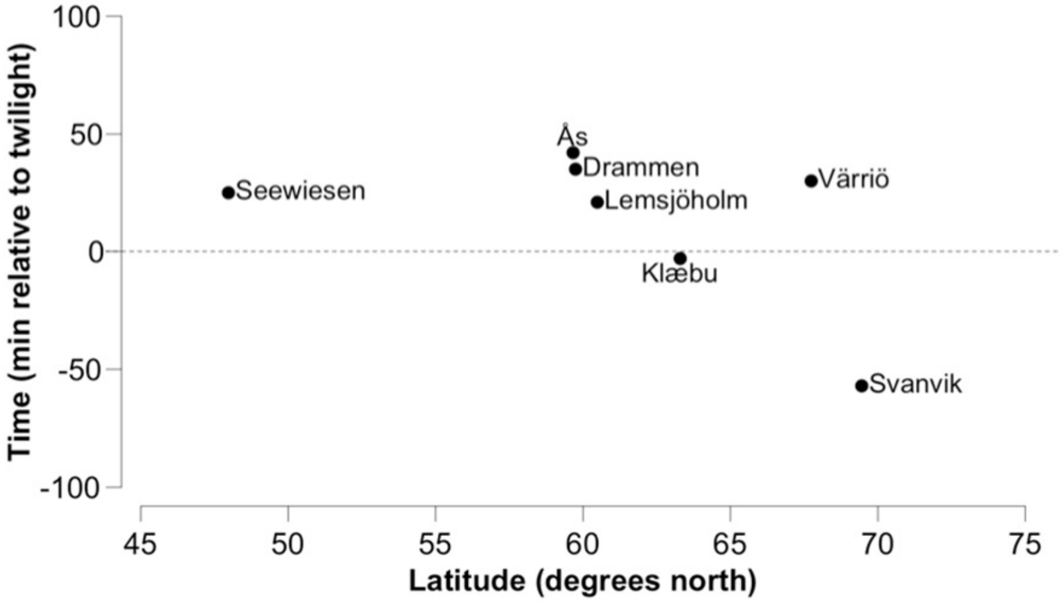

Figure 7. Onset of foraging relative to onset of morning civil twilight in Great Tits *Parus major*, in relation to latitude (°N) during midwinter. The datapoints were extracted from studies with different locations and latitudes, including own data (n = 7; see main text for detailed citations). The dashed horizontal line indicates the onset of twilight.

important role in foraging activity during winter (Lima 1986, McNamara & Houston 1990, Brotons 1997, Nakamura & Shindo 2001).

Onset of foraging in relation to latitude

Great Tits´ onset of foraging was significantly correlated with latitude, where foraging at the northernmost location started hours before sunrise, compared to minutes before sunrise at the southernmost location. Onset of foraging was not significantly correlated with twilight. Hence, twilight seemed to be the minimum light level needed to start foraging at all locations, except the northernmost location, where Great Tits started foraging well before twilight. We do not have any explanation for this, and environmental cues at high latitudes may deserve future study. Similar correlations have been shown elsewhere in Europe, where Coal Tits *Periparus ater* at higher latitudes in Scotland started mass gain earlier in the morning, compared to Coal Tits at lower latitudes in Spain (Polo et al. 2007). None of the populations of Coal Tits in Polo et al. (2007) were particularly limited by daylight

(7 h as absolute minimum daylength). Thus, one would expect the effect of daylength on foraging activity of Coal Tits to be even greater further north, where daylength is more limiting during winter. Moreover, Haftorn´s (1989) findings show that daylength may be one of the main drivers of mass gain and fat storage during winter at northern latitudes. Resident birds at higher latitudes store more fat during winter, than their counterparts at lower latitudes (Blem 1975, Nolan & Ketterson 1983). For this reason, one can expect that artificial light may affect onset of foraging to a greater degree further north, where daylength decreases quickly with increasing latitude during winter. Our results indicate that artificial light may influence the onset of foraging in the morning, and thereby the length of the period available for foraging during the day. Further, it indicates that when daylight is completely absent during polar night, twilight may represent the minimum amount of light level needed for birds to commence foraging.

Conclusion

This field study highlighted the positive effects that artificial light may have on foraging activity in resident birds and how daylength in relation to latitude affects foraging activity during winter. Findings from our field experiment show how artificial light may provide an opportunity to start foraging earlier in the morning when daylight is a limited resource. Moreover, the natural variation in daylength in relation to latitude may also play an important role in foraging activity of resident birds during winter. The magnitude of the effects of artificial light on resident birds during winter in the most northern areas has not yet been established, but one may expect that artificial light will have stronger effects than further south. Thus, it is important to understand the natural foraging adaptations of birds to polar nights and how urbanization and light pollution affects and possibly changes those adaptations, especially given steadily increasing human impacts across the globe, including northern areas.

Acknowledgements. We would like to thank Marlene Istad Rye for assistance with illustrating the schematic sketch of the experimental setup, Arild Johnsen for comments on a previous version of the manuscript and two anonymous reviewers for comments.

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