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The effect of artificial light and latitude on foraging activity in resident passerines in Northern Europe

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Abstract

Over the last couple of decades, there has been an increasing interest in the ecological consequences of artificial light on wildlife. At northern latitudes, winter is characterized by short days and low temperatures, compared to winter climate at lower latitudes. In these conditions, resident birds need a higher food intake to sustain their metabolism and maintain body temperature. Artificial light may prolong forage opportunities for resident birds during winter. The main objective of this thesis was to investigate if six resident passerine species would utilize artificial light by commence foraging before sunrise and continue after sunset. Further, by conducting a meta-analysis, an objective was to investigate if onset of foraging was correlated with latitude. Two feeding stations, one illuminated and one control, were placed in a forest area in Ås, Norway. A camera was placed in front of each feeding station to record daily activity of the passerines in December and February. In December, the great tit commenced foraging earlier relative to sunrise when artificial light was present, but was not affected by artificial light to continue foraging after sunset. In February, the great tit was not stimulated by artificial light to commence foraging before sunrise, nor continue to forage after sunset. Artificial light did not affect earlier onset of foraging at sunrise in *Poecile* sp. There was not enough data to do analyses for the other passerine species. Great tit´s onset of foraging was correlated with latitude. At the northernmost location, the great tit commenced foraging several hours before sunrise, compared to the southernmost location, where the great tit commenced foraging only a few minutes before sunrise. The great tit started foraging relatively early despite the absence of daylight at the northernmost location. These results suggest that some resident passerine species may utilize artificial light to prolong their foraging activity during midwinter, and that onset of foraging is limited by daylength at northern latitudes. Further, that early onset of foraging increases with increasing latitude, and that light levels at twilight might be the minimum light level needed for resident birds to commence foraging.

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Introduction

Over the last decades, there has been an increasing interest in the ecological consequences of artificial lighting on wildlife (Bird & Parker, 2014; Byrkjedal et al., 2012; Kotler, 1984; Rand et al., 1997; Rydell, 1992; Salmon et al., 1995; Van Doren et al., 2017). The increase in artificial light is strongly correlated with human urbanization, and as urbanization is predicted to expand, so is the usage of artificial light (Gaston et al., 2015; Hölker et al., 2010). On the one hand, urbanization can drive organisms away and reduce biodiversity by enhancing habitat fragmentation and loss (Concepción et al., 2015; Geslin et al., 2013). On the other hand, urban areas can create opportunities for organisms that can take advantage of the resources available. A range of animals, birds in particular, use urban landscapes as shelter, exploit the greater food opportunities, and utilize the heat emitted from cities and households (Ancillotto et al., 2015; Bateman & Fleming, 2012; Lausen & Barclay, 2006). The ecological consequences of artificial light are starting to be explored, but more research is needed to determine all 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 are alterations in reproduction (Russ et al., 2017; Zhang et al., 2014) and timing of singing (Da Silva et al., 2014; Kempenaers et al., 2010). The majority of studies on the effect of artificial light on birds focus on how it affects birds during 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, maintenance behaviors, such as foraging, which is crucial for survival, has been less explored in relation to artificial light. This emphasizes the need for more research regarding this topic, in particular since the majority of birds´ life span take place outside the breeding season.

There are studies of diurnal animals from a range of taxa that feed close to artificially lighted areas (Bolton et al., 2017; Frank et al., 2019; Heiling, 1999; Minnaar et al., 2015). Several of these studies are of birds utilizing artificial light when foraging (Bakken, 1977; Foley & Wszola, 2017; Lebbin et al., 2007; Russ et al., 2015; Santos et al., 2010). Common nighthawks (*Chordeiles minor*) have been observed foraging in artificial light nearby the Washington Monument together with bats (Chiroptera) after sunset (Foley & Wszola, 2017). Likewise, blue tits (*Cyanistes caeruleus*) and black-headed gulls (*Chroicocephalus ridibundus*) have been observed utilizing the same light source at night during winter (Blackett, 1970)**.** Furthermore, house sparrows (*Passer domesticus*) have been observed foraging in floodlights around the Empire State Building. The house sparrows foraged for insects several hours after sunset (Brooke, 1973).

Most of the studies of diurnal birds utilizing artificial light occurred during more favorable and clement environmental conditions. What would be the consequences of artificial light for 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 active, and some foraging, nearby 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, short days and low temperatures make foraging more challenging. Short days imply less time to forage and low temperatures demand a higher food intake to sustain metabolism through long and cold nights (King & Mewaldt, 1981; Newton, 1969; Nice, 1938). During short days, artificial light may have a greater impact on birds, since daylight already is a limiting resource. Smaller birds, such as titmice (*Baeolophus*), may be more exposed to low temperature 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 survival of resident titmice.

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

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

Clewley et al. (2016) and Da Silva et al. (2017) studied the effects of artificial light on foraging activity in resident passerines, but did not find any notable effects. However, both studies were conducted in Central Europe. Conducting a similar study further north might increase the effects of artificial light on foraging activity. Daylength decreases with increasing latitude in winter (List, 1949). Hence, northern latitudes may force passerines to start foraging earlier in the morning to optimize fat storage, and prevent starvation and hypothermia. In contrast to daylength, morning civil twilight (hereafter twilight) increases with increasing latitude (List, 1949). Thus, the light level during twilight might be adequate for foraging, and therefore might represent a potential time for the onset of foraging. Moreover, artificial lighting may enhance an even earlier start of foraging, offering light to make foraging easier.

Accordingly, I aim to study to which extent artificial light and latitude affect the foraging activity in resident passerines in the winter in Southern Norway. I predict that resident passerines will commence foraging earlier in the morning and extend foraging after sunset when (1) when artificial light is present and (2) when the temperature is considerably lower (more food is needed to prevent fat loss during the night), (3) artificial light will have less effect when the days are getting longer and the temperature increases. Finally, by conducting a meta-analysis, I predict that (4) earlier onset of foraging will increase with increasing latitude.

Materials and methods

Study site

The study area is located in Ås, Norway, a village in Viken municipality (Figure 1). 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 are mostly planted) mixed with shrubs. The two sites selected (site 1: 59° 38´40.2″ N, 10° 48´13.5″ E; site 2: 59° 38´ 37.6″ N, 10° 48´18.6″E) were 100 m apart (Figure 1). Distance to the closest road (a low traffic road) and settlements were > 100 m.

Figure 1. Map of the study area Ås, Norway with the location of the bird feeders; site 1 and site 2. Maps are provided by Kartverket (2020).

Experimental design

At each site, a single feeder (Supa feast wild bird feeder) with multiple food chambers (four food chambers, two on each side) was placed (Figure 2). The feeders stood 1.5 m above ground. The feeders were filled with whole sunflower seeds and were refilled every day. A camera (Brinno TLC200 Pro) was placed at each site 0.5 m away from the feeder. Only the food chambers facing the camera were open. The field of view of the camera covered the part of the feeder with open chambers and some of the vegetation around the feeder. The camera was kept in a water-proof container. An infrared-emitting light was placed right in front of the camera to light the feeder in dark conditions. At each site a LED spotlight (70W) was placed in a tree above the feeder to light the area of the feeder to simulate street lights. Each spotlight had one bulb and emitted white, warm light. The cameras were powered by rechargeable batteries, which were changed every day. The IR-lights were powered by batteries placed right next to the feeders and the artificial light by multiple 50 m extension cords to the closest house.

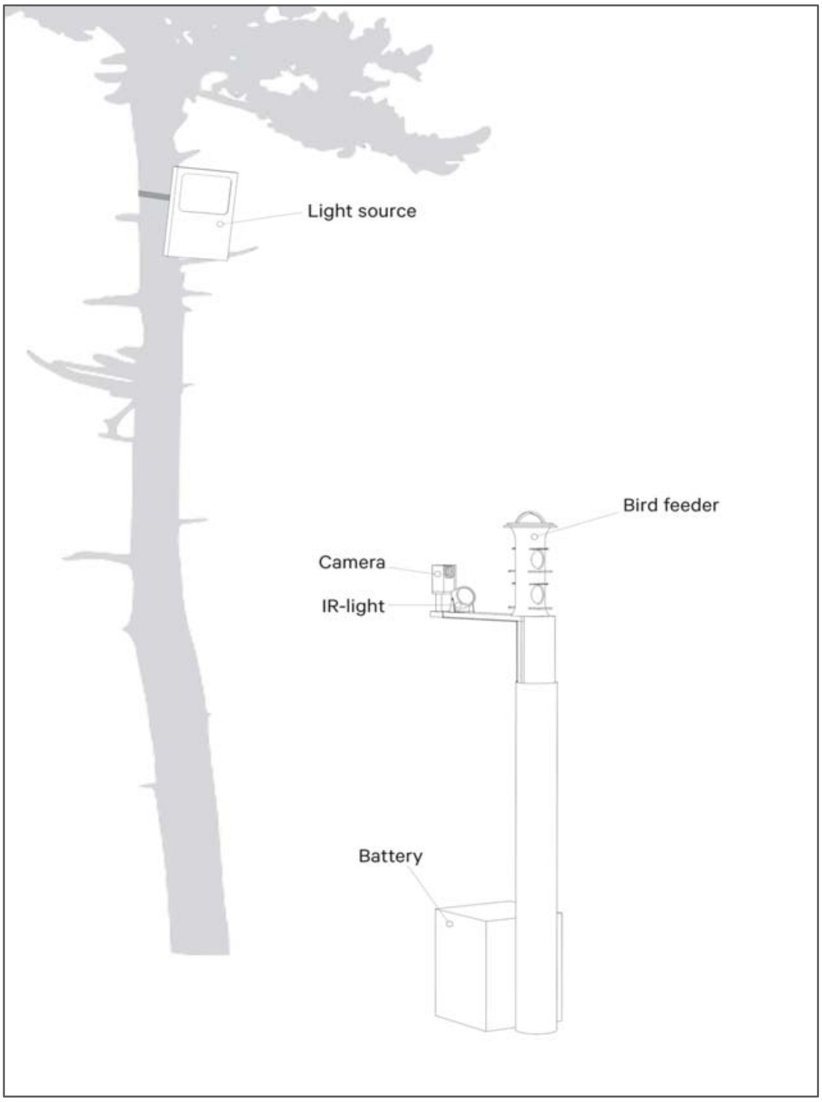

Figure 2. Schematically sketch of the experimental set up.

Experimental procedure

The first field experiment took place during 8-31 December and started in the morning on the 8 and ended in the evening on the 31. One site was illuminated (illumination phase), while the other was not (control phase). Illumination phase lasted for ten days at one site, parallel control phase lasted for ten days at the other site. After ten days, there was a break where both sites were without illumination for two days to allow the passerines to adjust to the light switch. After those two days, illumination phase was switched to the site that last had control phase (and vice versa) to control for habitat differences at the sites. For ten more days, one site had illumination phase, while the other site had control phase.

The experiment in February and March took place during 9 February – 9 March. It started 9 February in morning and lasted until 9 March in evening. Illumination phase lasted for seven days, parallel control phase lasted for seven days at the other site. After seven days, illumination phase was switched to the other site and vice versa the evening of the seventh day. The morning after the light switch, the next seven days period would start. Which site that was illuminated was switched every seventh day two hours after sunset. There were no breaks. The passerines quickly adapted to the light switch in December, therefore the breaks were omitted in February and March.

For both field experiments, the lights were manually turned on and off by switching which site that was connected to the extension cords. The light on the site that was illuminated was on for 24 hours for the whole period. The cameras were pre-programmed to record from two hours before sunrise until two hours after sunset. Throughout both field experiments, the illuminance in the area of the feeder was measured by using a light meter (Light Meter MT-906). Two types of measurement were conducted in the field. One to get a trend of the change in light conditions during sunrise and sunset (M1, see below) and another of the glares from the artificial light after sunset (M2, see below). Additionally, weather conditions were noted down daily at sunrise and sunset during the recordings (M3, see below).

Change in light conditions (M1)

The change in light conditions was measured during sunrise and sunset and lasted for two hours. During sunrise, the measurements started two hours before sunrise and lasted until the sun had risen (Figure 3). During sunset, the measurements started at the time the sun set and lasted for two hours after sunset (Figure 4). The light was measured every 20 minutes for both sites (a total of seven times). The light measurements were conducted during each seven- and ten days period. Two days of measurements were done in each period with two days in a row. Since both sites were measured on the same days, I had to first measure at one site before walking to the next site. The time difference for measurements at one site to the next was about 1 minute. To control for the time difference during measurements every 20 minutes between the two sites, I would switch which site that was measured first (i.e. if site 1 was the first one to be measured one day, the next day site 2 was the first to be measured). 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 measurements, lux was measured every first, fifth and tenth second when measuring every 20 minutes. The median value of the three measurements (first, fifth and tenth second) was used.

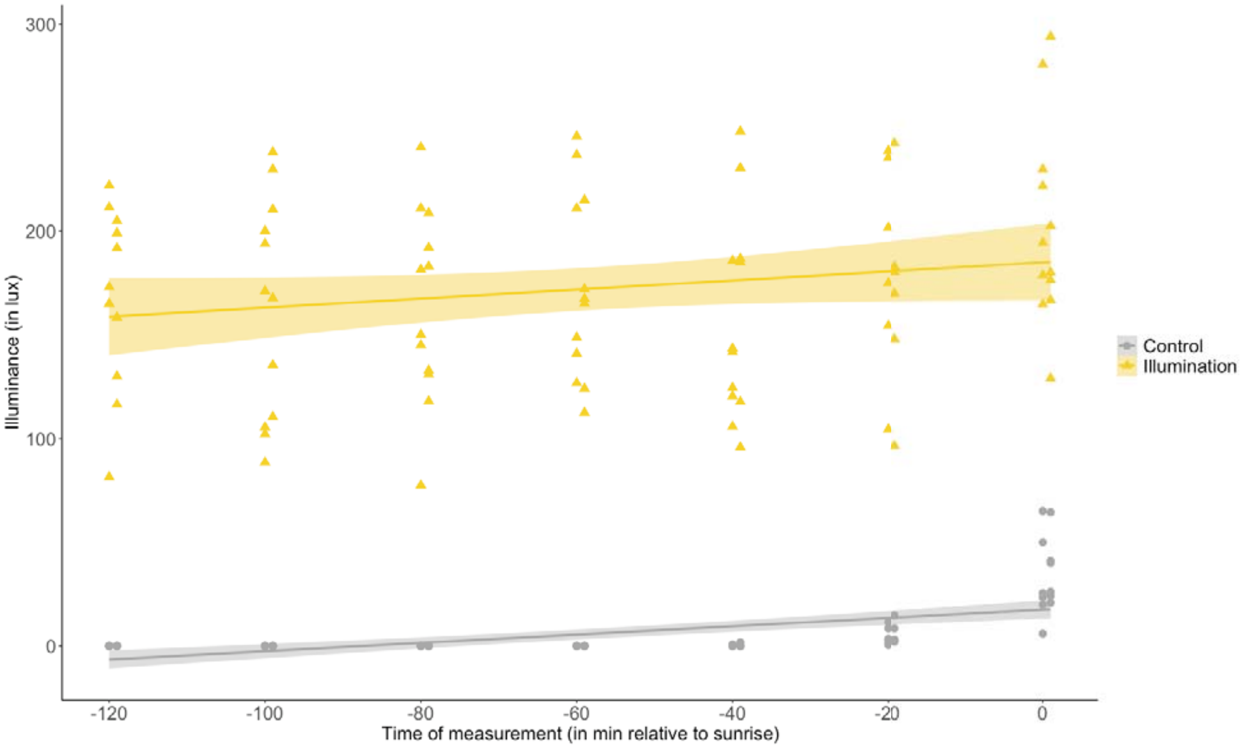

Figure 3. Change in light conditions (lux) during sunrise. The yellow (illumination) and grey (control) horizontal lines indicate the mean lux value. The yellow and grey areas around the horizontal lines indicate the 95% confidence intervals. The values of the y-axis indicate level of illuminance measured in lux. The values of the x-axis represent time in minutes relative to sunrise. The negative values indicate minutes before sunrise, where 0 is the time of sunrise.

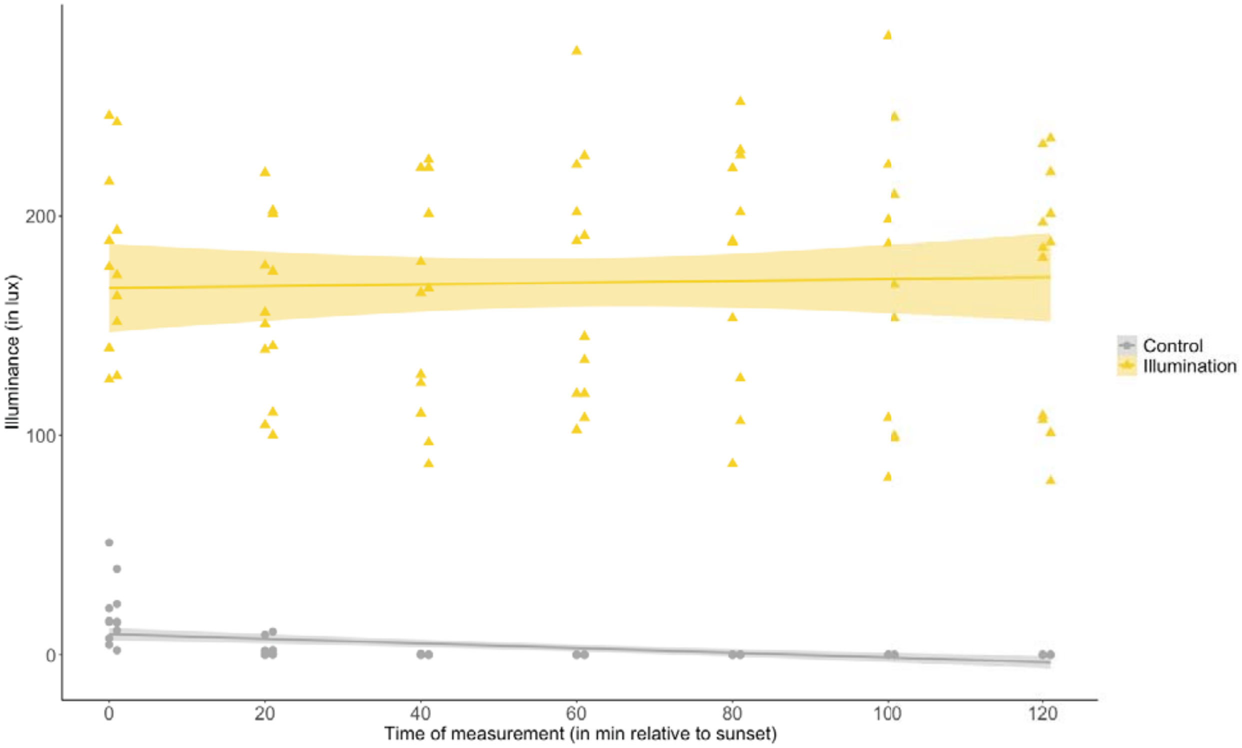

Figure 4. Change in light conditions (lux) during sunset. The yellow (illumination) and grey (control) horizontal lines indicate the mean lux value. The yellow and grey areas around the horizontal lines indicate the 95% confidence intervals. The values of the y-axis indicate level of illuminance measured in lux. The values of the x-axis represent time in minutes relative to sunset. The values indicate minutes after sunset, where 0 is the time of sunset.

Level of glare (M2)

In February, the level of glare (in lux) was measured after sunset in the area around the feeder as an additional measurement (Figure 5). Using the feeder as center, level of glare was measured in each cardinal direction at 0, 5, 10, 15, 25 and 30m away from the feeder (where 0m had the same spot of measurement as in M1, right next to camera). During these measurements, the light meter (and I) was 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 only measured at the feeder with artificial light.

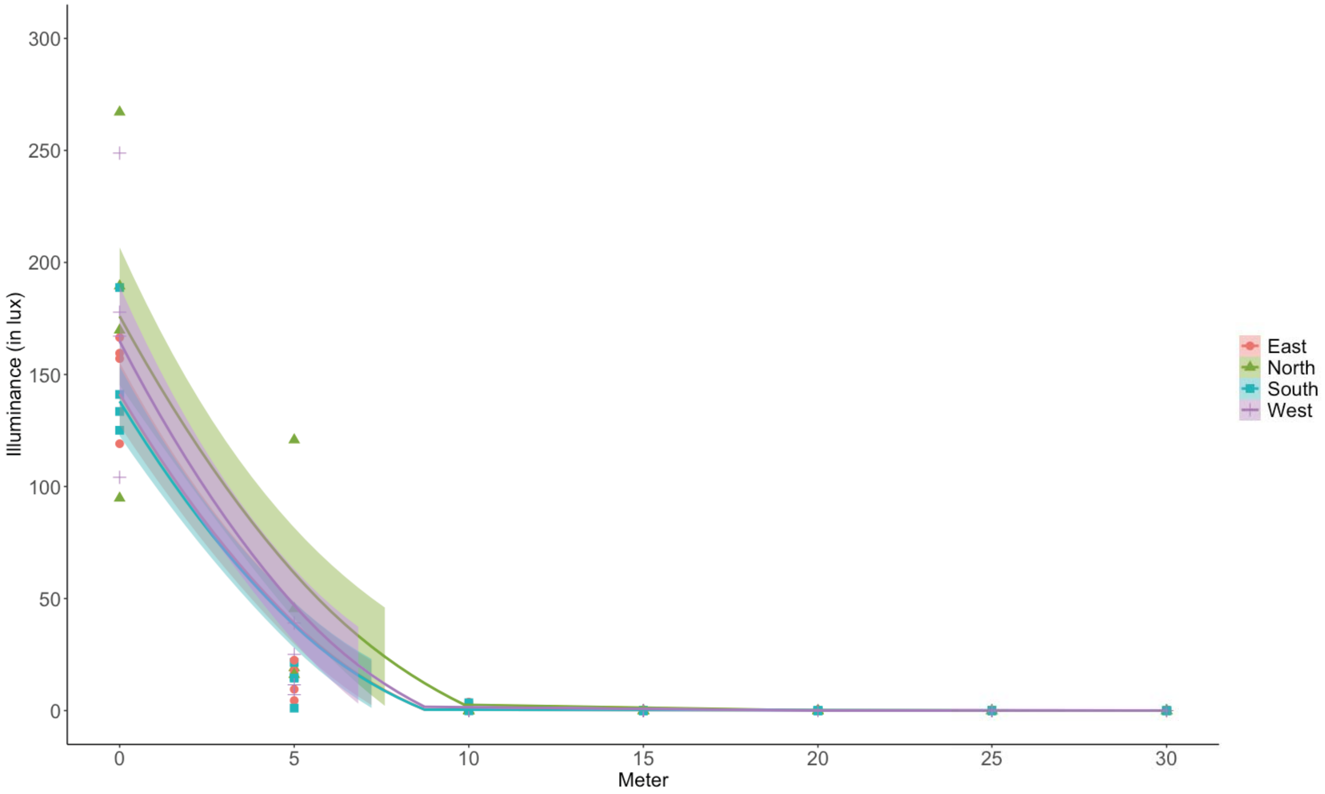

Figure 5. Level of glare (measured in lux) at sunset in the cardinal directions. The values of the x-axis indicate meters distance to a bird feeder. Lux was measured at 0, 5, 10, 15, 20, 25, and 30 meters distance to a bird feeder, where 0m is the spot of the feeder. The values of the y-axis indicate level of illuminance measured in lux. The red (east), green (north), blue (south), and purple (west) horizontal lines indicate the mean value of lux in each cardinal direction. The red, green, blue and purple areas around the horizontal lines indicate the 95% confidence intervals of lux in each cardinal direction.

Weather conditions (M3)

During the field experiment, weather conditions were measured daily at sunrise and sunset. Weather conditions included temperature (in degrees of Celsius), wind strength, cloud cover and precipitation. Wind strength was scored by using Beaufort wind scale. Cloud cover was determined as clear (0), partly cloudy (1), mostly cloudy (3) or overcast (4). Precipitation was determined as rain or snow (yes) or none (no). Daily timing of sunrise and sunset was extracted from timeanddate.no. The data for the weather conditions were extracted from yr.no.

Data extraction

Videos were collected each day, in the middle of the day or after the evening records to not disturb the birds during sunrise and sunset. All videos were saved on an external hard disk. The data was extracted manually by using VLC media player 2.2.5.1. For each day and for each site, all visits two hours before sunrise until one hour after sunrise were noted down (the camera ran from two hours before sunrise until one hour after sunrise). The same was the case for all visits one hour before sunset until two hours after sunset (the camera ran from one hour before sunset until two hours after sunset). Afterwards, the three first visits before sunrise and the three last visits after sunset for each species were converted into minutes and seconds relative to local sunrise and sunset. A bird was considered foraging whenever it was recorded taking a sunflower seed in its beak. The majority of visits were of birds foraging. Still, there were occasions were individuals of birds visited the feeders without taking any seeds. These observations made up 2.78% of the total amount of observations (1115). Additionally, red squirrels (*Sciurus vulgaris*) were foraging at the feeders. The red squirrels´ visits made up 7% of the total amount of observations.

The data analyses were run on the six passerine species appearing on the feeders, the great tit (*Parus major*), the blue tit, the coal tit (*Periparus ater*), the marsh/willow tit (*Poecile palustris/ Poecile montanus*) and the Eurasian nuthatch (*Sitta europaea*). The marsh and willow tit (hereafter *Poecile* sp.) were merged because species identification was often too challenging. I had no method to distinguish between different individuals of the six species. Therefore, I cannot exclude the possibility that the same individuals visited the same feeder several times or visited both feeders.

Site 1 was rarely visited during the whole field period. Consequently, this led to that analyses that compared the treatment illumination/control were mostly based on data from the same site, but at different time periods. In December, data for illumination phase is from 9 and 20-31 December. For control phase, the data is from 9-11, 13 and 15-17 December. In February and March, the data for illumination phase is from 15, 20 and 25-27 February and 3 March. For control phase, the data is from 16-20 and 22-23 February and 3 and 8 March.

Statistical analyses

For each species, their appearance at sunrise and sunset in relation to illumination was analyzed using unpaired two-sample Wilcoxon tests. Onset of foraging (relative to sunrise) and end of foraging (relative to sunset) were response variables and illumination (illumination/control) was the explanatory variable. The unpaired two-sample Wilcoxon tests were both two-tailed and one-tailed. I chose to do one-tailed tests since I expected the birds to commence foraging earlier at sites with illumination. One-tailed p-values are stated in addition to the two-tailed p-values.

I used multiple linear regression models to analyze the relation between foraging activity, illumination and temperature for each species. Onset of foraging (relative to sunrise) and end of foraging (relative to sunset) were the response variables. Illumination (illumination/control) and temperature were the explanatory variables. Overall, there were too few observations to include many explanatory variables. Therefore, the weather conditions cloud cover, wind and precipitation were omitted from the regression analyses. Temperature was the only weather variable used in the analyses since it´s included it the hypothesis with specific predications. There were in general few days with inclement weather, and the days that had inclement weather were evenly distributed between illumination and control phase.

Data for great tit had outliers from 9 December, the second day of the field experiment. To assess the effect of the outliers, I ran the same analyses without the outliers (onset of foraging 50.87, 52.17 and 53.24 minutes after sunrise) for great tit. Additionally, I ran diagnostic plots of the great tit dataset to assess the influence of the outlier on the linear regression model. The outliers are from the second day of the field experiment. The birds may therefore not have been adjusted to the light yet. Thus, there are both statistical and methodical arguments to remove the outliers from the analyses.

In December, blue tit, coal tit and Eurasian nuthatch had <5 observations at sunrise and sunset (Appendix 1). In February, only great tit had >5 observations at sunrise. The other species had <5 observations both at sunrise and sunset (Appendix 2). Thus, statistical analyses could not be executed and the analyses shown in the results are only for the species with >5 observations.

Meta-analyses were conducted using Spearman´s rank correlation coefficient and Pearson´s correlation coefficient analyses. For great tit, the onset of foraging relative to sunrise and twilight in relation to latitude (N°) were analyzed. To find studies with relevant data for the meta-analyses, I searched through a range of literature. The data for the meta-analysis were extracted from the result tables and texts of four studies (Table 2) with different locations and different latitudes (Da Silva et al., 2017; Haftorn, 1994; Pulliainen, 1980; von Haartman, 1975), including own 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, the mean onset was calculated. The mean onset of foraging was calculated using data from the result texts and tables that contained the individual onsets of foraging in great tit. The data was extracted from Table 1 in Da Silva et al. (2017), Table 1 in Haftorn (1994), the result text in Pulliainen (1980) and Table 1 in von Haartman (1975). The local time for sunrise and twilight at each location were extracted from timeanddate.no. For the location in Svanvik, Norway (Haftorn, 1994), there was no timing for sunrise because of the polar night at midwinter. For this reason, “sunrise” in Svanvik was defined as when the sun passes the location of the local meridian, as this is the time when the sun has the highest position on the sky.

All analyses were conducted using R-studio and the R stats package (R Core, 2018; RStudio, 2016). P-values lower than 0.05 were considered as significant. All figures were made using the packages ggplot2 and graphics in R-studio (Hadley, 2016; R Core, 2018).

Results

Foraging in great tit in December

In December, great tits commenced foraging significantly earlier relative to sunrise during illumination phase, compared to control phase (Figure 6, n = 19, two-tailed p = 0.0020, one-tailed p = 0.0010). During illumination phase, great tits commenced foraging on average 34.22 minutes before sunrise. During control phase, great tits commenced foraging on average 13.98 minutes before sunrise. Foraging started significantly earlier during illumination phase also when taking temperature into account (Table 1, p = <0.001). Some evidence was found for that onset of foraging was affected by temperature (p = 0.059) in the first visit, but not in the second and third visit (table 1). Illumination did not have an effect on the end of foraging at sunset (n = 9, two-tailed p = 0.90, one-tailed p = 0.65), nor did temperature (p = 0.90).

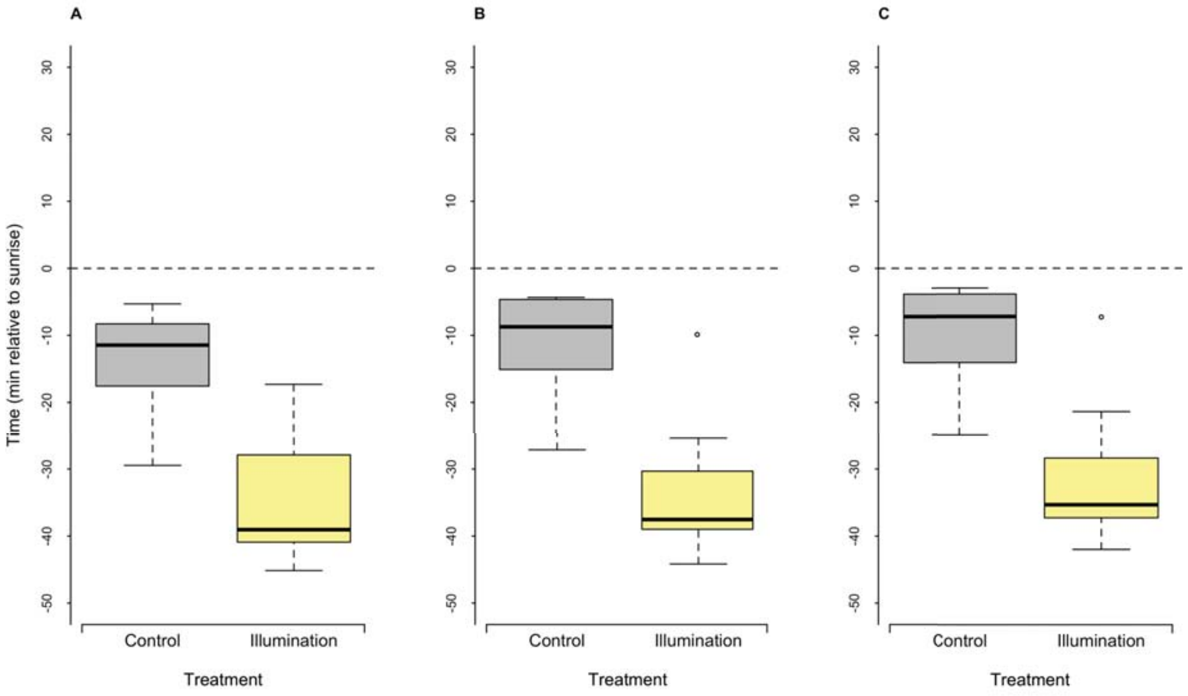

Figure 6. Onset of foraging in relative to sunrise in great tit (Parus major), December 2018. Shown are boxplots with first visit (A), second visit (B), third visit (C), medians (bold horizontal lines), upper – and lower quartiles (whole horizontal lines) and minimum and maximum values (vertical dashed lines). The boxplots represent a feeding station during illumination phase (yellow box plots) in A (n = 12), B (n =11), and C (n = 11) and control phase (grey box plots) in A (n = 7), B (n = 7), and C (n = 7). Negative values indicate time before sunrise and positive values indicate time after sunrise. The dashed horizontal line indicates sunrise

Table 1. Effect of illumination and temperature on the onset of foraging at sunrise in great tit (Parus major). Shown are first visit (n = 19), second visit (n = 18) and third visit (n = 18) with associated coefficients, in December 2018. Significant variables are highlighted in bold.

Visit no.[a]	Predictors	Estimate[b]	SE	t	p
1	intercept	-11.11	3.46	-3.22	0.0054
	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] Mean onset of foraging for first, second and third visit relative to sunrise.
[b] Minutes relative to sunrise.

Foraging in *Poecile* sp.

In December, *Poecile* sp. did not commence foraging earlier relative to sunrise during illumination phase (n = 9, two-tailed p = 0.16, one-tailed p = 0.95), compared to control phase. During illumination phase, *Poecile* sp. commenced foraging on average 33.68 minutes after sunrise. During control phase, *Poecile* sp. commenced foraging on average 9.50 minutes after sunrise. Temperature did not have an effect on earlier onset of foraging (Table 2). There were not enough data to do statistical analyses on the end of foraging relative to sunset in *Poecile* sp. Neither were there enough data to do statistical analyses on the onset of foraging at sunrise and end of foraging at sunset in the other four species.

Table 2. Effect of illumination and temperature on the onset of foraging at sunrise in marsh/ willow tit (Poecile palustris/ Poecile montanus). Shown are first visit (n = 9), second visit (n = 8) and third visit (n = 7) with associated coefficients, in December 2018. The species are merged (Poecile sp.).

Visit no.[a]	Predictors	Estimate[b]	SE	t	p
1	intercept	1.27	10.81	0.12	0.91
	illumination	18.56	15.41	1.20	0.27
	temperature	-2.60	2.11	-1.23	0.26
2	intercept	1.60	11.65	0.14	0.90
	illumination	20.62	16.97	1.22	0.28
	temperature	-2.29	2.26	-1.01	0.36
3	intercept	3.84	11.37	0.34	0.75
	illumination	28.41	18.82	1.51	0.21
	temperature	-2.22	2.21	-1.01	0.37

[a] Mean onset of foraging for first, second and third visit relative to sunrise.
[b] Minutes relative to sunrise.

Foraging in great tit in February

In February, illumination did not have an effect on onset of foraging in great tits (Figure 7, n = 14, two-tailed p = 0.95, one-tailed p = 0.47). During illumination phase, great tits commenced foraging on average 34.92 minutes after sunrise. During control phase, great tits commenced foraging on average 36.80 minutes after sunrise. Temperature did not have an effect on onset of foraging (Table 3). There were not enough data to do statistical analyses on the end of foraging at sunset. Neither were there enough data to do statistical analyses on the onset of foraging at sunrise and end of foraging at sunset in the other species.

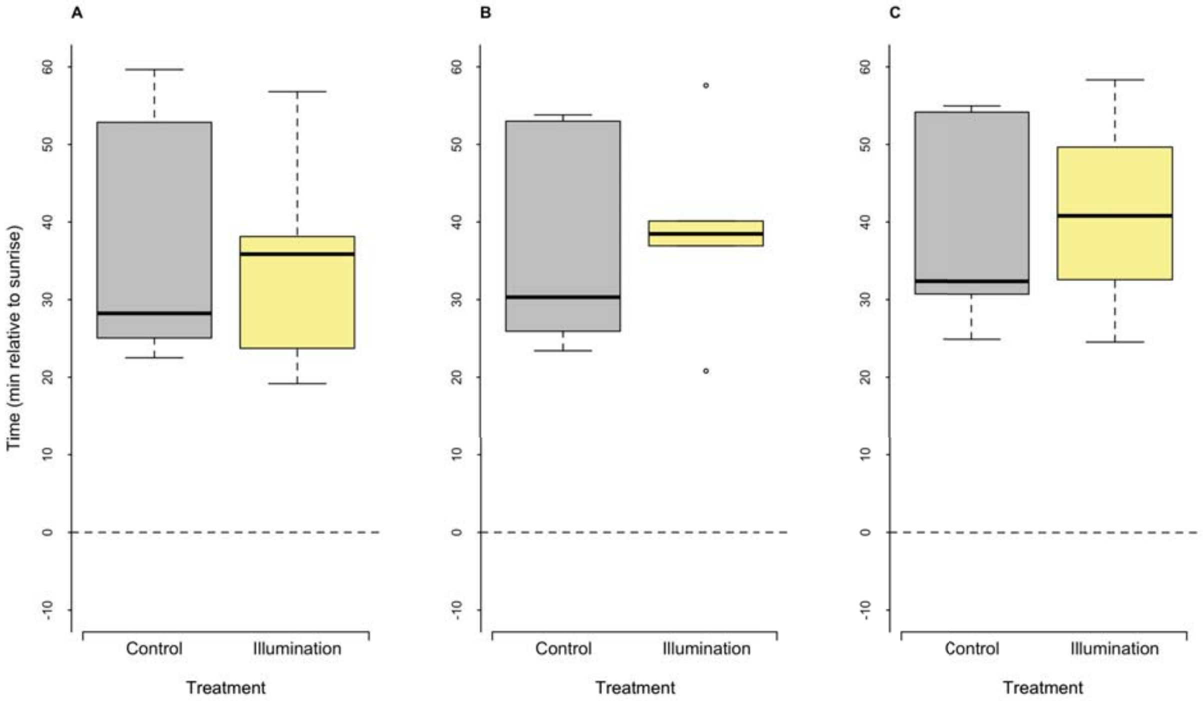

Figure 7. Onset of foraging (first visit) relative to sunrise for great tit (Parus major), February 2019. Shown are boxplots with first visit (A), second visit (B), third visit (C), median (bold horizontal line), upper – and lower quartile (whole horizontal lines) and minimum and maximum values (vertical dashed lines). The boxplots represent feeding station during illumination phase (yellow box plots) in A (n = 6), B (n =5), and C (n = 4) and control phase (grey box plots) in A (n = 9), B (n = 7), and C (n = 6). Negative values indicate time before sunrise and positive values indicate time after sunrise. The dashed horizontal line indicate sunrise.

Table 3. Effect of illumination and temperature precipitation on the onset of foraging at sunrise in great tit (Parus major). Shown are first visit (n = 15), second visit (n = 12) and third visit (n = 10) with associated coefficients, in February 2019.

Visit no.[a]	Predictors	Estimate[b]	SE	t	p
1	intercept	36.72	5.76	6.38	<0.001
	illumination	-1.86	8.22	-0.23	0.83
	temperature	0.07	1.85	0.04	0.97
2	intercept	39.16	6.49	6.03	<0.001
	illumination	1.81	8.26	0.22	0.83
	temperature	-1.82	2.04	-0.89	0.40
3	intercept	43.02	7.45	5.78	0.0012
	illumination	1.10	9.51	0.12	0.91
	temperature	-2.01	2.19	-0.91	0.41

[a] Mean onset of foraging for first, second and third visit relative to sunrise.
[b] Minutes relative to sunrise.

Meta-analyses

Great tits´ onset of foraging in relation to sunrise was negatively correlated with latitude (Figure 8, Table 7, n = 7, rho = -1, p = < 0.001). With increasing latitude, great tits commenced foraging earlier relative to sunrise. Great tits´ onset of foraging in relation to twilight was not significantly correlated with latitude (Figure 9, n = 7, rho = -0.61, p = 0.17), although at the northernmost site (Svanvik), great tits commenced foraging well before twilight.

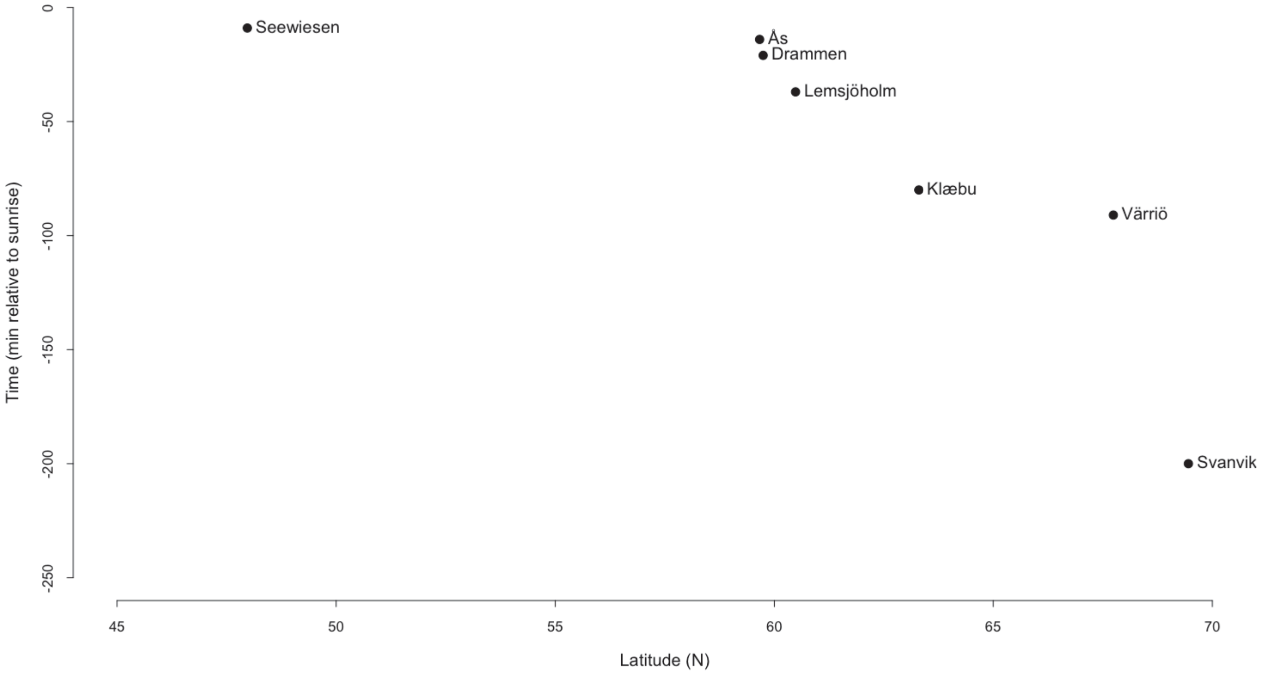

Figure 8. Onset of foraging at sunrise in great tits (Parus major) in relation to latitude (N°) during midwinter. Shown are data points with mean onset of foraging at different latitudes. The y-axis represents minutes before sunrise (negative values). The x-axis represents degrees of latitude. The datapoints are extracted from studies with different locations and latitudes, including own data (n = 7).

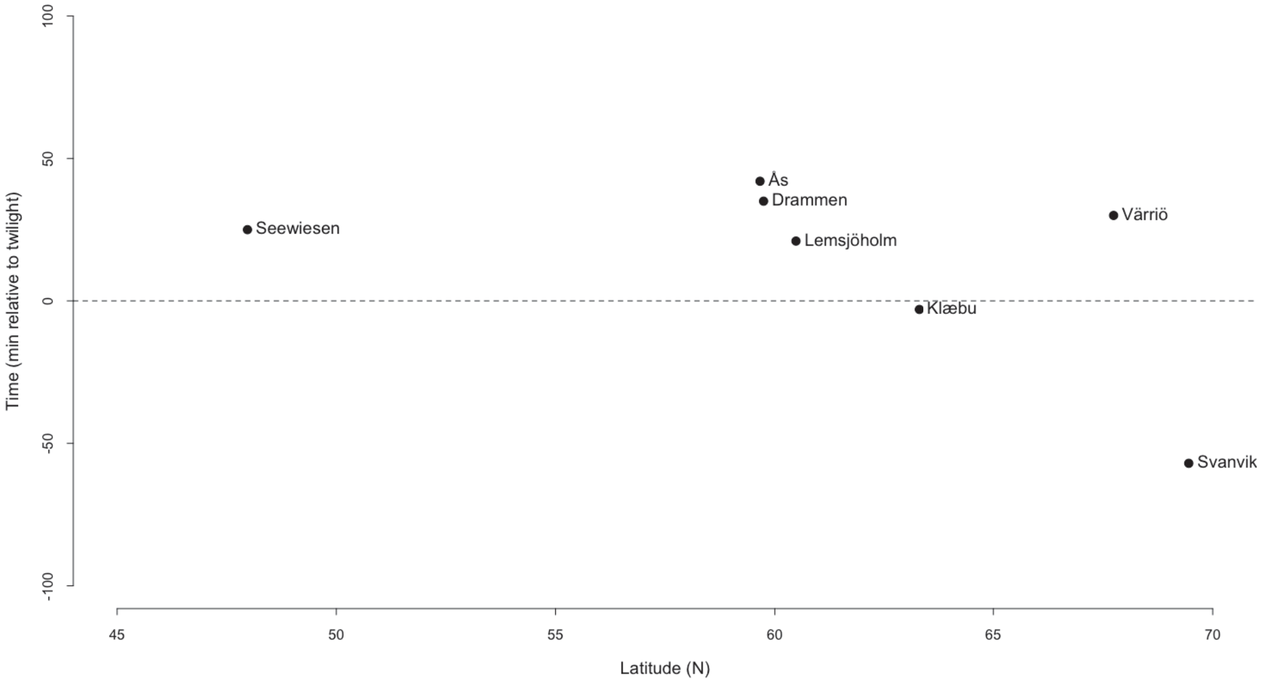

Figure 9. Onset of foraging at morning civil twilight in great tits (Parus major) in relation to latitude (N°) during midwinter. Shown are data points with mean onset of foraging at different latitudes. The y-axis represents minutes relative to morning civil twilight. The x-axis represents degrees of latitude. The datapoints are extracted from studies with different locations and latitudes, including own data. Negative values indicate time before morning civil twilight and positive values indicate time after morning civil twilight. The dashed horizontal line indicate twilight (n = 7).

Table 4. Mean onset of foraging in great tit (Parus major) at sunrise and morning civil twilight in relation to latitude and study site. Negative values indicate minutes before sunrise and morning civil twilight.

Area	Latitude (N°)	Min relative to sunrise	Min relative to twilight	Source
Seewiesen, Germany	47.97	-9	25	Da Silva et al., 2017
Ås, Norway	59.64	-14	42	Present study
Drammen, Norway	59.75	-21	35	Haftorn, 1994
Lemsjöholm, Finland	60.50	-37	21	von Haartman, 1975
Klæbu, Norway	63.25	-80	-3	Haftorn, 1994
Värriö, Finland	67.73	-91	30	Pulliainen, 1980
Svanvik, Norway	69.45	-200	-57	Haftorn, 1994

Discussion

All in all, there were too few observations to do statistical analyses for blue tit, coal tit and Eurasian nuthatch. Repeating the field experiment in another area, where the birds are used to supplemental feeding, could have provided data for the remaining species. Nevertheless, despite small sample sizes and lack of data for some species, there were sufficient data to provide evidence in support of several of my predictions on the response of great tits to artificial light.

In line with my first prediction, in December, great tits commenced foraging earlier at sunrise during illumination phase, compared to control phase. First visit, as well as second and third visit, were significantly affected by artificial light. *Poecile* sp. was not affected by the artificial light to commence foraging earlier relative to sunrise. Artificial light did not seem to affect the end of foraging relative to sunset in any of the species. There was limited evidence for my second prediction (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 second and third visit in relation to temperature showed similar trends. In concurrence with my third prediction, in February, great tits did not commence foraging earlier relative to sunrise, compared to the onset of foraging in December. Great tits commenced foraging earlier both during illumination phase and control phase in December, compared to the onset of foraging in February. In line with my fourth prediction, great tits´ onset of foraging in relation to sunrise was significantly correlated with latitude. At the northernmost location, great tits commenced foraging several hours before sunrise, while at the southernmost location great tits commenced foraging only minutes before sunrise. Onset of foraging in relation to twilight was not significantly correlated with latitude. Thus, twilight may be the minimum light level needed to commence foraging.

Foraging in great tit

Great tit´s earlier onset of foraging, in December, shows resemblance to the findings of Byrkjedal et al. (2012) and McNamara et al. (1994). Passerines were observed 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 (Becker et al., 2013; Czarnecka et al., 2019;

Minnaar et al., 2015; Negro et al., 2000; Rydell, 1991; Yurk & Trites, 2000). Though, my findings should not be surprising, particularly since feeding is more crucial during winter, and that small passerines, such as great tits, need a higher food intake to prevent hypothermia (Chaplin, 1974; King & Farner, 1966). In contrary, my results showed different patterns than previous findings (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 in Clewley et al. (2016) and Da Silva et al. (2017) were conducted at lower latitudes (Great Britain and Germany), compared to my study site (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, my results suggest that artificial light may serve as a beneficial variable during foraging in resident birds at northern latitudes in winter.

The differentiation in onset of foraging in December and February is in line 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 commenced foraging earlier at low temperatures (Baldwin & Kendeigh, 1938; Rogers & Reed, 2003). Additionally, feeding rates (weight gain per hour) were higher during midwinter (Haftorn, 1989). In December, onset of foraging in great tits was trending to be significant in relation to temperature. My results are trending in the same direction as previous findings, which show that resident birds increase fat reserves during the coldest months (Evans, 1969; Helms & Drury, 1960; King & Farner, 1966; Newton, 1969; Senar et al., 1992). These findings indicate that foraging and high food intake is more crucial during midwinter when temperature is at its lowest and daylength at its minimum. However, Fitzpatrick (1997) did not find any correlation between onset of foraging and temperature in resident tits during winter. Although onset of foraging in relation to temperature was not significant in my findings, it was trending towards being affected by temperature. A bigger sample size might have shown that temperature effects the onset of foraging. Moreover, it may also be due to the time chosen for extraction of temperature data. The temperature was extracted for the same date as the corresponding video recordings. Birds may adjust foraging activity in relation to an upcoming period with low temperatures (Evans, 1969). Several researches define temperature as a prime factor for winter fattening and foraging (Cresswell, 1998; Evans, 1969; Gosler, 2002; King &

Farner, 1966; Lehikoinen, 1987). Therefore, temperature may play a more important role on the onset of foraging, which my results were trending in the same direction as.

Other factors, such as food availability and snow cover, may also play an important role in foraging activity during winter (Brotons, 1997; Lima, 1986; McNamara & Houston, 1990; Nakamura & Shindo, 2001). In my field experiment, there were too few observations to take the environmental variables cloud cover, wind strength and precipitation into consideration. However, I cannot conclude that other environmental variables than temperature affect foraging activity, particularly since a range of findings show the contrary (Brotons, 1997; Da Silva et al., 2017; Grubb, 1978; Nakamura & Shindo, 2001; Renner et al., 2012). Numerous environmental variables may affect foraging activity, however, some weather variables may be more prominent than others.

Foraging in *Poecile* sp.

Poecile sp. was not affected by artificial light to commence foraging earlier at sunrise. This shows resemblance to the finding by Da Silva et al. (2017) where *Poecile* sp. was the species commencing foraging the latest at sunrise. Hoarding species, such as willow tit and marsh tit, commence foraging later in the morning, compared to non-hoarding species, such as great tit. (Brodin, 2000). On the contrary, there are also finding of hoarding species gaining body mass faster in the morning, than non-hoarding species (Lilliendahl, 2002). However, this might be a consequence of hoarding, as hoarding species can find the food they already collected to quickly regain optimal body weight. Moreover, the interspecific differences in size and foraging strategy in *Poecile* sp. and great tits may play an important role in my findings. *Poecile* sp. is smaller, and thus might have lesser fat reserves relative to body size than great tits (Pilastro et al., 1995). If this is true, *Poecile* sp. may not utilize the feeding stations to the same extent as great tits. Moreover, Haftorn (1989) found significant differences in body weight gain during midwinter in *Poecile* sp. and great tits. Thus, interspecific differences in foraging strategies and fat reserves might be the reason why I did not find any effects in *Poecile* sp.

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 at the southernmost location. Onset of foraging was not significantly correlated with twilight. Hence, twilight seemed to be the minimum light level needed to commence foraging at all location, except the northernmost location, where great tits commenced foraging well before twilight. These results are for the first time shown in this study. Similar correlations have been shown further south in Europe, where coal tits at higher latitudes in Scotland commenced 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) where particularly limited by daylight (7h as absolute minimum daylength). Thus, one would expect the effect of daylength on foraging activity in 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 the effect to be generally greater further north, where daylength decreases quickly with increasing latitude during winter. Thus, my results indicate that light may be a crucial resource for foraging and therefore has the greatest effects furthest north, where light is a strongly limiting resource during winter. Further, it indicates that when daylight is completely absent (polar night), twilight may be the minimum amount of light level needed for birds to commence foraging.

Conclusion

This thesis highlights the effects artificial light may have on foraging activity in resident birds and how daylength in relation to latitude affects foraging activity during winter. My findings show how artificial light may provide an opportunity to commence foraging earlier in the morning when daylight is a limited resource. Moreover, that daylength in relation to latitude may play an important role in foraging activity in resident birds during winter. To which extent artificial light affects resident birds during winter in the most northern areas is not yet established and more research is needed. Additionally, more research is needed to determine the effect of latitude in relation to daylength on foraging activity. More specifically, to look at the effects at the northernmost locations, where daylight is absent during winter and where artificial light most likely has the greatest effect. Thus, to understand birds´ natural foraging adaptations to polar nights and how urbanization, in terms of light pollution, affects and possibly changes those adaptations is important given steadily increasing human impacts across the globe, including northern areas.

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Appendix

Appendix 1. Mean onset and end of foraging in great tit (Parus major), marsh/ willow tit (Poecile palustris/ Poecile montanus), blue tit (Cyanistes caeruleus), coal tit (Periparus ater) and Eurasian nuthatch (Sitta europaea) at sunrise and sunset during illumination and control phase, December 2018. Negative values indicate time (in min) before sunrise and sunset, while positive values indicate time after sunrise and sunset. Sample size is shown in the parentheses (NA = No observations).

	Sunrise		Sunset	
Species	Illumination	Control	Illumination	Control
Great tit	-34.22 (12)	-13.98 (7)	-12.01 (6)	-23.20 (3)
Poecile sp.	33.68 (3)	9.50 (6)	-32.19 (2)	-35.09 (3)
Blue tit	55.72 (1)	-7.52 (3)	NA	NA
Coal tit	13.83 (1)	20.04 (3)	NA	NA
Nuthatch	51.22 (1)	22.18 (4)	-28.14 (2)	NA

Appendix 2. Mean onset and end of foraging in great tit (Parus major), marsh/ willow tit (Poecile palustris/ Poecile montanus), blue tit (Cyanistes caeruleus), coal tit (Periparus ater) and Eurasian nuthatch (Sitta europaea) at sunrise and sunset during illumination and control phase, February 2018. Negative values indicate time (in min) before sunrise and sunset, while positive values indicate time after sunrise and sunset. Sample size is shown in the parentheses (NA = No observations).

	Sunrise		Sunset	
Species	Illumination	Control	Illumination	Control
Great tit	34.93 (6)	36.80 (8)	NA	-42.63 (1)
Poecile sp.	43.16 (1)	20.81 (1)	-34.46 (1)	NA
Blue tit	34.15 (1)	NA	NA	NA
Coal tit	NA	-24.04 (1)	NA	NA
Nuthatch	NA	32.00 (2)	NA	NA

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