Breeding in the city: different reproductive choices in urban areas in Blue and Great Tits?

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Abstract

The phenomenon of urbanization is an increasingly large biodiversity threat. Urban ecosystems have been exposed to fast environmental changes causing many species to go locally extinct or adapt. Two bird species that are doing really well in urban areas are Blue and Great Tits. The effect of urbanization on these bird species has been extensively studied. However, most of these studies were comparative studies where the definition of urbanization is not very clear. Therefore, more replicate studies are needed that study the relationships between breeding characteristics and urbanization based on quantified urbanization gradients. In this study, we developed a method for quantifying urbanization into four different components; light pollution, habitat structure, vehicle disturbance and human disturbance. During five weeks of nest box monitoring, data on nest box occupation and laying date of an urban Blue and Great Tits population was acquired. The study site had variation in the degree of urbanization. These data were then analyzed in relation to the four urbanization components. We found that Blue Tits start laying eggs later in habitats with a high ecological value. Additionally, both Blue and Great Tits had a preference for nest boxes with high levels of vehicle disturbance. All other urbanization components were not sufficient to induce significant variation in occupation and laying date. My results suggest that differences in urbanization between nest box within one urban population of Blue and Great Tits is not sufficient to induce significant variation in occupation and laying date. These results contribute to our knowledge on the relationships between wildlife and urbanization.

Introduction

Urbanization is a major human-induced biodiversity threat (Branston et al 2021). In 1950 ca. 30% of the world population lived in cities, the 50% line was crossed in 2008 and this trend is not expected to be stopped in the near future (UN-habitat 2010). Urban areas generally have increased ambient temperatures due to the heat-island effect, are sources of light, sound and chemical pollution, vegetation has been replaced by buildings and roads and non-native species have increased (McKinney 2002 ; Foley et al. 2005). This process has caused many species to go locally extinct, although a few species are doing better than ever before (Sol, et al., 2013). In order to make cities more biodiverse and to conserve more wildlife within our urban areas, it is very important to understand the relationships and underlying mechanisms of urbanization on the impacted ecosystems.

The fast environmental changes resulting from urbanization have major impacts on wildlife, of which birds have been extensively studied in urban areas. Chemical pollution, caused by emission from industry, traffic and heating, has many direct health effects. For example on common bird species where enhanced bioaccumulation of heavy metals in the House Wren *Troglodytes aedon*, American Robin *Turdus migratorius* (Hoffer et al. 2010) and the House Sparrow *Passer domesticus* (Swaileh & Sansur 2006) have been demonstrated. Chemical emissions can also induce geochemical and nutrient cycle changes and changes in primary production (Grimm et al. 2008), which in turn might have indirect effects on the whole ecosystem via bottom-up control (Seress & Liker 2015). Light pollution is another form of ecological disturbance in cities and is known to affect animals' orientation, migration, foraging, reproduction and communication (Longcore & Rich 2004). In birds, light initiates singing behavior and therefore it influences territorial and courtship behavior. Moreover, especially migratory birds are affected as they get confused by artificial light because they use light cues to orientate. (Gauthreax & Belser 2006). Lastly, noise pollution can make it harder for many bird species to communicate due to elevated artificial background noise. This negatively impacts animal communication systems and behavior by masking sound signals that are related to territorial defense, mate attraction, alarm calls, pair-bond maintaining calls and begging calls of nestlings (Warren et al. 2006).

Due to the elevated ambient temperatures in cities, caused by the heat-island effect, the predator-prey relationships between arthropods and birds are altered. Higher urban temperatures can cause the phenology of vegetation to be altered such as earlier blooming dates (Neil & Wu 2006). This can cause earlier insect peaks and therefore earlier first egg laying dates in birds, as birds have to time nestling food demand to insect availability peaks (Gil & Brumm 2014). Food availability also plays a major role in clutch size as clutch size is constrained by resources a female needs to successfully produce and incubate eggs (Visser & Lessels 2001).

Two bird species that are very common in cities are Blue tits (*Cyanistes caeruleus)* and Great tits (*Parus major*) and these species are a good example of how wildlife is impacted by urbanization, but also how wildlife can adapt to these fast environmental changes. Halfwerk et al. 2011 found that great tits living near a noisy highway had lower clutch sizes and raised fewer chicks, but Great tits have also found a way to adapt; they can alter their song characteristics like amplitude or frequency in noisy areas to compensate for elevated noise levels (Slabbekoorn & Boer-Visser 2006). Great tits have been found to be bolder and more aggressive in urban areas compared to rural areas (Hardman & Dalesman 2017). The timing of caterpillar peaks is especially important for Blue and Great tits who time their reproduction like so, that this coincides with caterpillar peaks in availability (Branston et al. 2021), which in turn is dependent on the timing of budburst which can be earlier due to the heat-island effect in urban areas.

So the breeding location and the timing of reproduction of Blue tits and Great tits can have severe positive or negative fitness consequences, in relation to different levels of urbanization. However, it is hard to compare different studies on this topic because the definition of urbanization is not universal. Therefore it is important to also study these effects and relationships using a quantified urbanization gradient. In this research project, we aimed to develop a method for quantifying urbanization and test for relationships between breeding parameters and this urbanization gradient. This study focuses on the following research question: How do reproductive choices correlate to a gradient in urbanization in Blue tits (*Cyanistes caeruleus)* and Great tits (*Parus major*)? Supported by the following sub questions: How does nest box occupation vary along an urban gradient? How does timing of breeding vary along an urban gradient?

Multiple studies suggest that Great and Blue Tits living in urban areas have a lower fitness in terms of clutch size which is smaller in more urban areas (Halfwerk et al. 2011), food availability which is lower in urban areas where much of the vegetation is gone (Seress et al. 2015), and timing of reproduction; Branston et al. 2021 found that urban Blue Tits showed a higher degree of mismatch between peak nestling demand and peak caterpillar availability than their rural counterparts. Additionally there are many other negative fitness effects, some of them already mentioned above. Therefore I predict that Great and Blue Tits prefer nest boxes that are located in areas with low urbanization levels, which should result in high occupation levels in nest boxes with a low urbanization score and low occupation levels in nest boxes with high urbanization scores.

Multiple studies found no difference in breeding phenology between urban and forest blue tits (Branston et al. 2021; Pollock et al. 2017; Vaugoyeau et al. 2016). Therefore, I predict that the timing of breeding in Blue tits will not differ between different levels of urbanization. Furthermore, this same study found that urban Great tits laid their eggs earlier than their rural counterparts, which has also been found in other studies (Chamberlain et al. 2009 & and Caizergues et al. 2018). Therefore I predict that Great Tits reproducing in very urban breeding locations will start laying eggs earlier then Great Tits breeding in less urbanized locations.

This bachelor project is part of a long term monitoring project on Blue and Great tits and tries to contribute to our knowledge of the relationships between breeding characteristics and urbanization Blue and Great Tits.

Methods

Study population

In this study, an urban population of breeding Blue Tits and Great Tits in 77 nest boxes has been monitored over the course of six weeks during the breeding season. The nest boxes have been set up along an urbanization gradient on the Zernike campus of the University of Groningen (Figure 1). Some nest boxes have been placed within a small area of forest (the cluster of nest boxes in the top right) and some nest boxes were located on the campus surrounded by a varying amount of urban structures such as buildings, busy sidewalks and roads. Every Monday and Thursday, all nest boxes were checked and the following characteristics were documented: occupation, nest building stage, number of eggs, date of first egg, start of incubation (based on whether a incubating female was present or if not, temperature of the eggs), date of first hatchlings, number of hatched chicks and number of non-hatched eggs. The nest box checks were performed under license and disturbance was always kept to a minimum. From week 4 onwards, boxes were only checked once a week as this was sufficient to obtain all data and proved to be less disturbing for the breeding tits.

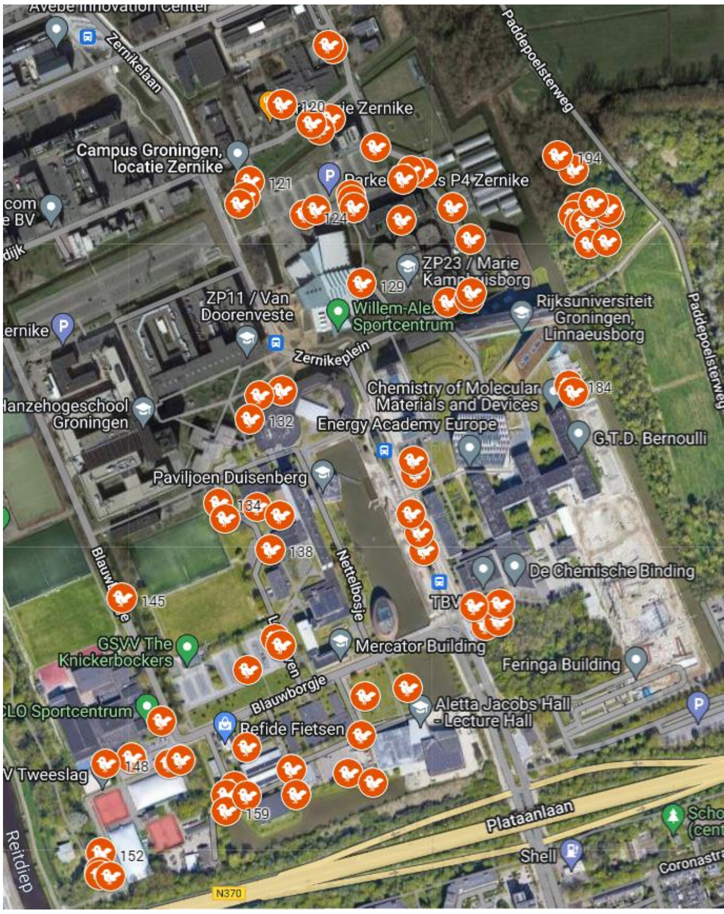

Figure 1, satellite map of the nest box locations studied during this project on the Zernike campus of the University of Groningen.

Quantification of the urbanization gradient

In order to quantify the gradient of urbanization, we used three different parameters as proxy for urbanization; road disturbance, habitat structure and light pollution.

Habitat scoring

To measure the habitat structure around all nest boxes, we defined a radius of 10 meters around each nest box where we studied the following parameters: number of trees, estimate of coverage of low (< 4 m) canopy as a percentage of sky coverage, estimate of high canopy as a percentage of sky coverage and estimate of surface coverage (%) using the following categories: 'grass/moss', 'shrubs', 'non-natural hard surfaces', 'uncovered soil', 'covered soil' and 'water' (appendix 1). The habitat scoring was always performed by two people to make sure that estimate bias was limited. A measuring tape was used to indicate the 10 meter radius.

In addition to these measures, we have noted tree circumference and species of all trees present within the 10-meter radius of a nest box. These measures were not included in our final analysis as they were not of additional relevance (circumference) for the PCA model or not accurate enough to warrant the quality of our research (species).

Road disturbance

In order to quantify the disturbance of the roads, traffic on these roads was counted. We allocated 21 relevant counting locations based on whether a road, bicycle path or parking lot had one or more nest boxes within their proximity (Figure 2). We defined the following categories of traffic: 'motorcycle/scooter', 'car', 'truck/bus', 'pedestrian', 'sitting people', 'bike', 'dog' and 'other' (appendix 2). To prevent the data to be biased by variation of traffic throughout the days, we defined five different time blocks; block 1 (8.30-10.29), block 2 (10.30 – 12.29), block 3 (12.30 – 14.29), block 4 (14.30 16.29), block 5 (16.30 – 18.29). At each location, traffic was counted once per time block in a standardized manner for 5 minutes. This process was repeated for a total of three days: two weekdays and one weekend day, making up a total of 315 counts.

Figure 2, schematic map of the research site on the Zernike campus of the University of Groningen. Red label = nest box, blue label = counting location.

Light pollution

ALAN was measured with a Lux-meter (Unitest digital lux meter, Beha Amprobe). Half of the measurements were done on the 10th and the other half on the 12th of may in 2022. These are the days before and after the new moon to minimize the influence of moonlight on the measurements. The measurements were done during astronomical darkness, which was approximately between 00:30 and 2:30 on these days. The measurements were carried out by placing the Lux-meter in front of the entrance hole.

Data analysis

All data analyses have been performed in RStudio, version 2023.03.1.

Principal component analysis (PCA)

The road disturbance and habitat score raw data both have multiple dimensions. Therefore, a PCA model was performed to organize, normalize and summarize the data. The PC values given by the model were used for further analysis. In the habitat score PCA, the variation was best explained by one PC value. In the road disturbance PCA, the variation was best explained by two PC values. In the further analyses, the PC value (PC1) of the habitat scores and both PC values (PC1 and PC2) of the road disturbance have been used.

Occupation data

For the occupation data (n = 77, 15 nest boxes were occupied by Blue Tits and 19 by Great Tits), four binomial GLM models were produced. Each model analyzed variation in the occupation data in relation to each four components of the urbanization data; habitat structure PC1, disturbance PC1, disturbance PC2 and light pollution. After this step, the Akaike Information Criterion (AIC) values of the models were compared to decide what model was the best predictor for the variation of the occupation data. The model with the lowest AIC value with a least a difference of 2 was considered as the strongest model.
A t-test was performed on the occupation data to test for species mean differences in habitat values. So for example for the light pollution data, all light pollution values of the nest boxes occupied by Blue Tits was compared to all light pollution values of the nest boxes occupied by Great Tits in this t-test. The same was done for the data on habitat structure, vehicle disturbance (PC1) and human disturbance (PC2).

Laying date data

The sample size for the laying date data was 34 nests. For the laying date data, eight Gaussian GLM models were produced. Again, in these models variation in the laying date data were analyzed in relation to each four components of the urbanization data. Per analysis, one model took the species interaction into account, whereas the other model did not. The species interaction model was only used if this improved the model (based on IAC values), if not then the model without the species interaction was used. In the end, four models were left to analyze the variation in laying date data to the four different components of urbanization. Again it was determined what urbanization component was best at predicting the variation in the laying date data.

Results

Principle components analysis (PCA)

Habitat score

The PCA result from the habitat scoring data shows two distinct groups within the habitat data; 1) grass & non-natural surface, 2) total canopy, low canopy, shrubs, covered soil, uncovered soil, water (Figure 3). The two groups are distinguishable by the PC1 axis which explains 43.7% of the variation in the data and is mainly computed out of group 2. Therefore PC1 is a proxy for ‘greenness’. PC2 explains 13.7% of the variation in the data but mainly captures variation in grass and uncovered soil, which is of low ecological value for Blue and Great Tits. Therefore, only the PC1 component was used for the statistical analysis. A positive PC1 value is correlated to an ecologically rich habitat. A negative PC1 value correlates to ecologically poor habitat.

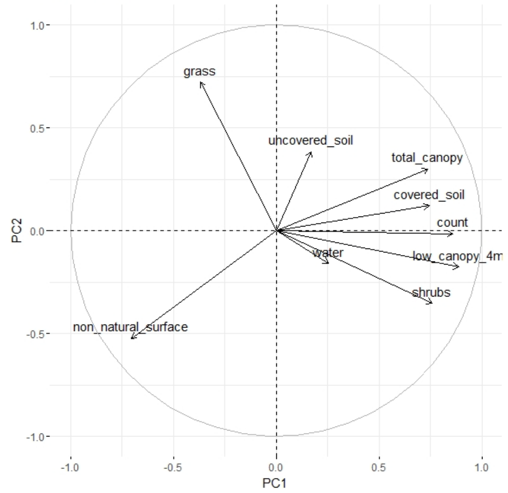

Figure 3, graph of the PCA habitat score results displaying PC1 and PC2.

Road disturbance

As seen in Figure 4, the PCA for road disturbance also yields two distinct groups of data: 1) individual persons and 2) motorized vehicles and bicycles. The difference between both groups is visible on both axes with PC1 explaining 33.2% of the variation and PC2 explaining 18.7% of the variation. The variation that is explained by PC1 is almost exclusively related to vehicles and bicycles, whereas the variation explained by PC2 is related to people, either walking or stationary. Because both components capture relevant information, we decided to use both values in our further analysis. A very negative PC1 value correlates to high levels of vehicle disturbance, whereas a very positive PC2 value corresponds to high levels of human disturbance.

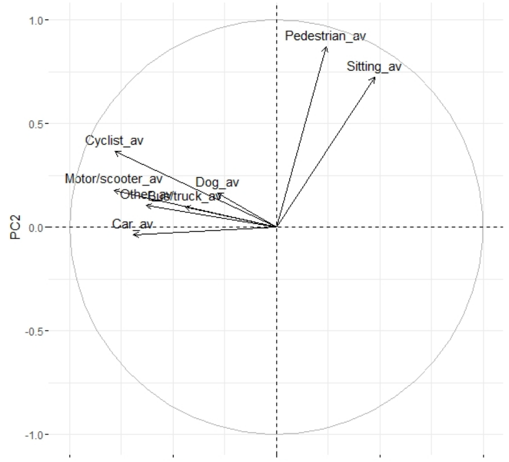

Figure 4, graph of the PCA road disturbance results displaying PC1 and PC2.

Relationships nest box occupation and urbanization components

The probability of occupation and light pollution graph shows a very weak positive trend with a very high standard error that is not significant (Table 1)(Figure 5.A).
Analyzing occupation in relation to the habitat structure yields a medium positive trend, but it is not significant (Table 1)(Figure 5.B).
Vehicle disturbance (PC1) does yield a strong and significant negative trend with occupation (Table 1)(Figure 5.C). The PCA results show that a more negative PC1 score is correlated with high levels of vehicle traffic and a more positive PC1 score is correlated to little vehicle traffic. So the relation between vehicle traffic and probability of occupation is actually positive.
Lastly, human disturbance (PC2) does not yield a significant trend in relation to occupation (Table 1)(Figure 5.D).
The t-tests show that there were no significant differences between Blue Tits and Great Tits all four analyses (Table 4).

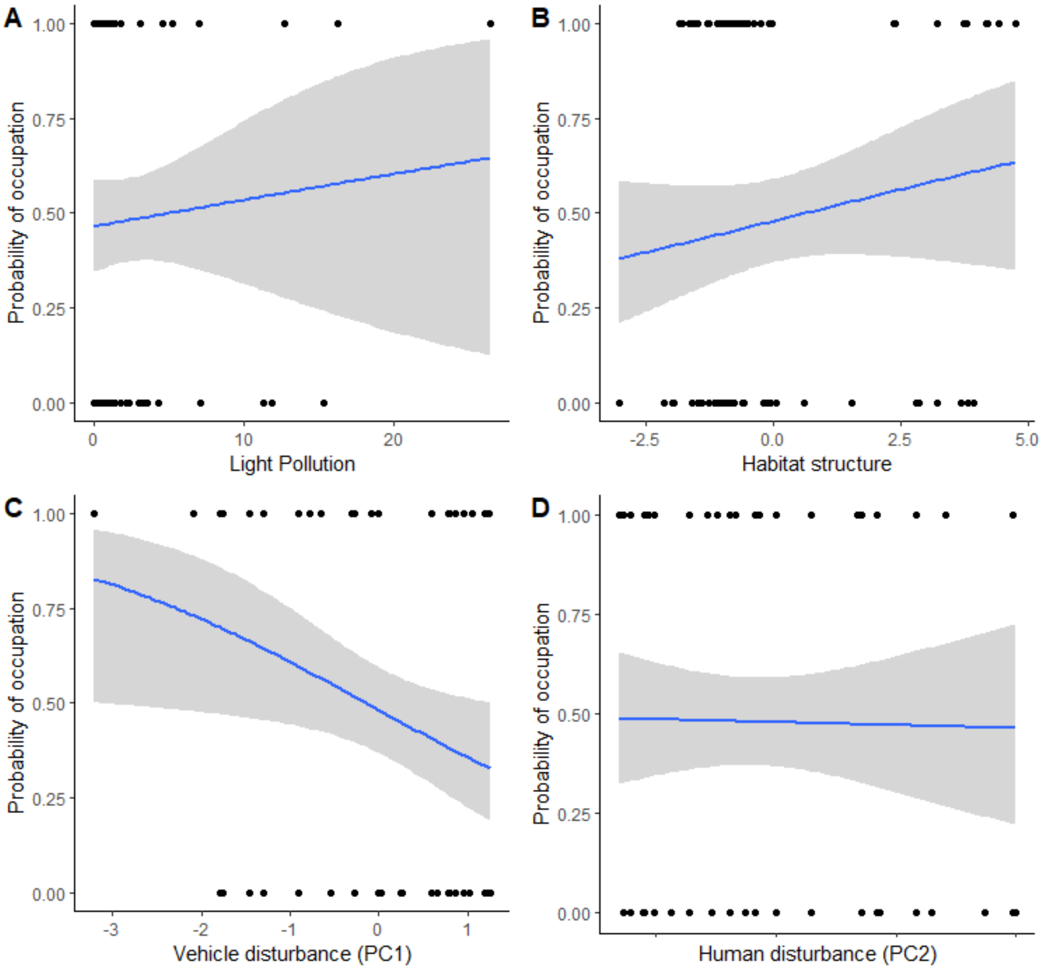

Figure 5, graphs showing the relationships between probability of occupation and light pollution (A), habitat score (B), vehicle disturbance (PC1) (C) and human disturbance (PC2) (D).

Relationships laying date and urbanization components

As seen in Figure 6.A, there is no trend in laying date in relation to light pollution (Table 2). Also, there is no significant difference between the reaction of Blue and Great Tits as the species interaction did not improve the model (difference in AIC values ≤ 2, Table 3), therefore the model without the species interaction was used.

Figure 6.B shows the relationship between laying date and habitat structure. Because there is a significant difference in this relationship between Blue and Great Tits (Table 3), the model with the species interaction was used. There is no trend for Great Tits but for Blue Tits there is a strong positive trend (Table 2). Blue Tits lay their eggs earlier with an increasing urban habitat, as seen in the graph this difference can be up to 20 days.

Vehicle disturbance (PC1) did yield a small negative trend in relation to laying date (Figure 6.C), but it is not significant (Table 2) and there is no significant difference between Blue Tits and Great Tits (Table 3), so the model without the species interaction was used.

There seems to be a small positive trend in the relation between human disturbance and laying date (Figure 6.D), but this trend is not significant (Table 2). Also, there is no significant difference between Blue and Great Tits (Table 3) so again, the model without the species interaction was used.

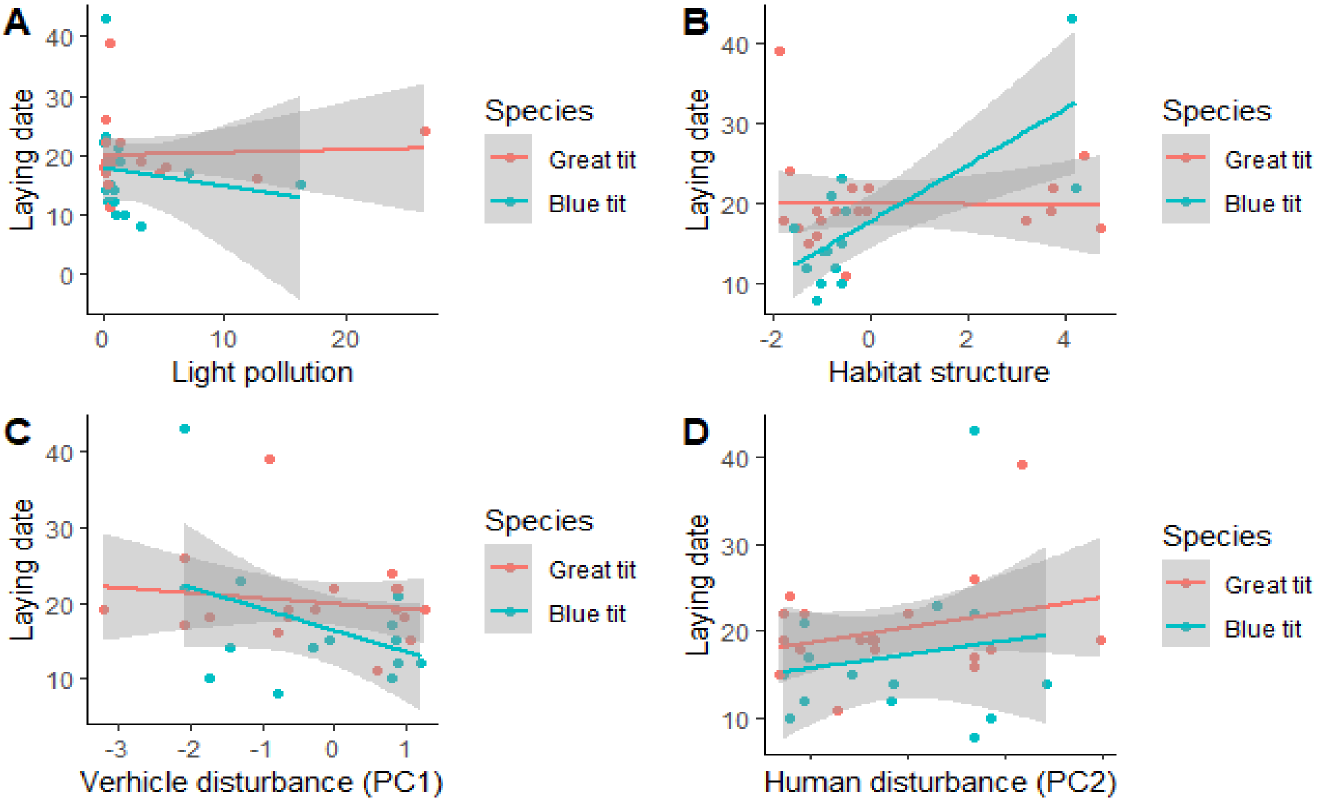

Figure 6, graphs showing the relationships between laying date and light pollution (A), habitat score (B), vehicle disturbance (PC1) (C) and human disturbance (PC2) (D).

Comparison of AIC values

For the probability of occupation, the vehicle disturbance (PC1) model has the lowest AIC value, followed by habitat score, light pollution and human disturbance PC2 (Table 1)

For laying date, the habitat score model has the lowest AIC value, followed by vehicle disturbance (PC1), human disturbance (PC2) and light pollution (Table 2).

Occupation	Habitat score				Disturbance PC1				Disturbance PC2				Light pollution			
	Est	SE	Z	P	Es	SE	Z	P	Est	SE	Z	P	Est	SE	Z	P
Intercept	-0.08	0.23	-0.36	0.72	-0.07	0.24	-0.31	0.75	-0.08	0.23	-0.36	0.72	-0.14	0.26	-0.54	0.59
Urbanization Score	0.13	0.118	1.14	0.25	-0.51	0.24	-2.18	0.03	-0.03	0.24	-0.12	0.90	0.03	0.05	0.53	0.60
AIC-value	109.29				105.44				110.61				110.34			

Table 1, results of the generalized linear models (GLM) on occupation and the four urbanization components; habitat structure, vehicle disturbance (PC1), human disturbance (PC2) and light pollution. Est = estimate, SE = standard error, Z = z-value, P = p-value.

Laying date	Habitat score				Disturbance PC1				Disturbance PC2				Light pollution			
	Est	SE	Z	P	Es	SE	Z	P	Est	SE	Z	P	Est	SE	Z	P
Intercept	20.02	1.36	14.73	2.82 e-15	19.63	1.59	12.33	1.72 e-13	20.39	1.63	12.50	1.22 e-13	20.13	1.78	11.31	1.58 e-12
Urbanization Score	-0.05	0.60	-0.09	0.93	-1.58	0.95	-1.66	0.11	1.67	1.30	1.28	0.21	-0.04	0.23	-0.20	0.85
Species	-2.20	2.04	-1.08	0.29	-3.02	2.37	-1.27	0.21	-3.04	2.41	-1.26	0.22	-3.03	2.48	-1.22	0.23
Species : Urbanization Interaction	3.55	1.05	3.39	1.98 e-3	-	-	-	-	-	-	-	-	-	-	-	-
AIC-value	222.37				232.43				233.55				235.27			

Table 2, results of the generalized linear models (GLM) on laying date and the four urbanization components; habitat structure, vehicle disturbance (PC1), human disturbance (PC2) and light pollution. Est = estimate, SE = standard error, Z = z-value, P = p-value.

AIC values of laying date models	**Habitat score**		**Disturbance PC1**		**Disturbance PC2**		**Light pollution**	
	BT + GT	BT * GT	BT + GT	BT * GT	BT + GT	BT * GT	BT + GT	BT * GT
AIC-value	231.40	222.37	232.43		233.55	235.54	235.27	236.76

*Table 3, AIC-value comparison of all laying date GLM's. BT + GT = model without species interaction, BT * GT = model with species interaction.*

Data	t	df	p-value
BT light pollution : GT light pollution	0.39	31.13	0.6992
BT habitat structure : GT habitat structure	0	36	1
BT vehicle disturbance (PC1) : GT vehicle disturbance (PC1)	0.03	30.98	0.98
BT human disturbance (PC2) : GT human disturbance PC2)	-0.07	30.96	0.94

Table 4, t-test results on the occupation data. BT = Blue Tits, GT = Great Tits.

Discussion

In this study I managed to develop a method for quantifying urbanization and identified multiple urbanization components that could potentially predict the laying date and/or the probability of nest box occupation. Two relationships were found; in Blue Tits there is a positive trend between laying date and habitat structure and there is a positive trend between probability of occupation and vehicle disturbance. All other comparisons did not yield significant trends, however the occupation results are quite consistent; occupation in relations to light pollution and habitat structure yielded slightly positive but not significant trends. The same accounts for the laying date results; in relation to vehicle and human disturbance there were slightly positive, but not significant trends in laying date. So, probability of occupation is not correlated with light pollution, habitat structure and human disturbance. This indicates that the intensity of artificial light at night at a nest box, the ecological value or 'greenness' of the habitat around the nest box within 10 meters and the disturbance by human (pedestrians and sitting/stationary people) do not seem to influence the preference for nest boxes in Blue Tits and Great Tits. Laying date is not correlated with light pollution, habitat structure (only for Great Tits), vehicle disturbance and human disturbance. This indicates that the intensity of artificial light at night at a nest box, the ecological value or 'greenness' of the habitat around the nest box within 10 meters (only for Great Tits), the amount of traffic on a road within 50 meters of the nest box and the disturbance by humans (pedestrians and sitting/stationary people) do not seem to influence the laying date in Blue and Great Tits.

Conclusions

A gradient in urbanization within one (semi-) urban population of breeding Blue and Great Tits was generally not sufficient to induce changes in the timing of breeding and preference of breeding location in Blue and Great Tits. Blue Tits did start laying eggs later in greener habitats and both Blue and Great Tits preferred nest boxes that had high vehicle disturbance.

Now I will discuss the different components separately.
Probability of nest box occupation increases in areas with high vehicle disturbance. So this indicates that both Blue and Great Tits in this studied population had a preference for nest boxes where there were high levels of vehicle disturbance. Occupation was also positively correlated to light pollution and habitat structure, even though this was not significant, it is consistent. This is opposite of what was hypothesized. Nevertheless, a possible biological explanation for this observed trend could be that Blue and Great Tits are safe from predation in urban areas. The Eurasian Sparrowhawk, Woodpeckers and Red Squirrels are three common predators of Blue and Great Tits where Woodpeckers and Red Squirrels feed on the chicks. The Eurasian Sparrowhawk is increasing in European urban habitats, it is a successful city-dwelling bird (Seress & Liker, 2015) and mainly large city parks contribute to the conservation of these birds of prey (Schütz & Schulze, 2018). Woodpeckers need large, multi-layered canopy and rich in deciduous tree species woodland patches (Myczko et al., 2014). Frölich et al. (2022) found that Woodpeckers select habitats with high abundance of trees or dead wood. Urbanization filters woodpecker assemblages by limiting the habitat-specialists and promoting habitat-generalists. Jokimäki et al. (2017) found that the relative squirrel abundance was twice as high in urban habitats than in forests in Finland. Fingland et al. (2021) found the same provided that greenspaces of high quality are maintained. They argue that this is possibly due to the widespread and reliable availability of human supplemental food alongside natural food resources. Additionally they state that road traffic incidents can be a major cause of mortality. So both Sparrowhawks, Woodpeckers and Red Squirrels in cities tend to concentrate in more green habitats, potentially arguing that Blue and Great Tits are safer in less green habitats, hence explaining the slightly positive (but not significant) trend between occupation and habitat structure. Additionally, high vehicle disturbance might protect Blue and Great Tits from Red Squirrels as traffic incidents are a major mortality source for the Red Squirrels, explaining the positive

correlation between occupation and vehicle disturbance. Therefore, taking the above into consideration, urban Blue and Great Tits might have a preference for urban nest boxes as they have a lower risk of predation there compared to natural nest boxes.
Laying date is positively correlated with habitat structure in Blue Tits. This indicates that Blue Tits tend to start laying eggs later in greener habitats, or habitats of high ecological value. This does not match with my hypothesis, as I did not predict a relation between urbanization and laying date in Blue Tits. This hypothesis was based on earlier findings by Branston et al. 2021, Pollock et al. 2017 and Vaugoyeau et al. 2016. A biological explanation is that due to the heat-island effect, plants and trees start blooming earlier in urban areas, therefore insect peaks will be earlier and therefore Blue tits have to start laying eggs earlier as well to match the peak in nestlings to insect food availability peaks. In the same study, Branston et al. 2021 also found that Blue Tits had a higher degree of mismatch between these peaks. Potentially, the Blue Tits in the population of our study were well adapted to the earlier blooming dates, resulting in a lower degree of mismatch.
All other analyses did not result in significant relationships, so most of the laying date and occupation data seem to not be affected by the urbanization components quantified in this study. There are multiple possible explanations for this. First of all, the Blue and Great Tits in this study population might already be greatly adapted to the urban surroundings. Therefore the variation in urbanization within the population area was not sufficient to explain variation in laying date and occupation. Secondly, we noticed that there was sufficient insect food availability, which also might have canceled out significant differences between urban and less urban nest boxes. Lastly, this year was a relatively cold spring. Therefore the increased ambient temperatures near more urban nest boxes (caused by the heat-island effect) could have actually been advantageous to the Blue and Great Tits. This might have canceled out any significant relationships.
A possible explanation for the difference between Blue Tits and Great Tits in the relation between laying date and habitat structure is that Great Tits might have adapted their foraging behavior to an urban life-style so that they fly further away from the nest box for foraging or that they are more flexible in their diet whereas Blue Tits did not. Great Tits are bigger than Blue Tits so they might fly longer distances more easily than Blue Tits. The location of the study site was at the border of a city so natural resources were relatively close by. For follow up studies on this long-term monitoring project, it would be an interesting research topic to investigate whether Great Tits travel further for foraging food than Blue Tits, and whether their diet differs. To do this, wild cameras could be installed in nest boxes that start filming when a Tit comes into the box. This way it can be documented what the diet consists of, and based on the time the foraging Tit is gone from the nest, an estimation of the distance traveled for foraging can be made. A more sophisticated and accurate method would be to catch some Blue and Great Tits, give them a chip that can track the GPS location and from this determine the traveled distance to the foraging ground. This way, it can also be documented where the foraging grounds are, and whether the Tits tend to forage at one location, or at multiple.

Shortcomings of this study

There are multiple methodological reasons as for why I did not find any strong relationships between laying date and occupation and the different urbanization components. The most important argument is that my hypothesis was mainly based on comparative studies, in which different populations from rural areas and urban areas were studied, while this study monitored one population with an urbanization gradient in the breeding locations. An urbanization gradient in one (semi-) urban population of Blue and Great Tits might not be sufficient to induce significant variation in laying date and occupation as the individuals might already be adapted to the urban life-style. Whereas the difference in urbanization between an urban and rural population that are not in contact with each other is sufficient for this variation in laying date and occupation.
This study was performed on a population in 77 nest boxes of which 34 boxes were occupied, 15 by Blue Tits and 19 by Great Tits. Especially the laying date sample size (34) was quite small. Many of the trends have a few data points that influenced the trend highly, but could also have been outliers. Due

to the low sample size it could not be determined whether this was the case. Additionally this study monitored only one breeding season. This year could have been an outlier in that due to the relatively cold spring, the Tits might have preferred the warmer urban nest boxes. The studied population was a (semi) urban population breeding at the boundary of the city of Groningen and therefore natural resources were relatively nearby anyway.

It is questionable how reliable the positive trend between possibility of occupation and vehicle disturbance is as the trend was just significant and the standard error margin is quite high, especially as the PC1 value gets to -2 to -3. Additionally, the positive trend between laying date and habitat score is also questionable, as the positive direction is mainly based on only two data points. They could be outlier but they could also be actually part of this trend. A higher sample size is needed to confirm or reject this relation.

For the road disturbance components (vehicle disturbance and human disturbance), we did not manage to account for the distance to the counted roads in our data analysis. Therefore a road that was 40 meters aways from a nest box counted as heavily as a road 2 meters away. This could have had influences on the results.

Taking the above into consideration, it would be beneficial to extend the scope of the population site. I propose to extend more nest boxes into the country side with more natural areas and towards the city with more urban areas. In this way, the area of the population size is extended, the sample size is increased and the differences of urbanization degree will be bigger. In this way, possible trends will potentially be clearer and the strength of the statistical analysis will be higher. Furthermore, our methods on quantifying the road disturbance and habitat score have worked well and can be used again.

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Appendix 1, the habitat scoring form.

Habitat scoring form:

Date	
Nestbox	
Observer	

Trees (*<30 cm counts as shrubs)

Count (total nr of trees)	
Small : 30-60 cm	
Medium: 60-120 cm	
Large: >120cm	
Species *note down nr of tree/species	
Canopy coverage *% of sky covered by canopy	

Habitat coverage in % (*All counts together must add up to 100%)

Grass/moss	%
Shrubs (eg hedges, brambles)	%
Hard, non-natural surface	%
Covered soil (eg leaf litter)	%
Uncovered soil (eg mud or sand)	%
Water surface	%

Remarks

Appendix 2, the disturbance counting form.

Road counting form

Observer: **Date:** **Time:** **Location:**

Vehicle type	**Counts**
Motorcycle/scooter	
Car	
Truck/Bus	
Pedestrian	
Sitting people	
Cyclist	
Dog	
Other	

Comments: