Growing up in the city- studies on the reproductive success of birds in rural and urban areas.

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Rijksuniversiteit Groningen

2018

Special thanks to Christiaan Both

Abstract

Urbanization is impacting habitats and wildlife worldwide, but little is known about the effects that this might bring on wildlife.The urban habitat has gained an increase in attention as some animal species, such as birds, have shown to be able to adapt to living in this urban landscape. In this thesis, I will look at the differences in reproductive output between urban and non-urban birds by discussing comparison studies. Studies done on urban factors such as effects of bird feeders & anthropogenic food, urban heat, anthropogenic sounds, artificial light, predation and pollution will be discussed. I determined which urban factors might have a reported influence on lay date, clutch size, egg size, fledgling size and fledgling success. This thesis concludes that birds in urban areas often differ in reproductive output compared to non-urban conspecifics. Urban areas, mostly-, (but not necessarily) show earlier lay dates and smaller clutch sizes, and a decrease in fledgling size and fledgling success. These effects and the severity of these effects largely differ per species and area studied.

Contents:

Introduction

According to the *Living Planet Rapport* that was released in October 2018, humanity has wiped out an estimated 60% of animal populations since 1970 (LPR. 2018). A large factor in this decline of populations is the loss of natural habitats due to human destruction. Large quantities of land are needed to satisfy the human need and the ever expanding world population. In March 2018, The Intergovernmental Platform on Biodiversity and Ecosystems Services (IPBES) released its *Land Degradation and Restoration Assessment* (LDRA) which found that only a quarter of land on Earth is now substantively free of the impacts of human activities (IPBES LDRA. 2018). This remaining 25% that is not impacted by humanity is projected to decline to just 10% in 2050. Deforestation plays an important role in this decline, as woodlands and forest are being cleared for agricultural and other purposes. About 27% of deforestation is being caused by urban growth, infrastructure expansion and mining (FAO FRA. 2016). The UN Habitat rapport on *The State of the Worlds Cities* from 2012 states that about 50% of the world populations lives in cities in 2008, and this is projected to increase to 70% in 2050 (UN-Habitat. 2012).

The loss of wildlife and natural habitats are a big concern for conservationists, but natural areas that are urbanized can also bring opportunities for some organisms that are able to adapt to an urban environment. The urban landscape, as a habitat, is not only gaining an increasing interest from the scientific community, but it has also gained attention from a wider public. In 2016, BBC's Planet Earth 2 released an episode on cities as habitats for wildlife, emphasizing the importance of these niches created by humanity.

In this thesis I want to explore the question what the effects upon the fitness are of an animal living in an urban environment, compared to animals living in a more natural environment? Can the urban environment actually increase the fitness of some animals? These are rather hard questions to answer, as so many factors affect an animals success in this new habitat. Differences in possible changes in fitness should be expected among species, cities and cultures, as well as the ability of the animal to cope with this new environment. In this study, the reproductive success of birds in cities will be compared with those in more natural habitats. Some avian species have shown to be able to adapt to live and nest in the city, and are therefore suitable for these type of comparison studies. These species of birds are often referred to as urban exploiters as they can show positive responses to levels of urbanization (Leveau. 2013).

Several studies have been performed on birds comparing the reproductive output between an urban environment and non-urban environment and can be found in table 2 in the appendix of this thesis. Comparison between urban and non-urban environments will be divided by factors represented in table 2 (Bird feeders and

anthropogenic food, Urban heat, Noise pollution, Artificial light, Predation and Pollution), as these factors might affect the reproductive success in birds between these two environments. These factors and their possible effects have been studied, and it is valuable to discuss them in order to give a wider perspective on the possible effects on urbanization.

The output of these studies can hopefully help us answer the main question of this thesis: *Does living in an urban environment affect the reproductive output in birds?* To help answer this question, comparisons will be made between clutch size, egg size, fledgling weight, fledgling success and laying date of the eggs.

Lay date has been included, as lay dates tend to differ between urban and non-urban habitats, causation of this difference can possibly be explained by several factors that will be described below. Later or earlier laying dates can cause a bird to be off sync with its natural food supply, which can possibly explain other differences found within studies. Earlier laying dates can also increase the chances of birds starting a second brood in the same year (Barba *et al.* 1995).

Methods

For studying the effects on urbanization on reproductive success in birds, theoretical research was performed using Web of Science, Smartcat and Google Scholar.

To get the best indication of possible effects on reproductive success within and outside of urban areas, I prioritised studies that included paired comparisons of urban with non-urban areas. As these studies used the same time-period and methodology and therefore might give the clearest indication on the effects of urbanization. All searches started with the words *bird* and *urban* after which words such as *breeding* and *reproductive success* were added. Furthermore, words such as *predation, pollution, heat, light, sound, noise, feeder, supplementary, food* and *feeding* were added to look for more information on precise topics. References from within articles were also used for complementary information. References from studies when used for meta-analyses were not used individually. Instead the information from the analyses was taken. This information can be found in table 2.

Results:

The results are divided by the factor that might influence a birds reproductive output. These sections are placed at random, and do not state the impact of this factor on the reproductive success.

Bird feeders & anthropogenic food

In order for birds to survive within an urban habitat, new food sources must be found as natural food sources tend to decrease. This can largely be explained by the loss of green areas and an increase in concrete buildings and roads. This decrease in flora means a decrease in edible seeds and fruits for birds, as well as a decrease in insects living of the plants. For the great tit (*Parus major*) an important food source during the breeding season are caterpillars. But caterpillar densities are lower in urban habitats than in their surrounding forests (Seress *et al*. 2018). New food sources within urban areas are available for birds that are able to adapt their diet.

Urban exploiters, such as the Australian silver gull (*Larus novaehollandiae*) have found a new food source in human discards. A study revealed that about 85% of their stomach contents consisted exclusively from human discards (Smith & Carlile. 1993).

Perhaps the biggest new food source for birds living in the cities comes from people that are actively feeding birds. Bird feeding has become a popular activity for humans; up to 43% of the US households feeds birds (Martinson & Flashpoler. 1993). The amount of people feeding birds is even higher in the UK, where an estimated 75% of people feed birds (Cowie & Hinsely. 1988). An estimated 500 000 tonnes of supplementary bird food is being provided to birds in the US and UK alone (O'Leary & Jones. 2006). The feeding of birds is often promoted by prominent organisations such as the British Trust for Ornithology (BTO) , The Royal Society for the Protection of Birds (RSPB) and many others (RSPB. 2002, BTO 2003). In the The Netherlands, Vogelbescherming Nederland actively sells bird food, seeds and feeders through their webshop (Vogelbescherming. 2018).

It is widely considered that feeding birds, especially during cold winters is good for birds (Brittingham *et al*. 1992). This makes sense, as natural food sources become more scarce. Food availability is a vital factor that can limit the size of bird populations. Supplementary feeding decreases the amount of birds dying from starvation (Newton. 2002). But not all birds benefit from this supplementary feeding, as the food that is being provided for birds is only suited for some species. Supplementary foods that is fed to birds often consists of bread, seeds, fats, peanuts or a combination of these (Plummer *et al.* 2013). In some cases, such as the Anna's Hummingbird (*Calypte anna)* special nectar feeders have been created, that allows the bird to increase in populations in urban areas (Greig *et al.* 2017). But for carnivorous and strictly insectivorous birds species, bird feeders offer limited to no direct benefits.

It is important to mention that the supplementary feeding of birds can also have negative effects, as weaker individuals are being allowed to survive and are able to recruit into the breeding population (Plummer *et al.* 2013). Feeders, especially ones that are not being cleaned on a regular basis, do contribute with the spread of diseases, both inter and intraspecific (Brittingham & Temple. 1988, Blanco *et al.*

2011, Adelman *et al.* 2015). Food dependency can also be brought up as a possible negative impact of supplementary feeding, although a research on black-capped chickadees (*Parus atricapillus*) did not find such an effect on food dependency and this not really been exemplified in other studies (Brittingham & Temple. 1992).

So what exactly are the effects of supplementary feeding on a birds reproductive success? Although some studies have been performed on the effects of supplementary feeding versus no supplementary feeding, no studies were found in which the supplementary feeding experiment was performed in an urban area, compared to a non-urban area. The lack of these type of studies can probably be explained by the difficulty of the experimental design, as many different factors should be taken into account that can assumably explain possible differences. Most studies performed are being carried out in non-urban areas where in similar habitats, (vegetation, latitude, etc) one group from a given species of bird was food supplemented and compared with a control. Duration of feeding often varied between studies and the results also varied per species.

One research by Meyrier *et al.* performed in Western jackdaws (*Corvus monedula*) compared the distance from jackdaw colonies to an urban environment to their reproductive success (Meyrier *et al.* 2017). Jackdaws are known to be opportunistic feeders, that can feed on both birdfeeders and anthropogenic waste. This research shows that clutch size and number of fledglings decreased with the distance to non-urban foraging grounds. This decrease in breeding parameters with distance to non-urban areas might be explained by a lack of natural foods (Chamberlain *et al.* 2009). This was tested by feeding some of the urban pairs with high quality foods during egg formation. This lead to an increase in egg weight and hatching success, but this eventually did not lead to a higher reproductive output as the chick survival was lower in the fed group than the non-fed group.

Therefore a second experiment was performed the year after, in which the parents of the experimental group were also fed during the chick rearing stage. This led to a higher chick survival rate in the experimental nests compared to the control nests, but this effect disappeared towards the end of the research, when the survival rate of fledglings decreased. This can possibly be explained by experimental design as supplemented food amounts might have been insufficient (Meyrier *et al.* 2017).

As studies on supplementary feeding in urban environments are lacking, effects of supplementary feeding on birds in more natural environments will now be discussed. These results can be interesting regarding the effects of urbanization on reproductive success, as we know that birds breeding in the city have access to supplementary feeds.

Two studies, performed in the blue tit (*Cyanistes caeruleus*), by Plummer *et al.* and by Robb *et al.* were done on the effect of winter provisioning in blue tits on their reproductive success (Plummer *et al*. 2013, Robb *et al.* 2008). In these studies, fed blue tit populations were compared to unfed populations in their reproductive success. In the study by Plummer *et al.* fat and fat+vitamin E were used as

supplementary food. Vitamin E was added, as it was hypothesized that shortage of this antioxidant might have been a limiting factor in hatching success. The study by Robb *et al.* used peanuts as supplementary food.

The results of these studies are rather interesting, as they are in contradiction to one another in regards of fledgling success. The study performed by Plummer *et al.* found no difference in lay date between fed and unfed birds, no effect on clutch size, and a decrease in fledgling size on average of -0.5gram for fat fed chicks and a decrease in weight on average of -0.4gram for chicks fed with fat + vitamin E. The fledgling success of fed chicks was also 8% lower compared to unfed chicks (Plummer *et al*. 2013). On the contrary, the research performed by Robb *et al*. found different results, as they found the lay date of fed birds to be about 2.5 days earlier. No effects on clutch size or chicks size, but an increase in fledgling success of almost one extra fledgling (Robb *et al.* 2008).

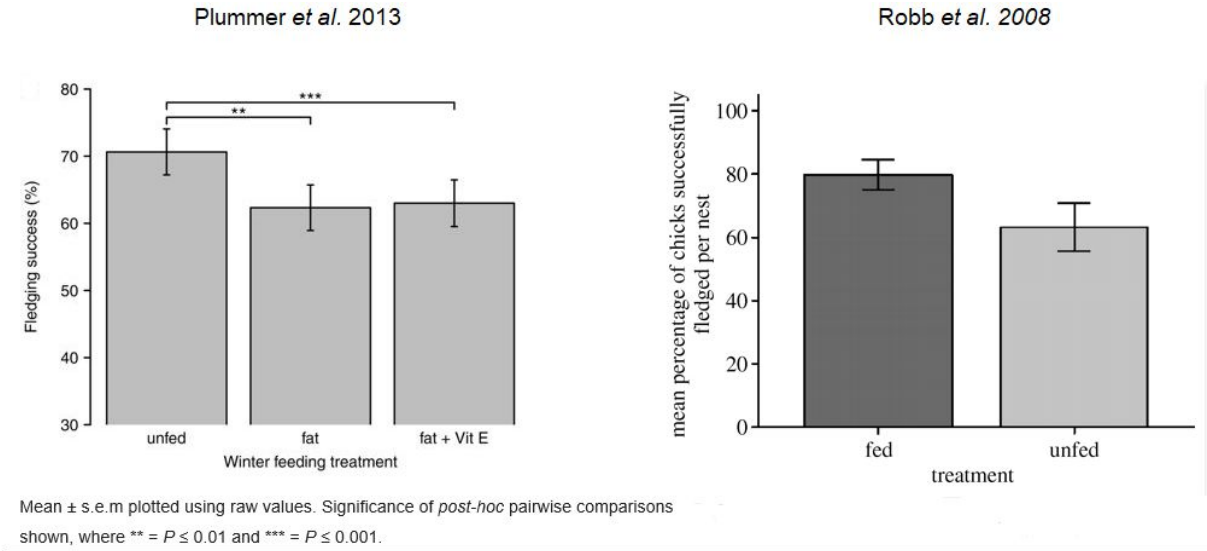

Figure 1: Differences in fledgling succes in the blue tit between Plummer *et al.* and Robb *et al.* Plummer shows a higher fledgling succes in unfed blue tits, while Robb *et al.* shows a higher fledgling succes in fed blue tits

So what can explain these differences? First of all it is important to mention that sample sizes between these two studies differed. Plummer *et al.* studies 362 nests whereas Rob *et al.* studied only 76 nest-boxes. As Plummer *et al.* performed their study over a period of three years compared to just one year in Robb *et al.* The results of Plummer *et al.* can be favoured over Robb *et al.,* due to bigger sample size and multiple years of data. Although different types of supplemented food were used, the difference between these two food sources is limited considering that peanuts contain high amounts of fat, as well as vitamin E (Alasalvar & Pelvan. 2011). However *Plummer et al.* mentioned in their comparison between their study and Robb *et al.* that peanuts contain, although in low amounts, Sulphur-containing amino acids, that can potentially limit reproduction in birds (Plummer *et al.* 2013). Both studies stopped with supplementary feeding well before the breeding season.

Two other factors that can possibly explain the differences between the different results are the location and the year in which the research was performed.

Blue tit populations might differ in response to supplementary food per location and some years are better years for blue tits to raise young then other years.

The scientific paper that probably gives the best indication about the effects of supplementary feeding on reproductive success is : *Food for thought: Supplementary feeding as driver of ecological change in avian populations* by Robb *et al.* from 2008 (Robb *et al.* 2008b). This review gives analyses of the effects of supplementary feeding on many species of birds, and summarizes their responses and results.

In the 59 studies they compared for laying date, they found earlier laying dates in 34 studies. These advances were usually less than a week, but sometimes could be as much as a month. The type of food that was given also impacted the laying date in some species, a study on the Florida scrub jay (*Aphelocoma coerulescens*) found that birds on a high-protein, high-fat diet were first to lay followed by high-fat, low-protein diet, followed by control (Reynolds *et al*. 2003). This can also be a possible explanation for the difference in lay date between Plummer *et al.* and Robb *et al.* in their studies on the effects of supplementary feeding on the blue tit.

A positive effect of supplementary feeding on clutch size was found in 28 of the 63 studies, while 34 studies found no effect of supplementary feeding. Egg size or quality increased in 14 of the 37 studies, while the remaining 23 studies found no effect. You could hypothesize that supplemented birds spend less time foraging, and therefore have more energy to spend on clutch size and egg quality. But this might not be the case in all studied species of birds, as it is unknown for what part the birds diets consisted of supplementary foods in many of these studies. Maybe the diet of the birds in the studies that show positive results consists for a larger part of supplementary food. Nutrient shortage can also be a limiting factor, as birds may profit from nutrients that can be found in supplemented foods (Such as vitamin E in peanuts) that are limited in their natural environment. Food supply can be a limiting factor in the species that show an increase in clutch size or egg quality, while this plays less of a role in species that do not show this increase. An increased clutch size can for some species have negative effects on the future reproductive output of the parental birds, as rearing more chicks can be costly and is therefore avoided (Monaghan & Nager. 1997).

Breeding parameter	Response to supplemental food					
	% positive (n)		% negative (n)		% no effect (n)	
Lay date	57.6	(34)	1.7	(1)	40.7	(24)
Clutch size	44.4	(28)	1.6	(1)	54.0	(34)
Egg size/quality	37.8	(14)	0.0	(0)	62.2	(23)
Incubation time	22.2	(2)	0.0	(0)	77.8	(7)
Hatching success	45.0	(9)	0.0	(0)	55.0	(11)
Chick growth rate	56.7	(17)	3.3	(1)	40.0	(12)
Fledging success	63.6	(28)	0.0	(0)	36.4	(16)

Table 1: Breeding parameters and the found responses to supplementary food in birds from Robb *et al.* 2008b. *n* is the amount of studies in which the given result was found. Studies used for this table can be found in Robb et al. 2008b.

A positive effect on fledgling success was found in 28 of the 44 studies, 16 studies found no effect of supplementary feeding on fledgling success. This makes the results of the research on blue tits by Plummer *et al*. all the harder to explain, as this study showed a higher fledgling success in unfed chicks versus fed chicks. Perhaps the fat and fat+vitamin E chosen as supplementary food sources in this study were not well suited for the blue tits (Plummer *et al*. 2013). Another difference to keep in mind is that the study by Plummer *et al.* only provisioned supplementary food during the winter period and stopped well before breeding, while most studies used in this review used also used supplemented food during the breeding period.

There are several ways in which supplemented food can have positive effects on fledgling success. The extra food can be used to feed the chicks, thereby decreasing the risk of starvation. Supplemented parents can also spend less time foraging and can therefore spend more time guarding the nest, which could decrease nest predation. A study on the Australian reed warbler (*Acrocephalus australis*) showed an increase of parental attendance on supplemented parents (Eikenaar *et al.* 2003). Supplemented food can also facilitate more selective foraging, which could increase the diet composition of the chicks (Grieco, F. 2002). Finally, supplementary feeding can lead to a reduction in aggression among chicks, thereby increasing chick survival. As is shown in a study on the Spanish imperial eagle (*Aquila adalberti* ; González *et al*. 2006).

This review by Robb *et al.* is a great summary of the possible effects of supplementary feeding on the reproductive success in birds. It largely shows positive effects of supplementary feeding on the reproductive output of birds. Which makes sense given the many ways described above in which supplementary feed can help birds during the nesting season. It is important to remember that these studies are not done in urban surroundings. Many of the species that are used for this research, such as the Spanish imperial eagle, nazca boobie (*Sula granti*) and other species are not found breeding in cities. Still, as we know that people actively feed birds in cities, and we know that several bird species nest in urban environments. This summary could give insights about the possible effects of bird feeding on reproductive success in cities.

Urban Heat

Worldwide, temperatures between cities and their surroundings differ. Despite differences in regional climates, urban areas tend to have higher air and surface temperatures than natural areas in what is known as the Urban Heat Island Phenomenon (Santamouris. 2014). As vegetation is removed, heat retaining asphalt and concrete buildings take over. These changes affect the near surface energy budget, by reducing evapotranspiration, mounting solar energy, absorbing surfaces and creating heat trapping canyon like urban morphology (Buyantuyev & Wu. 2010). Besides these effects, cities also produce excessive heat by building infrastructure and transportation (Buyantuyev & Wu. 2010). In the city of Phoenix in the United States, daily air temperatures have increased by 3.1°C and by a minimum of 5 °C during the night (Baker *et al.* 2002).

These differences in temperature in urban areas have an impact on the flora and fauna living within these habitats. Plants tend to flower earlier in urban habitats (Lu *et al.* 2006), which is hypothesized to lead to earlier insects peaks. This in turn, could be an explanation for earlier laying dates in urban areas from insectivorous birds. Information on this topic is limited, although one study did find that urban warming led to an increase of insect pests on street trees (Meineke *et al.* 2013). A study on caterpillar abundance in urban areas did however, not find an earlier peak in caterpillars in urban areas (Seress *et al.* 2018).

Information on the effect of the urban heat on the reproductive success of birds is limited, as no studies have been done in which the effect of this effect is assessed. A study done in Poland on the tawny owl (*Strix aluco)* found that tawny owls that nested in the central zone of Warsaw have an advanced laying date of about 40 days compared to tawny owls in a forest area near Warsaw. Urban pairs also brought up 0.2 less young compared to forest tawny owls (Gryz & Krauze-Gryz. 2018). The study suggests, among other things that urban heat could be an explanation for the earlier laying date, but shows no evidence for this claim.

A study done on four species of hole breeding birds, compared the location of a nestbox to the level urbanization in that given area and the results of this on laying date and clutch size. Differences between laying dates are found, but these differences were not corresponding with the level of urbanization. On the tit species used for this study, no results are found on clutch size regarding urbanisation level. However, the two flycatcher species show a decrease in clutch size with the level of urbanisation (Vaugoyeau *et al.* 2016). Urban heat is mentioned as temperatures differing between cities and less urban areas, but the study shows no further mention of how this might have affected the found results.

Little can be learned about urban heat from these given articles, as perhaps it makes more sense to look at the effects of climate change on breeding behavior. As the effects of global warming might be similar to those of urban heat. Studies have shown that for temperate-zone birds, temperature is an important cue enabling

breeding efforts to coincide with maximum food availability. Earlier breeding due to warmer temperatures have been recorded in many species of birds (Hinsley *et al.* 2016). These earlier laying dates do not necessarily have a negative impact, as long as food availability, such as insect densities also advances. Asynchronies do however occur and can potentially be harmful (Parmesan. 2007). The study on caterpillar densities by Seress *et al.* also shows possible asynchronies between caterpillar densities and insectivorous birds within urban areas (Seress *et al.* 2018). Little is known about the exact effects of urban heat on birds, and no research has been performed on the direct effects on urban heat on their reproductive output. Perhaps it is time to start thinking about possible experimental designs in which the effects of urban heat on birds and their reproductive output can be determined.

Noise pollution

Anthropogenic noise from sources as transportation, urbanization and industry are another aspect of urbanization that can influence wildlife. A research performed over two decades found that some species of wildlife are negatively impacted by these forms of noise pollution (Shannon *et al.* 2016). Effects of this in birds is widely studied, and can lead to alterations in communication, foraging efficiency, nestling physiology, adult physiology and many others. A great list of studies regarding each of these alterations can be found in Injaian *et al.* as we want to specify our topic to the effects of noise pollution on the reproductive success of birds (Injaian *et al.* 2018). Several studies have been performed on the effects of anthropogenic sounds on the reproductive success in birds, often by artificially mimicking urban sounds around some of the birds nests.

In the research by Injaian *et al.* as mentioned above, the effect of anthropogenic sounds on the reproductive success of tree swallows (*Tachycineta bicolor*) was performed (Injaian *et al.* 2018). 30 nest boxes were used in this experiment, of which 15 were exposed on a daily basis to six hours of playback of car sounds to mimic urban noise. This research specifically looked upon the effect of these sounds on the chicks of tree swallows and found that noise had a negative impact on the nestlings growth. Negative impacts were also found on the fledglings their body mass as well as tarsus length, skull size, tail, and wingchord length, as indicated in figure 2. Oxidative stress was measured in both experimental and control chicks. Oxidative stress is known as the imbalance between oxidant production and antioxidant capacity, and can be measured from blood samples. Oxidative stress was found to be higher in the exposed chicks, which might partly explain the differences on nestling growth. This study found no effect on fledgling success, although experimental young did show an increase in fledge latency of about 1.5days.

A second research by Injaian *et al.* on tree swallows looked at settlement patterns

and reproductive success in a similar set-up (Injaian et al. 2018b). This time the experiment consisted of 35 nest boxes, of which 19 were exposed to 6 hour urban noise playbacks per day. In this second study a delay of lay date of 3.8 days was found for parents exposed to noise pollution relative to controls, but was not significant. This delay might be explained by nest site choice. The researchers in this study hypothesized that higher quality individuals would prefer more quiet nest surroundings. Thus they played urban sounds on different levels of decibels and ranked which nest boxes were taken first. The adults of nest boxes that were first taken were given rank 1, followed by rank 2 etc. Tree swallows that lay eggs earlier in the season, usually produce larger clutches with higher quality eggs and have an increased flight ability in standardized flight test, and are therefore thought to be higher quality individuals. The tree swallows that ranked low (1,2 etc) prefered lower decibel nest boxes over the ones exposed to higher amounts of decibels, suggesting that lower-quality females settled in the noise-exposed nestboxes. Noise exposed parents laid 0.58 less eggs then control parents, this result was significant. This study found negative effects on nestling wingchord and tail length, but these results were not significant. Egg size and fledgling success were not assessed in this study.

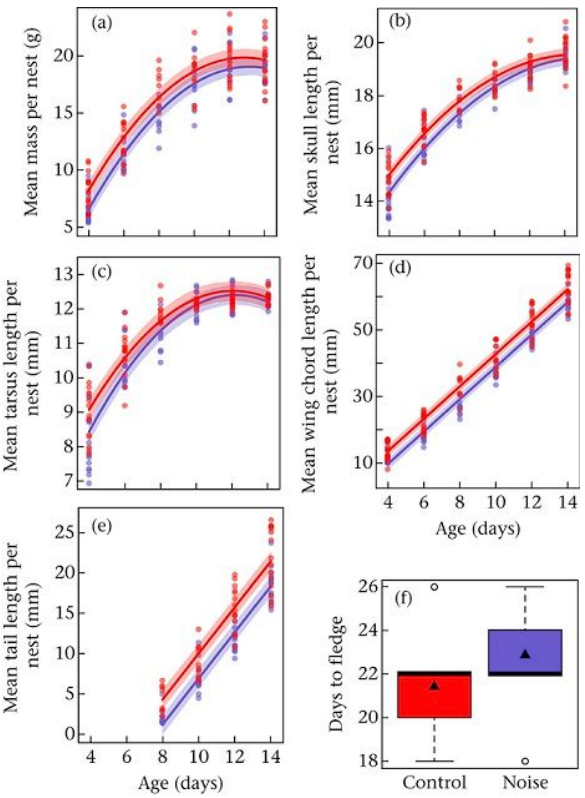

Figure 2: The effects of noise exposure to fledglings measures of growth and days to fledge. Exposed fledglings have a decreased body size in all categories (Injaian *et al.* 2018).

These similar studies look at different aspects of noise pollution on the reproductive success of tree swallows. The results of both studies combined show that tree swallows prefer settling in quiet habitats and that noise pollution negatively affects the reproductive output of tree swallows, with less eggs laid and lower quality offspring then control nests.

Three studies investigated the effects of urban noise on a clear urban exploiter : the house sparrow (*Passer domesticus ;* Marinin *et al.* 2017). Two of these studies were set-up in a similar way as the studies done on tree swallows. House sparrow nests were exposed to 6 hour playbacks of traffic noise daily during the nesting season, while control nests did not get this treatment. The study found no effects of noise exposure on the reproductive output of the house sparrow. The only difference found was a decrease in the metabolic rates of nestlings that were in the experimental group (Brischoux *et al.* 2017). However, the sample size of this study was rather low, as only 6 nests were exposed to noise playbacks. This low sample size might explain the limited effects that were found.

Another study done by the same group, also found no effects of the daily 6 hour

playbacks on the reproductive output. This study had a larger sample size, and used 21 nest boxes (Meillère *et al.* 2015). This might suggest that the effects of noise exposure are limited in house sparrows.

A study performed on Lundy Island however did find negative effects of noise pollution on house sparrows. The experimental house sparrows in this study bred in nest boxes surrounding a noise producing generator, and were compared to house sparrows from Lundy Island that were not exposed to this sound (Schroeder *et al*. 2012). Fledglings that were sound exposed weighed -0.74 grams less on average, and the fledgling success was decreased by 16%. Perhaps the amount of time exposed to urban noise has an impact on the reproductive output of house sparrows. As the generator produced sound 24 hours a day compared to the 6 hour playback loops of the other two studies done on house sparrows. Another study on the blue tit and the great tit also found no effects on reproductive output despite 24 hour exposure. In this study the birds were exposed to MP3 loops of traffic noise of 30 minutes that continued daily and nightly and were placed in a nest box that was placed above the experiment nests (Halfwerk *et al.* 2016).

More of these neutral effects were found in a study on Eastern Bluebirds, (*Sialia sialis*) when urban noise levels were measured around nest boxes and compared with each other in reproductive output (Kight *et al*. 2012). In this study, some negative trends on clutch size and fledgling success were found, but these were not significant and therefore questionable.

From the studies summarized above, effects of anthropogenic noise on reproductive success tend to be minimal, yet negative results were found in the studies on tree swallows and in the study on house sparrows by Schroeder *et al.* The results in tree swallows might be explained by the nest choice theory, in which lower quality females get more noise-exposed nest boxes, which can explain some of the negative results on reproduction. A similar result is found in great tits in the study by Halfwerk *et al.,* which showed that great tits had a preference for quiet nest box surroundings if they could choose. These results would implicate that some birds would choose quiet nesting places over noisy ones. An explanation for this preference for quiet nesting surroundings can be the negative effects of anthropogenic sounds on birds that are listed in Injaian *et al.* (Injaian *et al.* 2018). None of the studies discussed find any positive impacts of anthropogenic noises on reproductive output. Even within the studies that find no direct effects on traits like clutch size and fledgling success, indirect effects such as a decreased metabolism and increased oxidative stress in fledglings are being found. Therefore I can safely hypothesize that urban noise negatively affects urban reproductive success. More research needs to be done, as the current information regarding this subject is insufficient and the sample sizes are small. However it is feasible that anthropogenic noise impacts nesting urban birds in a negative way.

Artificial light

Another difference between urban and non urban areas is the amount of artificial light. Urban areas are often illuminated during the night for human comfort. Usage of artificial lights has shown an increase in the last 6 decades, and can negatively affect biodiversity and wildlife (Hölker *et al.* 2010). Therefore, the term light pollution is used in ecological studies when the impact of artificial light is considered. As light is an important zeitgeber for the biological clock in many organisms, artificial light could alter this biological clock and thereby affect the animals behavior (Hölker *et al.* 2010).

These differences can also be found in birds. Birds align their activity and physiology to time of day and time of year, via stimulation of photoreceptors (eyes) by sunlight to synchronize their internal circadian and circannual clocks (Dawson *et al.* 2001). Artificial light can therefore manipulate a birds biological rhythm. A study on the effects of artificial lights on blackbirds (*Turdus merula),* found that urban birds reached reproductive maturity 19 days earlier than their non-urban counterparts (Dominoni *et al.* 2015). Light pollution can alter dusk and dawn singing in songbirds, such as the blue tit (Kempenaers *et al.* 2010). A study done on great tits found that tit parents exposed to light, woke up earlier in the morning (Raap *et al.* 2015).

Limited information is available on the effects of artificial light on the reproductive success of birds. As experimental studies on the effect of light at night on fitness in a field situation with no other anthropogenic disturbances have rarely been performed (Spoelstra & Visser. 2014). You can hypothesize that urban lights might alter a birds circannual clock, and that this may lead to earlier lay dates in spring.

A study done on blue tits, compared blue tit nest boxes that were exposed to street light to those with natural light regimes. This study indeed found that the birds exposed to street lights had advanced laying dates of about 1.5 days compared to their non-exposed counterparts (Kempenaers *et al.* 2010). No results of this light exposure were found on clutch size. Another study was performed on the great tit and the pied flycatcher, (*Ficedula hypoleuca*) in which the effects of different colors of light was tested in natural areas in comparison with dark natural areas. This study found an earlier lay date in the great tit for green and white light in one year of this two year study. No earlier lay date was recorded for the pied flycatchers exposed to light (De Jong *et al.* 2015). No effects of this light exposure were found on clutch size or fledgling success.

Although light pollution can alter a birds behavior, little can be concluded about the impact of artificial light on reproductive success. The studies described above show that artificial light can lead to earlier lay dates, but find no effect on clutch size or fledgling success. The advancement of lay dates in these studies are minor and effects of this advancement are therefore likely to be restricted. This could explain

that no differences in clutch size or fledgling success were found, as parental birds would have been in a similar state at first lay than non-exposed birds while environmental conditions would be about the same. The impact of artificial light might also differ in impact per species, as no effects of light exposure were found in the pied flycatcher. Therefore, I conclude that the impact of light pollution might differ per species, but so far have been shown to be limited.

Predation

Predation might play an important role in differences in reproductive output between urban and non-urban birds. Predator densities in cities are often higher in comparison to their surrounding area, but some claim that predation rates tend to be lower. This phenomenon is known as the predation paradox (Fischer *et al.* 2012). This paradox can be explained by a lack of apex predators in urban areas. This leads to an increase in mesopredators, such as the magpie, crow, seagulls and mammals such as the fox and martin. Most of these species of predator, are omnivorous and can live just as well off of anthropogenic foods, which reduces the need to hunt (Fischer *et al.* 2012). This is not the case in all predators, as some species of urban predators such as the domestic cat (*Felis catus*), can have a devastating impact on some species of birds in urban populations. Even though most cats are being fed by their respective owners. (Baker *et al.* 2008).

The impact of predation on reproductive success is hard to assess on parameters such as lay date, clutch size, egg size, fledgling size and fledgling success. As predation commonly leads to complete loss of their nest. Therefore I will shortly discuss some articles regarding the differences in nest predation between urban and non-urban areas, as results found in these comparison studies vary widely. Some studies suggest that nest predation has decreased in urban compared to non-urban areas (Møller & Diaz. 2017), while other studies do not support these claims (Stracey, C. 2011). Probably the best article to read regarding nest predation is : *Avian productivity in urban landscapes: a review and meta-analysis* by Chamberlain *et al* (Chamberlain *et al.* 2009). This review displays that there is no consensus regarding the differences in nest predation between urban and non-urban areas in general. As differences in nest predation rates between urban and non-urban areas might differ per area and predator species.

As there is no consensus on possible differences in nest predation between urban and non-urban areas, it is hard to be conclusive about the effect of predation in urban versus non-urban environments. Differences between studies can perhaps be explained by many factors, such as bird species, predator species, predator

densities, the degree predators have adapted to urban living, different study areas and different levels of urbanization. It is therefore best to conclude that the impact of urban nest predation remains largely unknown, and that the impact of this on the reproductive success of birds might differ per area and species.

Pollution

Pollution, often caused by anthropogenic waste products and human activities, can have negative impacts on urban wildlife. Industrial manufacturing, combustion products or agricultural run-off can lead to elevated levels of metal (Burger. 1993). Once these metals are released into the environment they are hard to break down and persist in soils. Plants can take up these metals directly through root absorption after which they end up in the food chain (Hopkin. 1989). When these metals have entered the food chain, they can bioaccumulate, as they are being passed between trophic levels (Van Straalen & Ernst. 1991). Organisms occupying higher trophic levels, such as birds, are often affected by these higher concentrations of metals. Which could lead to both physical and neurological problems (Burger. 1993). Unfortunately, the effects of fauna feeding on polluted sites is not well documented and the understanding of these effects on ecosystems therefore remains undefined (Beyer *et al.* 2004). I could only find one comparative study that looked at the effect of pollution on the reproductive success in birds.

This study by Hofer *et al.* compared the nests of house wrens (*Troglodytes aedon*) between a polluted and a more natural environment (Hofer *et al.* 2010). They found that nestling feathers on the polluted site had significantly higher levels of pollutants, compared to the nestlings from the non-urban environment. Arsenic levels from urban nestlings were 14 times higher than from non-urban chicks. These differences however did not affect fledgling size, or fledgling success. This study did not look at possible effects on lay date, clutch size or egg size. It is important to mention that this study has a low sample size due to predation having only 19 experimental and 9 control nests left for sampling. Another aspect that should be taken into account is that the polluted area used in this study for comparison, has been abandoned for industrial use since the 1960's. And although significantly increased levels of pollutants were still found in the fledglings, these levels maybe even higher in industrial areas that are still in use, possibly affecting fledgling size and fledgling success.

Due to the limited research done on the effect of pollution on the reproductive success of birds, it is difficult to be conclusive regarding the possible effects that

these might implicate. As higher levels of pollutants have shown to have negative effects on both the birds physical and neuronal state (Burger. 1993), it is likely that this will also result on negative impacts on the reproductive output of birds. Leaving us with an nearly untouched topic for future researches.

Conclusion:

Does living in an urban environment affect the reproductive output in birds?

The studies discussed find predominantly negative effects of nesting in urban environments, although this might be compensated by less predation pressure and easy food access from bird feeders. Though we should keep in mind that there is no consensus over higher or lower predation pressure in cities, and that positive findings of food supplementation were found in field studies that did not take place in urban areas.

Most studies discussed find an advancement in lay date in urban areas compared to non-urban areas. These results are similar to the results described in the meta-analysis by Chamberlain *et al.* (Chamberlain *et al.* 2009). It is possible that these advanced lay dates are being caused by a combination of factors, such as food supplementation, warmer temperatures and artificial light.

Clutch size showed a tendency to decrease in urban areas in some of the discussed studies, although the study on the Western jackdaw revealed an increase. The analysis by Robb *et al.* also found positive effects of food supplementation on clutch size, but again we should take into consideration that these studies were not performed in urban areas. The negative effects on clutch size in urban areas for most species again match with the meta-analysis by Chamberlain *et al.,* which also finds that most species have a decrease in clutch size in urban areas.

Very little can be said about egg size, as most studies found no effects or did not look at differences in egg size.

Fledgling size also showed a decrease in some species when subjected to urban factors. Two studies done on the effect of noise pollution found a decrease in fledgling size when exposed to anthropogenic sounds. This decrease is likely causing alternative behaviors in parental birds, which could affect the feeding of nestlings, although the noise pollution might also affect the nestlings directly. Interestingly enough, the study on blue tits by Plummer *et al.* found negative effects of supplementary feeding on fledgling size, while Robb *et al.* analysis of food supplementation found positive effects on chick growth rate in 17 of their 30 assessed studies. Only one study in this analysis found negative growth rates on supplementary fed birds. Again, although these studies are not performed in urban

areas, it seems more likely that supplementary foods benefits nestlings, as supplemented food can reduce foraging time and can prevent starvation in fledglings. Not all the provided foods might be suitable for nestlings, but the indirect effects of supplemented food such as an increased parental attendance, selective foraging and reduction in aggression between chicks are beneficial. The decrease in fledgling size in urban areas is also found in most species in the meta-analysis by Chamberlain *et al.* Suggesting that supplemented food might have a smaller impact than is presupposed or that most birds studied in Chamberlain's *et al.* analysis had no access to supplemented foods.

Finally we come to the fledgling success, the strongest determinant of reproductive success. The discussed researches indicate in most cases that the urban factor discussed shows no effect on fledgling success. Suggesting that the effects of nesting in urban areas compared to non-urban areas are limited on a birds fitness. Some studies do find negative results on fledgling success, and the food supplementation studies find mostly positive results although we should bear in mind that they are not performed in urban areas. The studies that are discussed in this thesis often looks at a singular factor of urbanization, perhaps a combination of the given factors does give a more negative outcome as the effects of each factor piles up. The analysis by Chamberlain *et al.* states that the effects in urban birds on fledgling success largely differs per species. Therefore it is likely that urban factors can affect species of birds differently in their reproduction. Species that are known as urban exploiters are thought to be less affected by urbanization than other species, but future comparison studies between urban and non-urban environments should prove if this is indeed true.

Combining the answers of all given factors indicates that the urban environment can affect the reproductive output in birds, but that the effects largely differ per species and area. Some species can successfully raise young in urban environments and can show an increase in reproductive output, these urban populations are likely to be self-supporting. While other bird species show a decrease on reproductive output but it is uncertain if this leads to a population sink. And for some urban species studied, the urban habitat works as a sink (Padilla & Rodewald. 2015; Stracey & Robinson. 2012). As most bird species have been adapted to certain habitats and niches for many years, and given that the urban habitat and niches are relatively new perhaps birds need to adjust to their new habitats, and evolve within it to do just as good as their non-urban counterparts.

Appendix

Table 2: Comparison studies used for this thesis and their found effects on lay date, clutch size, egg size, young size and fledgling success. Given studies are separated by topic; bird feeders & anthropogenic food, urban heat, noise pollution, artificial light, pollution, predation and other. (N.A = No Available data in study) (N.E= No Effect or no significant affect was found).

Study	Design	Species and sample size	Lay date in urbanized area	Clutch size urbanized area	Egg size Urbanized area	Young size in Urbanized area	Fledgling success in Urbanized Area
Winter food provisioning reduces future breeding performances in wild birds	Research was performed in nine different woodlands over three years (three per year) split up into three different groups: Control, Winterfed with only fat and Winterfed with fat plus Vitamin E. Nest boxes in the area where checked regularly.	Blue Tit 362 nests	Experiment shows no difference in lay date, as it is performed in a forest area	Clutch size about the same between fed and unfed	N.A.	-0.5grams for fat fed chicks compared to unfed chicks. -0.4grams for chick fed with fat + Vit E compared to unfed chicks	-8% for fed chicks compared to unfed chicks
Happy to breed in the city? Urban food sources limit reproductive output in western jackdaw	In the theoretical research, Jackdaw colonies and their reproductive output (clutch size, egg size, amount of fledglings) was compared to	Jackdaws 34 nest boxes	N.A.	+0.37 egg in urbanized areas	Egg size about the same between fed chicks and rural chicks.	N.A.	-.88 fledgeling in urban area's

	the distances of the colonies to non urban environments. In the experiment, 15 and 19 nest boxes, split up between experiment and control, where used. about half of the nest boxes were given supplementary food (eggs or mealworms/maggots) and the results on clutch size, egg size, and fledglings was measured. Loggers were used to check if the parents got food from non-urban areas.				+1.4 for fed chicks vs unfed urban chicks.		
Winter feeding of birds increases productivity in the subsequent breeding season	Experiment in which 10 similar sites were randomly assigned to fed and unfed sites, feeding stopped 6 weeks prior to breeding season. Nest boxes of 76 blue tits were monitored.	Blue tit 45 fed and 31 unfed nest boxes	-2.5days for fed chicks although research not condemned in urbanized area	N.E	N.A	N.E	+0.9 chick in fed nests compared to unfed nests.
Food for thought supplementar	Analysis of studies performed on	Several species, several	+57.6 %advanced	+44.4 % positive	37.8% positive effect	56.7% positive effect on	63.6% positive effect on

y feeding as driver of ecological change in avian populations	the effect of feeding and productivity of a wide variety of birds	studies	laying date 40.7% no effect	effect on clutch size 54% no effect	62.2% no effect	growth rate 40% no effect	fledgling success 36.4% no effect.
Urban Heat:							
Influence of habitat urbanisation on time of breeding in the tawny owl	Tawny owl nests from the city were compared to tawny owl nests in a forest 70km away from the city. Lay date and amount of fledglings was recorded and compared.	Tawny owl, 45 urban tawny owl nest and 71 non-urban tawny owl nests	-40 days on average compared to non-urban tawny owls.	N.A	N.A	N.A	-0.2 young for urban birds
interspecific variation in the relationship between clutch size, laying date and intensity of urbanization in four species of hole nesting birds	Data of previous studies done on 4 birds species was used to compare laying date and other factors by comparing the location of nest boxes to the level of urbanization surrounding the nest boxes. After which a nest box was categorized for its intensity of urbanisation.	Blue Tits 101 study populations Great Tits 138 study populations Pied Flycatchers 23 study populations Collared flycatcher 66 study populations	Differences among habitats were found for al four species, but not with the intensity of urbanization	No significant effect on clutch size in blue tit and great tit Both the flycatchers clutch size decreased with the intensity of urbanisation.	N.A.	N.A.	N.A.

Noise pollution							
experimental anthropogenic noise impacts avian parental behaviour, nestling growth and nestling oxidative stress.	15 experimental nests were exposed to 6 hour playbacks of car noises to mimic urban noise pollution, the 15 control nests were not exposed to this sound. The noise pollution started two days after the last hatchlings hatched.	Tree swallows, 15 control and 15 experiment nests	N.A.	N.A.	N.A.	Negative impact on body mass, tarsus ,skull, tail and wing chord length for chicks exposed to noise.	Noise pollution caused no effect fledgling success between experiment and control. Experiment young did increase fledging latency
Effects of experimental anthropogenic noise on avian settlement patterns and reproductive success	The effect of noise pollution on tree swallows was studied by playing 6 hour playbacks along several nest boxes and compare these results with nest boxes that are not exposed to these noises.	Tree swallows, 19 experiment and 16 control nests	Egg laying delayed by 3.8 days in experiment nests	0.58 fewer eggs for nests exposed to noise pollution	N.A	N.E.	N.E.
Traffic noise decreases nestling metabolic rates in an urban exploiter	Experimental nest boxes were exposed to 6 hour playbacks of traffic sounds while control nest boxes were not exposed to this sound pollution. The sound pollution occurred during	House sparrow 6 experiment nest boxes 13 control nest boxes.	N.E	N.E	N.E	N.E although metabolic rate of experiment young was decreased	N.E.

	the entire first breeding attempt.						
Noise affects nest-box choice of 2 competing songbird species, but not their reproduction	Experiment in which the experimental nest boxes roofs were removed and a second nest box was added, in the second nest box an mp3 player was placed playing traffic noises in 30 min loops, day and night.	Great tit and Blue tit n=60 depending on calculation	N.A	N.E	N.E	N.E	N.E
Impact of chronic noise exposure on antipredator behavior: an experiment in breeding house sparrows	Speakers playing urban noise 6 hours per day were placed 3-4 meters away from experimental nest boxes. Sound exposure began when house sparrows have started to build their nests.	House sparrow 21 experimental nest boxes and 46 control nest boxes	N.E.	N.E.	N.A	N.A	N.E
Anthropogenic noise is associated with reductions in the productivity of eastern bluebirds	Sound recordings were made at nest boxes used to determine the amount of anthropogenic noise that each nestboxes was submitted to, after which these amounts of noise were	Eastern Blue, 43 nest boxes	N.A	Negative trend for brood size at higher levels of anthropogenic noise	N.A	N.A	Negative trend for fledgling success at higher levels of anthropogenic noise

	compared to the reproductive success of the eastern bluebird						
Passerine birds breeding under chronic noise experience reduced fitness	Nest boxes at a barn with a generator producing 68Db on average where compared to nest boxes in the environment of the barn, ranging from a light impact of the sound of the generator, to almost no impact of the sound. Young were cross-fostered to give a more detailed look on the effect of being raised in a noisy environment.	House sparrow 29 nest boxes at the barn with the generat or. 46 nest boxes in or on a quiet barn and 27 in a nearby wood.	N.E	N.E	N.A	-0.74 g Chicks that were reared but not necessa rily born in a noisy environ ment had a significa nt lower body weight	Survival rate of chick decrease s by 16% (from 0.25 to 0.21) when brought up under noise disturban ce
Artificial light							
Artificial night lighting affects dawn song, extra pair siring success and lay date in songbirds	Nest boxes of blue tits that were exposed to streetlight were compared to nest boxes that were exposed to a natural light regime	Blue tit 508 breedin g attempts 5165 offspring	+1.5 days advan ce under influen ce of streetli ght	N.E	N.A	N.A	N.A
Effects of nocturnal illumination on life-history	8 natural sites with nest boxes were illuminated with	Great tit (247 broods) and pied	No effects in pied flycatc	N.E	N.A	N.A	N.E

decisions and fitness in two wild songbird species	artificial light in different colors. The effects of this was compared to nest-boxes with natural light	flycatcher 113 broods	her Great tits showed an earlier laydate in 2013 in green and white lighted areas, but not in 2014.				
Pollution							
Metal accumulation and performance of nestlings of passerine bird species at an urban brownfield site	House wrens nests from an Urban polluted area were compared to a natural area with not much pollution.	19 house wren experimental nests and 9 control nests (many lost due to high predation rate)	N.A	N.A	N.A	N.E	N.E
Predation							
Avian productivity in urban landscapes: a review and meta-analysis	The results of several comparison studies, are used to compare the impact of urbanisation on laying date, clutch size, fledgling success etc.	Several species of birds	Earlier laying dates for urban birds in 16 of the 19 studies (and in 7 of	Clutch sizes in non urban areas are larger in general	N.A.	Out of 10 species, only one species of bird shows higher mean nestling weights in urban	No particular pattern across species, although a trend shows an increase in fledglings in

			the 13 studies using a significant test)			habitats. Several species show a significant increase in weight in non-urban areas.	non-urban areas. House sparrow show a significant increase in fledglings in urban areas.
Other							
Urban environments are associated with earlier clutches and faster nestling feather growth compared to natural habitats	Reproductive success of mountain chickadees in an urban environment was compared to the reproductive success of mountain chickadees in a forest. Nest boxes were placed in a forest and in urban area.	Mountain chickadees, data based on the results of a 146 nestlings	April 26 ± 5.6 days for urban birds May 15 ± 7 days for pairs in a natural habitat	N.E	N.A	N.E	N.E

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