



Norges miljø- og biovitenskapelige universitet

Master's Thesis 202260 ECTSFaculty of Environmental Science and Natural Resource Management

# Long-Term Changes in the Bird Community in Urban Green Spaces in Oslo, Norway

# Carmen Emilie Skjelvik

Master of Science in Tropical Ecology and Management of Natural Resources

# Preface

This master's thesis was written as part of my MSc in Tropical Ecology and Management of Natural Resources at the Faculty of Environmental Science and Natural Resource Management at the Norwegian University of Life Sciences. Due to the COVID -19 pandemic, I was not able to continue with my first master's project, where I intended to do field research in the Brazilian Amazon. Instead, I found this project where I could conduct my own fieldwork here in Oslo. The next few months consisted of learning all birds' songs and making sure I knew all the species. At that time, I had no idea that all this learning would probably stay with me for the rest of my life and enhance my recreational experience in nature. I am very grateful for the knowledge I have gained throughout this project!

With this thesis, I have completed a long journey during which I have learned a lot and gained a lot of experience. The care and support I have received have been outstanding, and I would like to thank all the people who have been there for me. First and foremost, I would like to thank my supervisor, Svein Dale, for giving me the opportunity to work on this project. I am grateful for his guidance, excellent feedback, and help with the statistical part of the project; he has been a fantastic supervisor for me. In addition, I would also like to thank my small study group for their help and good motivation throughout the writing process. I would also like to thank my better half, who helped me before and during the fieldwork by driving me to different locations so early that no one was awake yet except the birds and us.

Norwegian University of Life Sciences

Ås, 15 May 2022

Carmen Emilie Skjelvik

### Abstract

Urban areas are becoming increasingly dominant worldwide, and studies of long-term trends in urban bird populations are necessary to evaluate the impact cities have on wildlife and the ecosystem function upon which humans depend. However, few studies to date have examined long-term population trends of birds in urban areas. This study aimed to document the longterm bird population trends in urban green spaces. Birds were censused in 93 green spaces in Oslo, Norway. The first census was conducted in 2005-2007, and the second census was conducted approximately 15 years later, in 2021. Population trends for 45 breeding land bird species were considered, and ecological traits including body mass and brain size, migration strategy, nest site selection, diet, habitat preference, and red list status were considered as potentially contributing factors to population change. Additionally, population trends in Oslo were compared to national trends in Norway and Sweden to examine whether urban birds in Oslo exhibit different trends from the species in general. This study found evidence that migratory species declined relative to resident species, and populations of diet specialists and farmland species declined. Contrary to predictions based on previous studies of the importance of brain size for urban living, I found that brain size did not contribute to the long-term changes in the bird communities in Oslo. Overall, there was no significant change in the number of individuals or occupancy in Oslo over the last 15 years. The population trends were consistent with the temporal changes from the national counting in Sweden and close to observed population changes in Norway. These results suggest that population changes in urban environments are influenced by the same factors as the bird communities at the national scale. Thus, there was no evidence that urban bird species had population trends differing from those of birds at a wider scale.

# Table of Contents

| PREFACE  | I   |
|--|-----|
| ABSTRACT   | III |
| INTRODUCTION   | 1   |
| MATERIALS AND METHODS  | 5   |
| STUDY AREA   |     |
| Bird censuses  |     |
| STUDY SPECIES AND SPECIES CHARACTERISTICS                          |     |
| STATISTICAL ANALYSIS   | 8   |
| Ecological variables   |     |
| Long-term population changes                                       |     |
| Aggregated analysis of the ecological variables and Swedish trends | 10  |
| RESULTS  | 11  |
| LONG-TERM POPULATION CHANGES                                       | 11  |
| Ecological variables   |     |
| Body and brain mass  | 13  |
| Migration strategy   | 14  |
| Nest site  |     |
| Dietary preference   | 16  |
| Habitat preference   | 17  |
| Red list status  | 18  |
| URBAN CHANGES IN RELATION TO NATIONAL TRENDS                       | 19  |
| AGGREGATED ANALYSIS  | 21  |
| DISCUSSION   | 22  |
| LONG TERM CHANGES  | 22  |
| Ecological traits  |     |
| URBAN TRENDS VERSUS NATIONAL TRENDS                                |     |
| Ecological significance  | 26  |
| CONCLUSION   | 27  |
| REFERENCES   | 28  |
| APPENDIX   | 37  |
| Appendix 1   | 37  |

## Introduction

Today, more than half of the world's population lives in urban areas (Ritchie & Roser, 2018), and during the last century, the shift from natural to man-made habitats has occurred at an unprecedented scale (Marzluff & Ewing, 2001; Shochat et al., 2006; Liu et al., 2018). It is now undeniable that urbanization negatively impacts biodiversity (Aronson et al., 2016; Fidino et al., 2021; McDonald et al., 2020; Pyšek et al., 2004). Cities are usually located in biodiversity hot spot areas, and the associated habitat loss caused by urbanization is a major driver of species extirpations or extinctions (Czech et al., 2000; McDonald et al., 2008; Myczko et al., 2014). In addition, biodiversity has declined significantly worldwide in recent years for several taxa (Butchart et al., 2010). Among the threats to biodiversity include changes in agricultural practices, habitat loss, degradation, illegal hunting, invasive and alien species (IUCN, 2015), and climate change (Møller et al., 2010; Parmesan & Yohe, 2003; Parmesan, 2007; Walther et al., 2002). It has been demonstrated that numerous bird species in Europe have experienced significant population declines, particularly those associated with agricultural systems (Donald et al., 2006; Gregory et al., 2005; Reif, 2013; Tucker & Heath, 1994), and those that migrate long distances (Heldbjerg & Fox, 2008; Sanderson et al., 2006; 2016; Thaxter et al., 2010).

As cities continue to grow and urbanize worldwide, the selective pressure on species in these areas will likely increase, forcing species to either adapt to the novel conditions or disappear. Still, some species persist and, at times, thrive in cities. The diversity is often favored by these (usually few) tolerant species that manage to adapt and persist under this higher degree of urbanization (McKinney, 2006). Populations can be categorized as 'winners' or 'losers' according to whether they are thriving or declining in their environment (McKinney & Lockwood, 1999).

Cities usually have green spaces suitable for certain species, and most of these green spaces are public parks or cemeteries. The vegetation usually includes introduced non-native species of trees, grasses, and bushes, managed lawns, and removal of mid-story canopy (Luck & Smallbone, 2010). In addition, urban areas often have a high food abundance and low predation risk, which explains the global pattern of high urban bird densities (Shochat, 2004). However, while food resources for urban birds may be abundant at the population level (Marzluff, 2001), it might be scarce at the individual level due to intense competition (Sol et al., 1998).

Changes in abundance and occupancy are essential components of biodiversity change and contribute in different ways to biotic change (Dornelas et al., 2019). Whether the urban bird community compositions are unique because of the selection of certain species (winners) with specific characteristics or if other factors influence the composition of the urban communities has been explored (Bonier et al., 2007; Dale et al., 2015; Møller, 2009; Seress & Liker, 2015). It has frequently been reported that urbanization favors residency rather than migration (Croci et al., 2008; Møller et al., 2014), urbanization favors species that are generalists (e.g., review by Chance & Walsh, 2006), species that nests high and in cavities rather than ground nesters (Jokimäki et al., 2016) and species with a broad environmental tolerance (Bonier et al., 2007). Conversely, other researchers suggest that the bird diversity in urban areas, such as Oslo, is influenced mainly by the diversity of birds found in the surrounding habitat (Dale et al., 2015; Møller et al., 2012; Sol et al., 2014), suggesting that the urban bird communities result from immigration from the surrounding landscapes. Because species traits have been linked to extinction risk in various taxa, from higher plants (Smart et al., 2005), to primates (Purvis et al., 2000), it is important to identify these ecological, life history, and behavioral traits. As these traits might contribute to species declines and extinctions, we can learn more about the underlying mechanisms, predict which species will face problems, prioritize research and conservation efforts, and develop management strategies (Kotiaho et al., 2005; Vercauteren et al., 2010).

An insufficiently explored process is how the urban environment has changed the long-term composition of species inhabiting urban areas. Long-term studies provide us with essential insight into ecological processes at different scales, such as populations, communities, and ecosystems. Additionally, long-term research in urban areas allows us to understand trends and dynamics that could have gone unnoticed in short-term studies. However, long-term urban ecological datasets are extremely scarce (Fidino et al., 2022). This is primarily due to the lack of exploration into the urban ecology of cities, and this has only increased in recent decades (Magle et al., 2012). Long-term research in urban areas is important because urbanization has a homogenizing effect on biodiversity as natural habitats are reduced (Liang et al., 2019; McKinney, 2006; Newbold et al., 2018). As birds are well-known and well-studied, they are often used as surrogates for other biodiversity elements and could act as a good indicator of the ecosystem's health (Gregory et al., 2008). Urban bird studies have contributed to the field of urban ecology, and many of the patterns observed within urban systems are demonstrated with birds (Aronson et al., 2014; Blair, 1999; Crooks et al., 2004; Marzluff, 2008). Still, these studies

have mainly focused on patterns and processes at different spatial scales, and most of the studies are conducted over a short time period (Marzluff, 2001).

To explore how species composition changes over time in a city, the urban bird communities of 93 green spaces in Oslo, Norway, were studied. Between 2005 and 2007, these green spaces were censused in the breeding season (Dale et al., 2015; Dale, 2018). I repeated these censuses to examine how the urban bird community has changed, and whether changes in the bird community are influenced by ecological traits such as brain and body size, migratory behavior, nest site selection, diet, habitat preference, and red list status. In addition, national population trends were used to test whether population changes in Oslo were unique to Oslo or followed national trends. I hypothesized that urban birds are subject to specific selection pressures. Based on this hypothesis, I predict that urban birds with specific traits that are particularly well adapted to urban environments are likely to exhibit positive population trends. For the specific ecological traits:

- I predict that there has been a shift in Oslo over the past 15 years towards species with larger brains. Although Dale et al. (2015) found no effect of brain size on urban living in Oslo, several researchers have found that brain size facilitates population change in which species with larger brains are more successful in urban and novel environments (Carrete & Tella, 2011; Maklakov et al., 2011; Overington et al., 2009; Sayol et al., 2020; Sol et al., 2005). This can be explained by the fact that brain size is widely considered to be one of the primary mechanisms through which animals cope with novel environmental changes, facilitating population persistence when there is an unpredicted change in the environment (Price et al., 2003; Sol et al., 2013). However, these studies demonstrating that larger brains are favored do not address the long-term changes in urban communities as this research does.
- There is also evidence of an ongoing trend favoring species with larger bodies, while species with smaller bodies are declining more rapidly (Inger et al., 2015). This study only considered land bird species, and other large-bodied species, including geese, whose populations have generally increased, were not included. Therefore, I do not predict that body size is related to population changes in Oslo.
- I predict that there has been a decline in migratory species, primarily long-distance migrants. Several studies have found that long-distance migrants breeding in Europe show

the most considerable population declines (Heldbjerg & Fox, 2008; Sanderson et al., 2006; Thaxter et al., 2010) and that residency is favored in urban areas (Møller et al., 2014).

- Dale et al. (2015) found that high and cavity-nesting species are the most successful species in the urban environment of Oslo. Additionally, one of the most consistent effects of urbanization is on ground-nesting birds, whose abundance will be negatively affected by urbanization (Clergeau et al., 2006; Dale, 2018; Evans et al., 2011; Hedblom & Söderström, 2010; Jokimäki & Huhta, 2000; McLain et al., 1999). Hence, I predict a positive population trend for species nesting high and in cavities and a decline for groundnesting species.
- Research on European bird communities shows that the most successful urban adapters tend to be omnivorous species (Chace & Walsh, 2006; Evans et al., 2011; Kark et al., 2007; Le Viol et al., 2012; Møller, 2009), a sort of generalist species. Hence, I predict a decline in specialist species and an increase in generalist species.
- Farmland birds represent the group of birds that have shown the most negative population decline in Europe (Donald et al., 2001; Inger et al., 2015; Kamp et al., 2021; Pain & Pienkowski, 1997; Tucker & Heath, 1994). Hence, I predict that there has been a similar decline for farmland species in Oslo.
- I predict a decline for species categorized as threatened in the Norwegian Red List, similar to the decline in Norwegian national trends (Stokke et al., 2021).

As urbanization continues, selection pressures on species will likely increase, eventually leading to a loss of species that cannot survive high levels of urbanization. If this is the case, I would expect species richness to decline. Although several researchers have reported that the composition of urban bird communities is unique due to the selection of species with specific traits, one could, on the other hand, also argue that urban birds may be influenced by the same factors as bird populations on a larger scale. Thus, the urban species composition in Oslo would reflect large-scale (Norwegian or Swedish) patterns of change in species population in the regional pool (Fidino et al., 2022; Murgui, 2014; Ward et al., 2018). If this is the case, species population trends within Oslo should therefore reflect overall national trends.

# Materials and methods

## Study area

The study was carried out in Oslo, the capital of Norway. Oslo is located in the southeastern part of Norway (59.91° N, 10.75° E), and the municipality of Oslo had a population of 699 827 in 2021 during this study (Statistisk sentralbyrå, 2022). Oslo is surrounded by hills, forests, and the fjord in several directions. To the north and east perimeter of the city, two vast forested areas (*Marka*) border to the urban Oslo. Approximately 310 km<sup>2</sup> of the total area of the Oslo Municipality (454 km<sup>2</sup>) lies within *Marka*, and the population density for the urban areas is 4 859 inhabitants per km<sup>2</sup>. The city of Oslo has many parks and green areas within the city core. Parks, cemeteries, and other green spaces were censused in this project, aiming to cover nearly all green spaces larger than 1 ha in the built-up areas of Oslo (Dale, 2018). I surveyed the bird community of 93 green spaces in the city of Oslo and around the city center (Figure 1). The green spaces were the same in 2021 as those recorded during the first censuses conducted in 2005-07.



*Figure 1.* Map of the study area in Oslo, Norway (made in Google Maps). The dark gray areas represent the 93 green spaces surveyed in 2005-2007 and 2021. In some cases, sites were so close to each other that they merged on the map.

The vegetation of the 93 green spaces included in this study varied; most of the spaces consisted of managed parkland with some natural vegetation. Deciduous forests and mixed forests dominated the natural vegetation. There was a gradual gradient from the city center of Oslo to

the borders of *Marka*, from residential and commercial buildings to residential areas with a considerable amount of vegetation. The 93 green spaces in Oslo included in this study were divided into three zones according to the degree of urbanization: (1) The inner zone (n = 22) consisted of residential, commercial, and office buildings, while the green spaces were mostly restricted to parks and cemeteries. (2) The middle zone (n = 20) was located between Ring Roads 2 and 3, and included a similar environment to the inner zone, but more houses had gardens, and undefined green spaces became more frequent. (3) The outer zone (n = 51) was located outside Ring Road 3 and consisted mainly of residential areas with a mix of apartment buildings and many individual houses with gardens. Due to a strict ban on constructing houses outside the designated boundaries of *Marka*, the periphery of the city forms an abrupt boundary with the adjacent non-urban habitat. Coniferous forests were the predominant forest type on the periphery of the city, outside the border to *Marka*. Minor changes were detected in only a few sites (n = 3); hence population changes are unlikely to be related to habitat changes

#### **Bird censuses**

The bird censuses were conducted during the breeding season from late April to the middle of June 2021. Each of the 93 urban green spaces was censused two times, giving a total of 186 individual censuses. In 2005-07, three censuses were conducted at different times of the breeding season. The two censuses from 2005-07 chosen to use as a comparison to the two censuses in 2021 were often conducted in the same year (n = 83), and the remaining (n = 10) were held in different years. In order to evenly distribute the 2021 visits in the different time periods used in 2005-07, 51 visits were made in the early period, 67 visits during the middle period, and 68 visits during the late period (sum of 186 = two visits per green space). All visits to the 93 green spaces in 2021 were similar to those in the dataset from 2005-07; for example, if the two visits were early and mid-period, the same was done in 2021. The three time periods during which the census was conducted were made up of the early period (22. April - 15. May), the middle period (16. May - 29. May), and the late period (30. May - 15. June).

A census consisted of walking slowly through each site with care to avoid double counting. The paths were chosen to cover each green space evenly, and no parts of the sites were more than 100 meters away from the paths used (Dale et al., 2015). The censuses usually began at sunrise, at the earliest 04:15 am, and finished around 09:00 am (latest at 10:15). In line with the previous studies in Oslo (Dale et al. 2015; Dale 2018), sites in the city center were visited

earlier in the morning than the other sites in order to avoid traffic noise and human disturbance, which may reduce bird detection rates.

In windy or rainy conditions, the censuses had to be postponed. The time spent at each site increased with the size of the site. The minimum time spent at each site was 10 minutes, and the maximum time was 1 hour and 30 minutes. The mean of the median time spent at all sites in 2021 was 27 minutes, while in 2005-07, the mean of the median time spent at sites was 25.2 minutes. The slight increase in time spent at the sites was due to my inexperience with bird identification at the beginning of the fieldwork period. Both the 2005-07 and 2021 censuses aim to register all individuals and determine the occupancy of urban birds; therefore, this is unlikely to have affected the results.

#### Study species and species characteristics

Only breeding land bird species were considered during the bird censuses of Oslo; species entirely dependent upon wetlands and passage migrants were excluded from the study. The species were recorded as either present or absent (occupancy), and the total number of individuals of each species at each of the 93 green spaces. While a wide range of ecological factors and life-history traits have been linked to urban bird community composition and population changes, I focused on seven features of the species ecology that could affect their ability to utilize urban areas. Present in at least four sites in at least one of the time periods (2005-07 or 2021), species were classified in relation to the following ecological traits:

- Body and brain mass: data was taken from Dale et al. (2015). Relative brain mass values were the residuals from a regression analysis of brain mass on body mass.
- Migratory strategy: species were initially classified as either resident (n = 19) or migratory (n = 26) based on Dale et al. (2015). Note that species in which only a minor portion of the population is a resident are classified as migratory. Migratory species were then separated into short-distance migrants (n = 13) and long-distance migrants (n = 13) based on "Norsk Ringmerksatlas" (Bakken, 2006).
- Nest sites: species were classified into four groups following Dale et al. (2015); (1) ground (n = 4) or (2) low in bushes (< 2 m above ground, n = 12), (3) high in trees (> 2 m above ground, n = 12), or (4) in cavities (n = 17).
- Diet: species were classified as being either specialists or generalists based on their dietary preference; data was taken from Dale (2018). Feeding specialists (n = 21) were insectivorous

and predatory species, and feeding generalists (n = 24) were omnivorous and granivorous species (many of which also supplement the diet with insects during summer).

- Habitat preference: species were classified into four habitat types following Dale et al. (2015); (1) breeding predominantly in coniferous forests (n = 6), (2) breeding predominantly in mixed and deciduous forests (n = 21), (3) breeding predominantly in farmland habitats (n = 15), and (4) breeding predominantly in urban areas (n = 3).
- Red list status: The species' red list status was based on the Norwegian Red List (Stokke et al., 2021). Species were classified as threatened (n = 6) and red-listed as Critically Endangered (CR), Endangered (EN), Vulnerable (VU; n = 1), or Near Threatened (NT; n = 5), or not red-listed as Least Concern (LC; n = 38). One species (*Columba livia*) was not categorized in the red list and excluded from further analysis.

### Statistical analysis

#### Ecological variables

All statistical tests included species (n = 45) present in  $\ge$  4 of the green spaces in at least one of the time periods (2005-07 and 2021). A Kruskal-Wallis test was used to analyze the relationship between population trends and habitat preference (four categorical variables: farmland, mixed, coniferous forest, urban) and nest-site preference (four categorical variables: cavity, high, low, ground). The association between migration status (two-level categorical variable; migratory and resident, short- and long-distance migrants), dietary preferences (two-level categorical variable; threatened and non-threatened), and change in species occupancy and the number of individuals was examined using Mann-Whitney U- tests. All statistical tests were considered statistically significant when p < 0.05.

#### Long-term population changes

The analysis of changes in urban bird communities in Oslo between 2005-07 and 2021 was carried out using paired t-tests. The associations between the two types of change in the bird community in Oslo, the percentage change in occupancy and the number of individuals, were analyzed with a Pearson's correlation test.

To test whether there is an association between population trends in Oslo, Norway, and Sweden, I conducted nine GLM analyses. First, the Norwegian data from the Pan-European Common Bird Monitoring Scheme (PECBMS) were used to determine whether bird species in Oslo have changed according to national trends. PECBMS collects survey data from all participating countries from 1996 to 2017. To match the time period in Oslo, I compared the trends in Oslo to the Norwegian national trends, selecting the period 2007-2017. Since we are interested in relative rather than absolute changes for the species, I had to calculate index values for the species in the PECBMS report by dividing all values from the later years by the values from 2007. The slope value was used directly in the analysis (index versus year), and the slope estimates were used as the annual change index. As most of the censuses done 15 years ago in Oslo are from 2006 and 2007, it would be logical to use the data from 2006 in the PECBMS report. However, one reason for using the data from 2007 is that TOV-E (the national bird census website in Norway) does not provide pre-2007 data. Therefore, I found it more appropriate to use the period from 2007 to 2017. The PECBMS dataset for national trends in Norway lacked data for 9 of the 45 species of interest.

For this reason, data on Swedish bird populations (Green et al., 2020), which contain data on 44 of the 45 species (data were missing for *Carduelis cannabina*), were also used to compare the population trends observed in Oslo. This Swedish report, entitled "Övervakning av fåglarnas populationsutveckling" (Green et al., 2020), contained information on the annual percentage change for species from 1996 to 2020 and did not require the calculation of index numbers for species, so it could be used directly to compare the population trends. Species covered by both the Norwegian and Swedish monitoring showed similar trends (Table 1). However, the population change for the birds of interest in the Swedish report (Green et al., 2020) covered a relatively long time period (1996-2020).

To match the time period in Oslo, I also used the Swedish PECBMS dataset, which had the possibility to select a specific time period, chosen to be 2007 to 2017. As with the Norwegian PECBMS data, it was necessary to calculate the index numbers for each species. If information was not available for a species in some of the earlier years in the dataset (in this case, there was no data for one species in 2007), I excluded that year from the analysis and calculated the index starting in 2008. The period from 2007 to 2017 (n = 44) in the Swedish PECBMS dataset showed a strong, statistically significant relationship with the Norwegian (PECBMS) national trends (Table 1). In addition, Spearman's rank-order correlation tests were performed due to some outlier values.

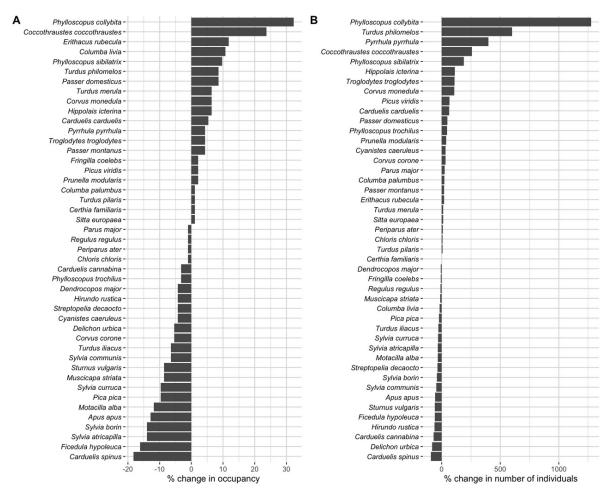
Aggregated analysis of the ecological variables and Swedish trends

Generalized linear models with Gaussian error and an identity link function were used to analyze the relationship between ecological variables and the change in occupancy and number of individuals in Oslo. Four multiple regressions were conducted; either the change in occupancy or the number of individuals in Oslo over the past 15 years as the independent variable. The dependent variables, brain and body size, migration, nest site, habitat, diet, and red list status were all included in the same analysis. Swedish trends (1996-2020 and 2007-2017) were included as dependent variables in each analysis. Norwegian data from the Pan-European Common Bird Monitoring Scheme (2007-2017) were not included in the combined analysis, because there was no significant relationship between the variables and the population trend in Oslo. Groups of variables were excluded if they contained fewer than two species. In the final table, p-values < 0.1 are shown. All analyses were performed using the integrated development environment Rstudio in the statistical software R (version 4.1.1; R Core Team, 2021).

## Results

#### Long-term population changes

Exactly the same number of species was observed in the 93 green spaces surveyed in Oslo in 2005-07 as in 2021 (n = 58). Summing all species found in more than four green spaces, 45 species in 20 families were observed in Oslo. Of those, 24 species declined, and 21 increased in occupancy (Figure 2A). The number of individuals declined for 20 species, increased for 24, and remained stable for one (Figure 2B). The change in the total number of individuals was - 1.149 %, and the change in occupancy of bird species in Oslo over the last 15 years was -1.094 %. There was no statistically significant change either for the percentage change in occupancy (t = 0.33, df = 44, p = 0.74) or the percentage change in the number of individuals (t = -0.56, df = 44, p = 0.58).



*Figure 2.* (*A*) The percentage change in occupancy of bird species along with (*B*) the percentage change in the number of individuals of each species in Oslo from 2005-2007 to 2021. Based on species (n = 45) found in  $\ge 4$  of the green spaces.

Thus, the occupancy and the total number of individuals of urban bird species have remained nearly unchanged in Oslo over the past 15 years. Although there were no statistically significant changes for the bird community in Oslo as a whole, some species have experienced substantial population increases or decreases (Figure 2).

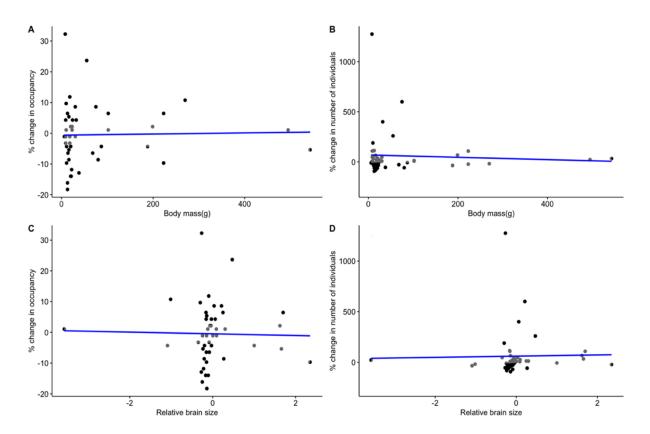
The dominant species among the birds with the steepest positive occupancy trend in Oslo in the last 15 years are *Phylloscopus collybita* and *Coccothraustes coccothraustes*. In contrast, *Carduelis spinus, Ficedula hypoleuca, Sylvia atricapilla, Sylvia borin,* and *Apus apus* had the steepest negative trend in occupancy (Figure 2A). *Phylloscopus collybita* was also the species with the steepest increase in the number of individuals. The second and third species with the steepest increase in the number of individuals were *Turdus philomelos* and *Pyrrhula pyrrhula*. However, these species were not very common and only increased with a few individuals. Considering that only the percentage change is presented in Figure 2B, the increase appears more dramatic than it is. In addition, the number of individuals of *Coccothraustes coccothraustes* also increased substantially. Species that experienced the greatest decrease in the number of individuals *plichon urbica, Carduelis cannabina, Hirundo rustica, Ficedula hypoluca, Sturnus vulgaris,* and *Apus apus* (Figure 2B).

Changes in the urban bird community of Oslo showed a statistically significant relationship between change in occupancy and the number of individuals (Pearson's correlation test: t = 6.52, df = 43, p = < 0.001), indicating that there is a relationship between change in occupancy and number of individuals in Oslo during the last 15 years. A complete table of species trends can be found in the Appendix (Appendix 1).

#### **Ecological variables**

#### Body and brain mass

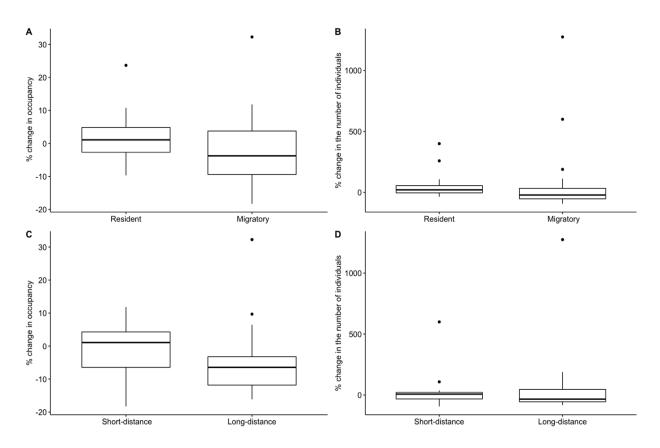
The results of the analysis showed that neither relative brain size nor body mass was correlated with the changes in urban bird communities that have occurred in Oslo over the past 15 years (Figure 3). Specifically, there were no significant relationship between body mass and the percent change in occupancy (R = 0.89, n = 45, p = 0.89; Figure 3A) and percent change in the number of individuals (R = -0.061, n = 45, p = 0.69; Figure 3B). Similarly, no significant relationship was found considering relative brain sizes and the population changes in Oslo (percent change in occupancy: R = -0.024, n = 45, p = 0.88; Figure 3C and percent change in the number of individuals R = 0.022, df = 45, p = 0.88; Figure 3D).



**Figure 3.** The association between the percentage change in occupancy and the percentage change in the number of individuals in relation to (A and B) body mass measured in grams and (C and D) relative brain size. A negative value on the x-axis indicates a small brain size compared to body size and vice versa. Black points represent the species (n = 45), and the blue line is the regression line.

#### Migration strategy

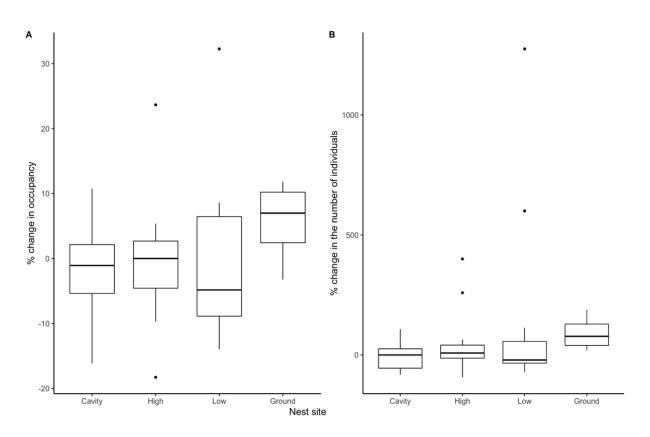
There was no significant association between the percentage change in occupancy and whether the species was migratory or resident (W = 181.5, n = 45, p = 0.14; Figure 4A). In contrast, there was a significant difference between migratory and resident species when analyzing the change in the number of individuals (W = 160, n = 45, p = 0.046) in Oslo over the last 15 years, indicating a decline in migratory species (Figure 4B). Furthermore, when separating the migratory species into two groups; short-distance migratory species and long-distance migratory species, there was no significant difference between the two groups concerning population change in Oslo (percentage change in occupancy: W = 61, n = 45, p = 0.24; Figure 4C and percentage change in the number of individuals: W = 74, n = 45, p = 0.61; Figure 4D).



**Figure 4.** (A and B) Migratory species (n = 26) and resident species (n = 19) and their association with the percentage change in occupancy and the number of individuals, and (C and D) short-distance (n = 13) and long-distance (n = 13) migratory species and their association with the percentage change in occupancy and the number of individuals in Oslo over the last 15 years.

#### Nest site

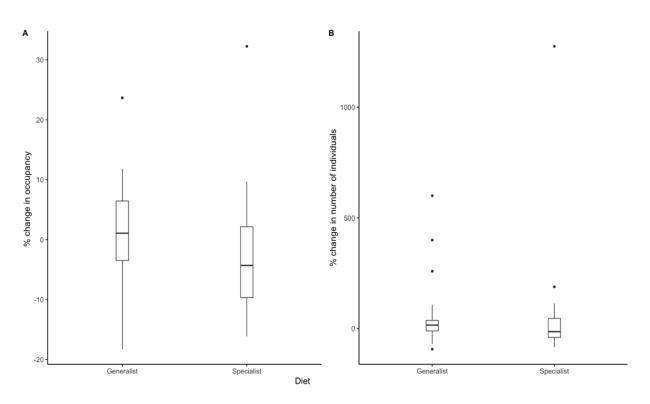
Nest-site selection did not appear to be associated with percentage change in occupancy (H = 4.48, df = 3 p = 0.21; Figure 5A) or number of individuals (H = 3.34, df = 3, p = 0.34; Figure 5B) in Oslo over the last 15 years. Although there was no significant difference between the nest site selection groups, ground-nesting species appeared to have the highest average population increase (Figure 5).



**Figure 5.** The association between nest site selection and (A) percentage change in occupancy and (B) the percentage change in the number of individuals in Oslo over the last 15 years. Nest site selection was grouped as cavity (n = 17), high (n = 12), low (n = 12), and ground-nesting (n = 4) species.

#### Dietary preference

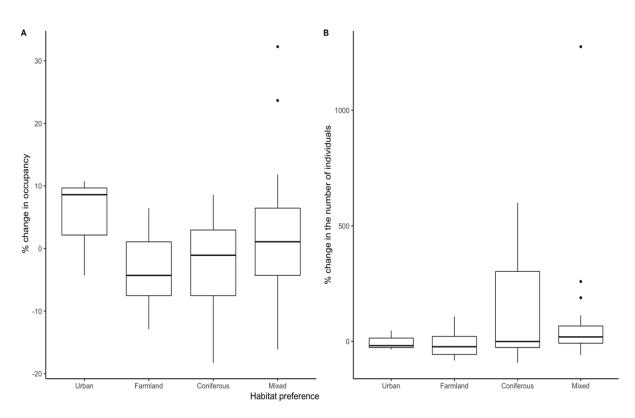
Over the last 15 years, changes in the population trends of the bird species in Oslo were associated with the diet of the species (Figure 6). Specifically, the two dietary groups significantly differed when considering the bird communities' change in percentage occupancy (W = 348.5, n = 45, p = 0.029; Figure 6A). However, when the percentage change in the number of individuals and the dietary preference groups was considered, there was no significant difference between the two groups (W = 304, n = 45, p = 0.24; Figure 6B).



**Figure 6.** The association between dietary preference and (A) the percentage change in occupancy and (B) the percentage change in the number of individuals in Oslo over the last 15 years. The species were categorized as either generalist (n = 24) or specialists (n = 21). The outlier for change in specialist species is the Phylloscopus collybita

#### Habitat preference

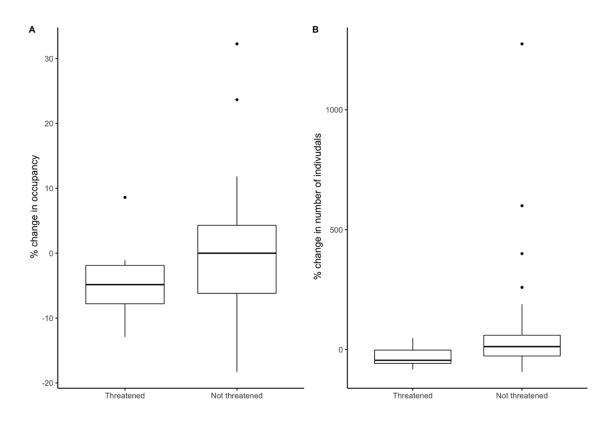
There was no significant difference between the breeding habitat groups (urban, farmland, coniferous, and mixed forests) and the species population trend either in the percentage change in occupancy (H = 3.72, df = 3, p = 0.29; Figure 7A) or the number of individuals (H = 4.74, df = 3, p = 0.19; Figure 7B) in Oslo over the last 15 years.



**Figure 7.** The association between habitat preference and (A) percentage change in occupancy and (B) percentage change in the number of individuals in Oslo over the last 15 years. Species were categorized as breeding predominantly in urban areas (n = 3), breeding predominantly in farmland habitats (n = 15), breeding predominantly in a coniferous forest (n = 6), and breeding predominantly in deciduous and mixed forests (n = 21).

#### Red list status

There was no significant difference between the two groups of threatened and not threatened species, and their population change in either occupancy (W = 143.5, n = 44, p = 0.32; Figure 8A) or change in the number of individuals (W = 168, n = 44, p = 0.066; Figure 8B) in Oslo over the last 15 years. Even though there was no statistically significant difference between the two groups, Figure 8 indicates that the species considered threatened have declined compared to the not threatened species.



**Figure 8.** The association between red list status and (A) the percentage change in occupancy and (B) the percentage change in the number of individuals in Oslo over the last 15 years. Species were categorized as either threatened species, including species in the red list category VU and NT (n = 6), or not threatened (LC; n = 38).

# Urban changes in relation to national trends

The population trends from Oslo, Norwegian national trends (2007-2017; PECBMS), and two Swedish national trends (1996-2020; Green et al., 2020 and 2007-2017; PECBMS) were compared through GLM analysis (Table 1).

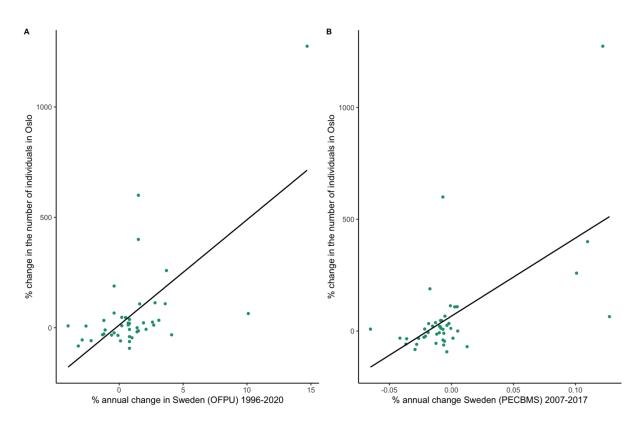
### Table 1

Changes in urban bird populations in relation to national trends of the species, analyzed using GLM analysis. The Swedish population trends were from 1996-2020 (OFPU) and 2007-2017 (PECBMS), and the Norwegian trends were also from 2007-2017 (PECBMS). The change in Oslo was based on total percentage change over 15 years, while those of Sweden and Norway were annual percentage changes.

| Independent<br>variable | Dependent variable         | n  | Estimate | SE     | t-value | p-value | Spearman<br>rank<br>correlation |
|-------------------------|----------------------------|----|----------|--------|---------|---------|---------------------------------|
| Sweden 1996-2020        | Change in occupancy Oslo   | 44 | 1.69     | 0.408  | 4.16    | <0.001  | 0.38<br>p = 0.01003             |
|                         | Change in individuals Oslo | 44 | 47.68    | 8.23   | 5.79    | <0.001  | 0.46<br>p = 0.0015              |
|                         | Norway 2007-2017           | 35 | 49.36    | 23.09  | 2.14    | 0.040   | 0.45<br>p = 0.0072              |
| Sweden 2007-2017        | Change in occupancy Oslo   | 44 | 0.0024   | 0.0005 | 4.70    | <0.001  | 0.42<br>p = 0.0038              |
|                         | Change in individuals Oslo | 44 | 3496.02  | 684.24 | 5.11    | <0.001  | 0.42<br>p = 0.0044              |
|                         | Sweden 1996-2020           | 43 | 0.0099   | 0.0012 | 7.92    | <0.001  | 0.75<br>p = < 0.001             |
|                         | Norway 2007-2017           | 35 | 0.73     | 0.24   | 3.095   | 0.004   | 0.47<br>p = 0.004               |
| Norway 2007-2017        | Change in occupancy Oslo   | 35 | 67.71    | 75.72  | 0.89    | 0.38    | 0.15<br>p = 0.39                |
|                         | Change in individuals Oslo | 35 | 3252.19  | 1893.6 | 1.72    | 0.095   | 0.25<br>p = 0.15                |

Both the Swedish trends appeared to be statistically significantly related to the population changes in Oslo during the last 15 years, to the Norwegian national trends (Table 1) and between the two Swedish trends. There was no significant relationship between the population trends in Oslo and Norway, although the data appears to be connected.

Based on the significant association between the population trends in Sweden and Oslo (Table 1), Figure 9 was made to illustrate this change. Considering the strong relationship (p < 0.001) between the change in the number of individuals and the change in occupancy in Oslo over the last 15 years, only the change in the number of individuals is presented (Figure 9).



*Figure 9.* The percentage change in the bird community in Oslo over the last 15 years against (A) the estimated change per year in Sweden from 1996-2020 and (B) the estimated annual percentage change per year in Sweden from 2007-2017. The green points represent the species (n = 44).

Most species are centered around zero, suggesting a stable trend and little change (Figure 9). Considering the outliers caused by the high number of individuals of *Carduelis carduelis* (from the PECBMS report) and *Phylloscopus collybita* in Oslo for the past 15 years (Figure 9), a Spearman rank correlation test was conducted. The test indicated that the significant associations were weak correlations (0.20 to 0.39) to strong correlations (0.70 to 0.89; Cohen et al., 2013), and all significant associations were also significant in the test (Table 1).

## **Aggregated analysis**

A combined analysis was performed to assess the effects of all ecological variables and Swedish trends on population change in Oslo. Table 2 shows that the significant relationships are similar when different independent and dependent variables are combined.

#### Table 2

Urban bird population changes in relation to all ecological variables and Swedish population trend as dependent variables. The Swedish population trends were from 1996 to 2020 (OFPU) and 2007 to 2017 (PECBMS). Nest site selection in cavities and habitats in coniferous forests were used as the references for analyzing these groups of four levels. Generalist species were used as the reference for specialist species. Groups with p - values less than 0.1 are shown in the table, and the variables in a group where one of the groups in the variable is significant. Ecological variables with  $\leq 2$  species in that group were excluded from the table below.

| Independent variable                    | Dependent         | Estimate | SE     | t-value | p-value |
|---|-------------------|----------|--------|---------|---------|
|   | variables         |          |        |         |         |
| Change in occupancy in Oslo             | Sweden 1996-2020  | 1.73     | 0.54   | 3.19    | 0.00337 |
|   | Nest site: High   | 0.48     | 4.16   | 0.11    | 0.91    |
|   | Nest site: Low    | 4.029    | 5.33   | 0.76    | 0.46    |
|   | Nest site: Ground | 12.04    | 6.19   | 1.95    | 0.061   |
| Change in occupancy in Oslo             | Sweden 2007-2017  | 178.86   | 40.14  | 4.46    | <0.001  |
|   | Nest site: High   | -244.11  | 87.41  | -2.79   | 0.00901 |
|   | Nest site: Low    | -56.58   | 96.79  | -0.59   | 0.56    |
|   | Nest site: Ground | 8.59     | 5.56   | 1.54    | 0.13    |
| Change in number of individuals in Oslo | Sweden 1996-2020  | 64.71    | 10.42  | 6.21    | <0.001  |
|   | Habitat: Farmland | -281.12  | 104.56 | -2.69   | 0.0118  |
|   | Habitat: Urban    | -263.25  | 198.79 | -1.32   | 0.20    |
|   | Habitat: Mixed    | -235.94  | 90.27  | -2.61   | 0.0141  |
| Change in number of individuals in Oslo | Sweden 2007-2017  | 5543.90  | 833.71 | 6.65    | <0.001  |
|   | Nest site: High   | -244.11  | 87.41  | -2.79   | 0.0090  |
|   | Nest site: Low    | -56.57   | 96.79  | -0.59   | 0.56    |
|   | Nest site: Ground | -28.029  | 115.56 | -0.24   | 0.81    |
|   | Habitat: Farmland | -294.57  | 95.38  | -3.09   | 0.0043  |
|   | Habitat: Urban    | 42.14    | 192.57 | 0.219   | 0.83    |
|   | Habitat: Mixed    | - 187.65 | 84.42  | -2.22   | 0.0339  |

According to the analysis, there was a significant difference between high and cavity-nesting species. The population of the high-nesting species appeared to decrease compared to the cavity-nesting species. It also appears that farmland and mixed habitat species have declined compared to coniferous forest species in Oslo over the past 15 years (Table 2).

## Discussion

#### Long term changes

Several studies have reported that European birds are declining at an alarming rate (Burns et al., 2021; Gross, 2015; Inger et al., 2015; Lehikoinen et al., 2019). In contrast, this study found that the bird population in Oslo has not declined significantly over the past 15 years. Some assemblage surveys might support this result, as they have suggested a more balanced picture of change (Dornelas et al., 2019; Vellend et al., 2013; 2017). Furthermore, the population dynamics of the urban bird community of Oslo appear to primarily reflect the general national trends in Sweden. Swedish population trends were also the strongest of all the dependent variables for change in the Oslo bird community, suggesting that the same species increased or decreased. Similar population trends between Oslo and Sweden were expected, primarily because of the similarities in climate, environment, and proximity between the two countries. On the other hand, the population change in Oslo and the Norwegian national trends did not appear to be significantly related. A possible explanation for the absence of a relationship might be that there were fewer species in the Norwegian dataset than in the Swedish dataset. Meanwhile, the Swedish and Norwegian datasets showed similar trends and had a significant relationship.

It should be noted that not all patterns at local (Oslo) and large spatial scales (Norway and Sweden) coincide. For instance, the *Passer domesticus* population underwent an increase in Oslo over the past 15 years, while national trends show population declines in both Norway and Sweden. Similarly, there are several well-publicized declines in widespread European birds, such as *Passer domesticus* (De Laet & Summers-Smith, 2007). This example highlights the necessity of comprehensive ecological studies, as there are geographic differences in population trends of certain species.

#### **Ecological traits**

Several researchers have found an association between relative brain size in birds and success in urban environments (Carrete & Tella, 2011; Maklakov et al., 2011; Overington et al., 2009; Sayol et al., 2020; Sol et al., 2005). Behavioral plasticity has also been linked to reduced extinction risk in birds (Ducatez et al., 2020), which has been linked to increased brain size (Lefebvre et al., 1997; Reader & Laland, 2002; Sol et al., 2002; 2013). Contrary to predictions

based on previous studies of the importance of brain size for urban living, I found that brain size had no effect on population change in urban Oslo over the past 15 years. Other researchers support these findings, where brain size did not affect urbanization success (Dale et al., 2015; Evans et al., 2011; Kark et al., 2007; Møller & Erritzøe, 2015). Furthermore, it has been objected that brain size may not be a valuable measure of behavioral flexibility and innovation (Healy & Rowe, 2007). To my knowledge, this is the first study based on long-term trends in urban areas in relation to brain size.

Furthermore, some have argued that body size may contribute to population change, with an ongoing trend favoring species with larger body sizes, while species with smaller bodies decline more rapidly (Inger et al., 2015). On the contrary, others found that a larger body size makes species more susceptible to extinction because it typically correlates with lower annual fecundity (Bennett et al., 2005). Nevertheless, this study found no evidence to support the idea that body mass influences population trends.

Migration strategy is one of the key life-history strategies of migratory birds, and these are expected to be very susceptible to environmental change (Newson et al., 2016). When species cannot cope with the new and changing environment, it might result in population declines or species extinction (Parmesan, 2007; Thomas et al., 2004). The declines of migratory species are well documented (e.g., Kramer et al., 2018; Sanderson et al., 2006), and this study found supporting evidence that migratory species are declining. Different hypotheses for this decline have been suggested, including climate change and habitat change in breeding wintering grounds (Vickery et al., 2014). Bowler et at. (2019) reported that long-distance migrants are primarily insectivores, and several studies have reported insect abundance to decline in Europe (Conrad et al., 2006; Hallmann et al., 2017; Thomas et al., 2004; Valtonen et al., 2017). Hence, this could potentially affect bird species that feed on insects across a bottom-up trophic cascade, where fewer insects have adverse effects on the insectivore species populations. In addition, the ongoing climate change will adversely affect species directly (via their thermal niches) and indirectly (through habitat change). Climate change results in milder winter conditions which may favor residents and short-distance species and might cause competition that disadvantages migrants (Lemoine & Böhning-Gaese, 2003). Residents and short-distance migrants would be at an advantage due to their access to the best breeding grounds (Sanderson et al., 2006). Warmer temperatures will particularly threaten urban species adapted to colder environments because urban areas typically have a milder climate than surrounding non-urban habitats

(Lepczyk et al., 2017), a phenomenon known as the "urban heat island" effect (Isaksson, 2018). These species might find it more challenging to inhabit urban areas because urban areas might favor species living in the south as they migrate north, potentially driving the future urban bird community to become more influenced by warm-adapted species.

In the habitats of most bird species, their populations are naturally constrained by factors such as the availability of food resources, competition, nesting sites, disease, and predation, as well as the carrying capacity of breeding birds in the environment, which is usually limited by nesting sites and food sources (Price et al., 1988). According to the results of the analysis, nest site selection was insignificant when considered alone but significant when combined with other ecological variables, suggesting that species that nest high declined compared to species that nest in cavities. On the contrary, several researchers have suggested that urban birds that are both high nesters and cavity nesters, appear to be more successful in urban areas (Antonov & Atanasova, 2002; Croci et al., 2008; Dale et al., 2015; Kosinski, 2001; Lancaster & Rees, 1979). A high nest placement will reduce disturbances of humans in cities or predation pressures; predation rates have been shown to increase with urbanization (Jokimäki & Huhta, 2000; Matthews et al., 1999). However, habitat availability could act as a limiting factor for high nests. It has consistently been reported that ground nesters are decreasing as urbanization increases (Clergeau et al., 2006; Dale, 2018; Hedblom & Söderström, 2010; Jokimäki & Huhta, 2000; McLain et al., 1999). On the contrary, ground nesters showed some tendencies of an increase in numbers in this study. This could be explained by the fact that some researchers, in contrast to others, have found that urbanization does not consistently change avian nest predation rates (Chamberlain et al., 2009; Kosinski, 2001).

Due to the negative effects of urbanization on local primary productivity (Imhoff et al., 2004), and the preference for generalist species in areas of low primary productivity (Evans et al., 2005), it is consistently reported that generalist species appear to be the most successful urban adapters (Chace & Walsh, 2006; Evans et al., 2011; Kark et al., 2007; Møller, 2009). Typically, generalist species have wide niche breadths, lay multiple clutches, and have broad diets, making them possibly more successful in urban environments (Callaghan et al., 2019). Additionally, changes in the climate have been reported to favor generalist species (Davey et al., 2012); having a broad food niche could be advantageous in a changing environment. The analysis of this study agrees with this observed pattern, with an increase in occupancy of diet generalists over time in Oslo. Species with a broader food spectrum have become more

common in Oslo's green spaces over the past 15 years. This finding may suggest that selection pressures on the landscape have shifted in favor of species that are capable of taking advantage of the heterogeneous resources offered by a highly urbanized city, filtering out non-generalist or poorly adapted species at the local scale (Aronson et al., 2016). Additionally, Bowler et al. (2019) and Møller (2019) reported declines that primarily affected insectivores (specialists) among European bird species. As the number of generalists increased in occupancy, I expected species richness to decrease as well, but this was not observed.

In the multivariate approach, farmland and mixed forest species exhibited significant declines over the past 15 years compared to cavity-nesting species in Oslo; however, the declines were not significant when considered alone. Numerous other researchers have also confirmed a negative population trend for farmland species in several European countries in recent years (e.g., Chamberlain et al., 2000; Wretenberg et al., 2006). Additionally, species in mixed forests showed a significant decrease in the multivariable approach but not when considered alone. Due to the complexity of these relationships in a multivariate approach like this, it is difficult to decide which results are spurious. However, the intensification of agricultural practices is believed to have had a considerable negative effect on the bird populations in Europe (Donald et al., 2001). Population trends from Sweden over the last 30 years also confirm that the largest relative decline has been seen amongst birds of the agricultural landscapes and woodland species, whereas farmland birds have generally fared worst (Ottvall et al., 2009). A general increase in intensive forestry and agriculture and the closure of farms could be the cause. Farmlands and forests provide habitats for many bird species in this country. Therefore, sustainable use of the biodiversity and biological resources of our avian fauna can be achieved by expanding conservation priorities beyond the boundaries of designated protected areas.

#### Urban trends versus national trends

Several researchers suggest that the composition of urban bird communities is unique due to the selection of species with specific ecological traits (i.e., residents, generalists, high and cavity nesters; Chace & Walsh, 2006; Jokimäki et al., 2016; Lancaster & Rees, 1979; Møller et al., 2014). However, the present study found that population changes in urban areas of Oslo over the 15 years reflect large-scale temporal shifts in distribution and abundance, similar to the findings of Murgui (2014) and Ward et al. (2018). Thus, population dynamics in urban areas are influenced by factors occurring at different spatial scales, and bird communities are

subject to the same threats and pressures as others. This suggests that the traits favored by species in urban areas are not unique to urban areas but generally apply to a wider geographical scale. In addition, the general traits that are preferred in urban areas overlap with those reported in studies of national trends (e.g., Davey et al., 2012; Vickery et al., 2014). Nevertheless, few species live their own lives secluded in urban areas; several species have urban populations associated with non-urban populations, and many of the species are migratory birds that may overwinter in non-urban areas.

#### **Ecological significance**

In this study, we contribute to an area in which little attention has been given - the temporal dynamics of urban bird populations and communities. Additionally, many national monitoring programs have overlooked urban areas in long-term surveys. It is difficult to find long-term ecological records for most cities, perhaps due to their perception as inadequate for wildlife (Fidino & Magle 2017). This is unfortunate because it appears that most species are persisting in the city. Studies of urban birds have focused on patterns and processes at different spatial scales, and the majority of studies have been conducted over relatively short time periods. Such studies tend to fit within standard funding cycles or within the duration of a typical graduate program. Long-term studies are needed to better understand and predict how slow or subtle temporal processes, rare events, and complex phenomena affect urban bird populations and communities (Fidino & Magle, 2017; Foster et al., 2002; Turner et al., 2004; Wolkovich et al., 2014). In addition to considering the intrinsic value of species and their persistence, this also underlines the importance of species populations to the functioning of ecological systems and the provision of ecosystem services.

# Conclusion

The present study has provided insight into the changes in the urban bird community composition in Oslo over the past 15 years. Although few studies have examined the long-term trends and dynamics of urban bird populations, such research is essential for understanding the decadal trends and dynamics of urban bird populations. According to this study, no significant changes have occurred in the urban bird community in Oslo. Overall breeding bird population trends in Oslo coincide with those reported at the national level. Furthermore, the ecological variables that I identified as contributing to population changes in Oslo are similar to the factors that have affected populations more broadly. For example, migratory species have declined relative to resident species. Populations of diet specialists and farmland species have declined. Thus, species on different spatial scales likely face similar pressures despite geographical differences. Contrary to the expectations of previous studies based on brain sizes' importance to urban success, I found no correlation between relative brain size and species population trends in Oslo over the past 15 years. Moreover, the study found no evidence that urban bird species exhibited divergent trends from the species at broader scales. Thus, the results of this study do not support the notion that urban birds exhibit drastically different population trajectories than non-urban birds.

## References

- Antonov, A. & Atanasova, D. (2002). Nest-site selection in the Magpie *Pica pica* in a highdensity urban population of Sofia (Bulgaria). *Acta ornithologica*, 37 (2): 55-66. doi:10.3161/068.037.0201
- Aronson, M. F., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S., Cilliers, S. & Clarkson, B. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, 281 (1780): 20133330. https://doi.org/10.1098/rspb.2013.3330
- Aronson, M. F., Nilon, C. H., Lepczyk, C. A., Parker, T. S., Warren, P. S., Cilliers, S. S., Goddard, M. A., Hahs, A. K., Herzog, C. & Katti, M. (2016). Hierarchical filters determine community assembly of urban species pools. *Ecology*, 97 (11): 2952-2963.
- Bakken, R., Tjørve. (2006). Norsk ringmerkingsatlas. Vol. 2.—Stavanger Museum, Stavanger.
- Bennett, P. M., OWENS, I. & Nussey, D. (2005). phylogeny, ecology and threats. *Phylogeny* and Conservation: 317.
- Blair, R. B. (1999). Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? *Ecological Applications*, 9 (1): 164-170. https://doi.org/10.1890/1051-0761(1999)009[0164:BABAAU]2.0.CO;2
- Bonier, F., Martin, P. R. & Wingfield, J. C. (2007). Urban birds have broader environmental tolerance. *Biology Letters*, 3 (6): 670-673.
- Bowler, D. E., Heldbjerg, H., Fox, A. D., de Jong, M. & Böhning-Gaese, K. (2019). Longterm declines of European insectivorous bird populations and potential causes. *Conservation Biology*, 33 (5): 1120-1130. https://doi.org/10.1111/cobi.13307
- Burns, F., Eaton, M. A., Burfield, I. J., Klvaňová, A., Šilarová, E., Staneva, A. & Gregory, R. D. (2021). Abundance decline in the avifauna of the European Union reveals cross-continental similarities in biodiversity change. *Ecology and Evolution*, 11 (23): 16647-16660. https://doi.org/10.1002/ece3.8282
- Butchart, S. H. M., Walpole, M., Collen, B., Strien, A. v., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., et al. (2010). Global Biodiversity: Indicators of Recent Declines. *Science*, 328 (5982): 1164-1168. doi: doi:10.1126/science.1187512
- Callaghan, C. T., Major, R. E., Wilshire, J. H., Martin, J. M., Kingsford, R. T. & Cornwell, W. K. (2019). Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos*, 128 (6): 845-858.
- Carrete, M. & Tella, J. L. (2011). Inter-Individual Variability in Fear of Humans and Relative Brain Size of the Species Are Related to Contemporary Urban Invasion in Birds. *PLoS one*, 6 (4). doi: ARTN e18859 10.1371/journal.pone.0018859
- Chace, J. F. & Walsh, J. J. (2006). Urban effects on native avifauna: a review. *Landscape and Urban Planning*, 74 (1): 46-69. doi: https://doi.org/10.1016/j.landurbplan.2004.08.007
- Chamberlain, D. E., Fuller, R. J., Bunce, R. G. H., Duckworth, J. C. & Shrubb, M. (2000). Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, 37 (5): 771-788. doi: https://doi.org/10.1046/j.1365-2664.2000.00548.x
- Chamberlain, D. E., Cannon, A. R., Toms, M., Leech, D. I., Hatchwell, B. & Gaston, K. (2009). Avian productivity in urban landscapes: a review and meta-analysis. *Ibis*, 151 (1): 1-18. https://doi.org/10.1111/j.1474-919X.2008.00899.x

- Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L. & Dinetti, M. (2006). Avifauna homogenisation by urbanisation: Analysis at different European latitudes. *Biological Conservation*, 127 (3): 336-344. doi: https://doi.org/10.1016/j.biocon.2005.06.035
- Cohen, L., Jarvis, P. & Fowler, J. (2013). Practical Statistics for Field Biology: John Wiley & Sons.
- Conrad, K. F., Warren, M. S., Fox, R., Parsons, M. S. & Woiwod, I. P. (2006). Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, 132 (3): 279-291. https://doi.org/10.1016/j.biocon.2006.04.020
- Croci, S., Butet, A. & Clergeau, P. (2008). Does Urbanization Filter Birds on the Basis of Their Biological Traits. *The Condor*, 110 (2): 223-240. doi: 10.1525/cond.2008.8409.
- Crooks, K. R., Suarez, A. V. & Bolger, D. T. (2004). Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biological Conservation*, 115 (3): 451-462. https://doi.org/10.1016/S0006-3207(03)00162-9
- Czech, B., Krausman, P. R. & Devers, P. K. (2000). Economic Associations among Causes of Species Endangerment in the United States: Associations among causes of species endangerment in the United States reflect the integration of economic sectors, supporting the theory and evidence that economic growth proceeds at the competitive exclusion of nonhuman species in the aggregate. *BioScience*, 50 (7): 593-601. doi: 10.1641/0006-3568(2000)050[0593:Eaacos]2.0.Co;2
- Dale, S., Lifjeld, J. T. & Rowe, M. (2015). Commonness and ecology, but not bigger brains, predict urban living in birds. *BMC Ecology*, 15 (1): 12. doi: 10.1186/s12898-015-0044-x
- Dale, S. (2018). Urban bird community composition influenced by size of urban green spaces, presence of native forest, and urbanization. *Urban Ecosystems*, 21 (1): 1-14. doi: 10.1007/s11252-017-0706-x
- Davey, C. M., Chamberlain, D. E., Newson, S. E., Noble, D. G. & Johnston, A. (2012). Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, 21 (5): 568-578. doi: https://doi.org/10.1111/j.1466-8238.2011.00693.x
- De Laet, J. & Summers-Smith, J. (2007). The status of the urban house sparrow Passer domesticus in north-western Europe: a review. Journal of Ornithology, 148 (2): 275-278. doi:10.1007/s10336-007-0154-0
- Donald, P. F., Green, R. & Heath, M. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London*. *Series B: Biological Sciences*, 268 (1462): 25-29. doi: 10.1098/rspb.2000.1325
- Donald, P. F., Sanderson, F. J., Burfield, I. J. & Van Bommel, F. P. (2006). Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems & Environment, 116 (3-4): 189-196. https://doi.org/10.1016/j.agee.2006.02.007
- Dornelas, M., Gotelli, N. J., Shimadzu, H., Moyes, F., Magurran, A. E. & McGill, B. J. (2019). A balance of winners and losers in the Anthropocene. *Ecology Letters*, 22 (5): 847-854. doi: https://doi.org/10.1111/ele.13242
- Ducatez, S., Sol, D., Sayol, F. & Lefebvre, L. (2020). Behavioural plasticity is associated with reduced extinction risk in birds. *Nature Ecology & Evolution*, 4 (6): 788-+. doi: 10.1038/s41559-020-1168-8
- Evans, K. L., Greenwood, J. J. & Gaston, K. J. (2005). Dissecting the species–energy relationship. *Proceedings of the Royal Society B: Biological Sciences*, 272 (1577): 2155-2163. https://doi.org/10.1098/rspb.2005.3209

- Evans, K. L., Chamberland, D. E., Hatchwell, B. J., Gregory, R. D. & Gaston, K. J. (2011). What makes an urban bird? *Global Change Biology*, 17 (1): 32-44. doi: https://doi.org/10.1111/j.1365-2486.2010.02247.x
- Fidino, M. & Magle, S. B. (2017). Trends in long-term urban bird research. *Ecology and Conservation of Birds in Urban Environments*: 161-184. doi:10.1007/978-3-319-43314-1
- Fidino, M., Gallo, T., Lehrer, E. W., Murray, M. H., Kay, C. A., Sander, H. A., MacDougall, B., Salsbury, C. M., Ryan, T. J. & Angstmann, J. L. (2021). Landscape-scale differences among cities alter common species' responses to urbanization. *Ecological Applications*, 31 (2): e02253. https://doi.org/10.1002/eap.2253
- Fidino, M., Limbrick, K., Bender, J., Gallo, T. & Magle, S. B. (2022). Strolling through a Century: Replicating Historical Bird Surveys to Explore 100 Years of Change in an Urban Bird Community. *The American Naturalist*, 199 (1): 000-000. doi: 10.1086/717052
- Foster, D. R., Motzkin, G., Bernardos, D. & Cardoza, J. (2002). Wildlife dynamics in the changing New England landscape. *Journal of Biogeography*, 29 (10-11): 1337-1357.
- Gaston, K. J. (2008). Biodiversity and extinction: the importance of being common. *Progress* in *Physical Geography*, 32(1), 73-79. https://doi.org/10.1046/j.1365-2699.2002.00759.x
- Gaston, K. J. (2010). Valuing common species. *Science*, 327(5962), 154-155. doi:10.1126/science.1182818
- Green, M., Haas, F., Lindström, Å. & Nilsson, L. (2020). Övervåkning av fåglarnas populationsutveckling: Lunds Universitet.
- Gregory, R. D., Van Strien, A., Vorisek, P., Gmelig Meyling, A. W., Noble, D. G., Foppen,
  R. P. & Gibbons, D. W. (2005). Developing indicators for European birds.
  *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360 (1454):
  269-288. https://doi.org/10.1098/rstb.2004.1602
- Gregory, R. D., Vořišek, P., Noble, D. G., Van Strien, A., Klvaňová, A., Eaton, M., Gmelig Meyling, A. W., Joys, A., Foppen, R. P. B. & Burfield, I. J. (2008). The generation and use of bird population indicators in Europe. *Bird Conservation International*, 18 (S1): S223-S244. doi: 10.1017/S0959270908000312
- Gross, M. (2015). Europe's bird populations in decline. *Current Biology*, 25 (12): R483-R485. doi: https://doi.org/10.1016/j.cub.2015.05.057
- Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H. & Hörren, T. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PloS one*, 12 (10): e0185809. https://doi.org/10.1371/journal.pone.0185809
- Healy, S. D. & Rowe, C. (2007). A critique of comparative studies of brain size. Proceedings of the Royal Society B: Biological Sciences, 274 (1609): 453-464. https://doi.org/10.1098/rspb.2006.3748
- Hedblom, M. & Söderström, B. (2010). Landscape effects on birds in urban woodlands: an analysis of 34 Swedish cities. *Journal of Biogeography*, 37 (7): 1302-1316. doi: https://doi.org/10.1111/j.1365-2699.2010.02299.x
- Heldbjerg, H. & Fox, T. (2008). Long-term population declines in Danish trans-Saharan migrant birds. *Bird Study*, 55 (3): 267-279. https://doi.org/10.1080/00063650809461532
- Inger, R., Gregory, R., Duffy, J. P., Stott, I., Voříšek, P. & Gaston, K. J. (2015). Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters*, 18 (1): 28-36. doi: https://doi.org/10.1111/ele.12387
- Isaksson, C. (2018). Impact of urbanization on birds. Bird species: 235-257.

- IUCN, B. I., European CommissionI, UCN Species Survival Commission (SSC). (2015). European Red List of birds. doi:https://doi.org/10.2779/975810, acc.no. 978-92-79-47450-7
- Jokimäki, J. & Huhta, E. (2000). Artificial Nest Predation and Abundance of Birds Along an Urban Gradient. *The Condor*, 102 (4): 838-847. doi: 10.1093/condor/102.4.838
- Jokimäki, J., Suhonen, J., Jokimäki-Kaisanlahti, M.-L. & Carbó-Ramírez, P. (2016). Effects of urbanization on breeding birds in European towns: Impacts of species traits. *Urban Ecosystems*, 19 (4): 1565-1577. doi: 10.1007/s11252-014-0423-7
- Kamp, J., Frank, C., Trautmann, S., Busch, M., Dröschmeister, R., Flade, M., Gerlach, B., Karthäuser, J., Kunz, F. & Mitschke, A. (2021). Population trends of common breeding birds in Germany 1990–2018. *Journal of Ornithology*, 162 (1): 1-15. doi:10.1007/s10336-020-01830-4
- Kark, S., Iwaniuk, A., Schalimtzek, A. & Banker, E. (2007). Living in the city: can anyone become an 'urban exploiter'? *Journal of Biogeography*, 34 (4): 638-651. doi: 10.1111/j.1365-2699.2006.01638.x
- Kosinski, Z. (2001). Effects of urbanization on nest site selection and nesting success of the Greenfinch *Carduelis chloris* in Krotoszyn, Poland. *Ornis Fennica*, 78 (4): 175-183.
- Kotiaho, J. S., Kaitala, V., Komonen, A. & Päivinen, J. (2005). Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences*, 102 (6): 1963-1967. doi: https://doi.org/10.1073/pnas.0406718102
- Kramer, G. R., Andersen, D. E., Buehler, D. A., Wood, P. B., Peterson, S. M., Lehman, J. A., Aldinger, K. R., Bulluck, L. P., Harding, S. & Jones, J. A. (2018). Population trends in Vermivora warblers are linked to strong migratory connectivity. *Proceedings of the National Academy of Sciences*, 115 (14): E3192-E3200. doi: https://doi.org/10.1073/pnas.1718985115
- Lancaster, R. K. & Rees, W. E. (1979). Bird communities and the structure of urban habitats. *Canadian Journal of Zoology*, 57 (12): 2358-2368. doi: https://doi.org/10.1139/z79-307
- Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindström, Å., Pearce-Higgins, J. W., Reif, J., Van Turnhout, C. & Devictor, V. (2012). More and more generalists: two decades of changes in the European avifauna. *Biology Letters*, 8 (5): 780-782. doi: https://doi.org/10.1098/rsbl.2012.0496
- Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. (1997). Feeding innovations and forebrain size in birds. *Animal Behaviour*, 53: 549-560. doi:10.1006/anbe.1996.0330.
- Lehikoinen, A., Brotons, L., Calladine, J., Campedelli, T., Escandell, V., Flousek, J., Grueneberg, C., Haas, F., Harris, S., Herrando, S., et al. (2019). Declining population trends of European mountain birds. *Global Change Biology*, 25 (2): 577-588. doi: https://doi.org/10.1111/gcb.14522.
- Lemoine, N. & Böhning-Gaese, K. (2003). Potential Impact of Global Climate Change on Species Richness of Long-Distance Migrants. *Conservation Biology*, 17 (2): 577-586. doi: https://doi.org/10.1046/j.1523-1739.2003.01389.x
- Lepczyk, C. A., Aronson, M. F. J., Evans, K. L., Goddard, M. A., Lerman, S. B. & Macivor, J. S. (2017). Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation. *Bioscience*, 67 (9): 799-807. doi: 10.1093/biosci/bix079
- Liang, C., Yang, G., Wang, N., Feng, G., Yang, F., Svenning, J.-C. & Yang, J. (2019). Taxonomic, phylogenetic and functional homogenization of bird communities due to land use change. *Biological Conservation*, 236: 37-43.

- Liu, X., Hu, G., Chen, Y., Li, X., Xu, X., Li, S., Pei, F. & Wang, S. (2018). High-resolution multi-temporal mapping of global urban land using Landsat images based on the Google Earth Engine Platform. *Remote Sensing of Environment*, 209: 227-239. doi: https://doi.org/10.1016/j.rse.2018.02.055
- Luck, G. W. & Smallbone, L. T. (2010). Species diversity and urbanisation: patterns, drivers and implications. *Urban Ecology*: 88-119.
- Mace, G. M., Norris, K., & Fitter, A. H. (2012). Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology & Evolution, 27(1), 19-26. doi: https://doi.org/10.1016/j.tree.2011.08.006
- Magle, S. B., Hunt, V. M., Vernon, M. & Crooks, K. R. (2012). Urban wildlife research: past, present, and future. *Biological Conservation*, 155: 23-32. doi: https://doi.org/10.1016/j.biocon.2012.06.018
- Maklakov, A. A., Immler, S., Gonzalez-Voyer, A., Liljestrand Rönn, J. & Kolm, N. (2011). Brains and the city: big-brained passerine birds succeed in urban environments. *Biology Letters*, 7 (5): 730-732. doi: 10.1098/rsbl.2011.0341
- Maklakov, A. A., Immler, S., Gonzalez-Voyer, A., Rönn, J. & Kolm, N. (2011). Brains and the city: big-brained passerine birds succeed in urban environments. *Biology Letters*, 7 (5): 730-732. doi:10.1098/rsbl.2011.0341
- Marzluff, J. M. (2001). Worldwide urbanization and its effects on birds. In Marzluff, J. M., Bowman, R. & Donnelly, R. (eds) Avian Ecology and Conservation in an Urbanizing World, pp. 19-47. Boston, MA: Springer US. doi: 10.1007/978-1-4615-1531-9\_2
- Marzluff, J. M. & Ewing, K. (2001). Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology*, 9 (3): 280-292. doi: 10.1046/j.1526-100x.2001.009003280.x
- Marzluff, J. M. (2008). Island biogeography for an urbanizing world how extinction and colonization may determine biological diversity in human-dominated landscapes. *Urban Ecology*, pp. 355-371: Springer. doi: 10.1007/978-0-387-73412-5 23
- Matthews, A., Dickman, C. R. & Major, R. E. (1999). The influence of fragment size and edge on nest predation in urban bushland. *Ecography*, 22 (4): 349-356. doi: https://doi.org/10.1111/j.1600-0587.1999.tb00572.x
- McDonald, R. I., Kareiva, P. & Forman, R. T. (2008). The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, 141 (6): 1695-1703. doi: https://doi.org/10.1016/j.biocon.2008.04.025
- McDonald, R. I., Mansur, A. V., Ascensão, F., Crossman, K., Elmqvist, T., Gonzalez, A., Güneralp, B., Haase, D., Hamann, M. & Hillel, O. (2020). Research gaps in knowledge of the impact of urban growth on biodiversity. *Nature Sustainability*, 3 (1): 16-24. doi:10.1038/s41893-019-0436-6
- McKinney, M. L. & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14 (11): 450-453. doi: https://doi.org/10.1016/S0169-5347(99)01679-1
- McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127 (3): 247-260. doi: https://doi.org/10.1016/j.biocon.2005.09.005.
- McLain, D. K., Moulton, M. P. & Sanderson, J. G. (1999). Sexual selection and extinction: the fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands. *Evolutionary Ecology Research*, 1 (5): 549-565.
- Møller, A. P. (2009). Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, 159 (4): 849-858. doi: 10.1007/s00442-008-1259-8

- Møller, A. P., Fiedler, W. & Berthold, P. (2010). (Eds.). *Effects of Climate Change on Birds*: OUP Oxford.
- Møller, A. P., Diaz, M., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Mänd, R., Markó, G. & Tryjanowski, P. (2012). High urban population density of birds reflects their timing of urbanization. *Oecologia*, 170 (3): 867-875. doi: 10.1007/s00442-012-2355-3
- Møller, A. P., Jokimäki, J., Skorka, P. & Tryjanowski, P. (2014). Loss of migration and urbanization in birds: a case study of the blackbird (Turdus merula). *Oecologia*, 175 (3): 1019-1027. doi: 10.1007/s00442-014-2953-3
- Møller, A. P. & Erritzøe, J. (2015). Brain size and urbanization in birds. *Avian Research*, 6. doi: ARTN 810.1186/s40657-015-0017-y
- Møller, A. P. (2019). Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecology and Evolution*, 9 (11): 6581-6587. doi: https://doi.org/10.1002/ece3.5236.
- Murgui, E. (2014). Population trends in breeding and wintering birds in urban parks: a 15year study (1998-2013) in Valencia, Spain. *Revista Catalana d'Ornitologia*, 30: 30-40.
- Myczko, Ł., Rosin, Z. M., Skórka, P. & Tryjanowski, P. (2014). Urbanization level and woodland size are major drivers of woodpecker species richness and abundance. *PLoS* one, 9 (4): e94218. doi: https://doi.org/10.1371/journal.pone.0094218
- Newbold, T., Hudson, L. N., Contu, S., Hill, S. L., Beck, J., Liu, Y., Meyer, C., Phillips, H. R., Scharlemann, J. P. & Purvis, A. (2018). Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLoS Biology*, 16 (12): e2006841. doi: https://doi.org/10.1371/journal.pbio.2006841
- Newson, S. E., Moran, N. J., Musgrove, A. J., Pearce-Higgins, J. W., Gillings, S., Atkinson, P. W., Miller, R., Grantham, M. J. & Baillie, S. R. (2016). Long-term changes in the migration phenology of UK breeding birds detected by large-scale citizen science recording schemes. *Ibis*, 158 (3): 481-495. doi: https://doi.org/10.1111/ibi.12367
- Ottvall, R., Edenius, L., Elmberg, J., Engström, H., Green, M., Holmqvist, N., Lindström, Å., Pärt, T. & Tjernberg, M. (2009). Population trends for Swedish breeding birds. *Ornis Svecica*, 19 (3): 117-192. doi: https://doi.org/10.34080/os.v19.22652
- Overington, S. E., Morand-Ferron, J., Boogert, N. J. & Lefebvre, L. (2009). Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour*, 78 (4): 1001-1010. doi: 10.1016/j.anbehav.2009.06.033.
- Pain, D. J. & Pienkowski, M. W. (1997). Farming and birds in Europe: the common agricultural policy and its implications for bird conservation: *Academic Press*.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421 (6918): 37-42. doi:10.1038/nature01286
- Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, 13 (9): 1860-1872. doi: https://doi.org/10.1111/j.1365-2486.2007.01404.x
- Price, T., Kirkpatrick, M. & Arnold, S. J. (1988). Directional selection and the evolution of breeding date in birds. *Science*, 240 (4853): 798-799. doi: 10.1126/science.3363360
- Price, T. D., Qvarnstrom, A. & Irwin, D. E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society B: Biological Sciences*, 270 (1523): 1433-1440. doi: 10.1098/rspb.2003.2372
- Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267 (1456): 1947-1952.

- Pyšek, P., Chocholousková, Z., † Pyšek, A., Jarošík, V., Chytrý, M. & Tichý, L. (2004). Trends in species diversity and composition of urban vegetation over three decades. *Journal of Vegetation Science*, 15 (6): 781-788. doi: https://doi.org/10.1098/rspb.2000.1234
- Reader, S. M. & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, 99 (7): 4436-4441. doi: https://doi.org/10.1073/pnas.062041299
- Reif, J. (2013). Long-term trends in bird populations: a review of patterns and potential drivers in North America and Europe. *Acta Ornithologica*, 48 (1): 1-16.
- Ritchie, H. & Roser, M. (2018). Urbanization. *Our world in data*. Published online at OurWorldInData.org. Retrieved from: 'https://ourworldindata.org/urbanization' [Online Resource]
- Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J. & Van Bommel, F. P. (2006). Longterm population declines in Afro-Palearctic migrant birds. *Biological Conservation*, 131 (1): 93-105. doi: https://doi.org/10.1016/j.biocon.2006.02.008
- Sanderson, F. J., Pople, R. G., Ieronymidou, C., Burfield, I. J., Gregory, R. D., Willis, S. G., Howard, C., Stephens, P. A., Beresford, A. E. & Donald, P. F. (2016). Assessing the performance of EU nature legislation in protecting target bird species in an era of climate change. *Conservation Letters*, 9 (3): 172-180. doi: https://doi.org/10.1111/conl.12196
- Sayol, F., Sol, D. & Pigot, A. L. (2020). Brain Size and Life History Interact to Predict Urban Tolerance in Birds. *Frontiers in Ecology and Evolution*, 8. doi: ARTN 58 10.3389/fevo.2020.00058
- Seress, G. & Liker, A. (2015). Habitat urbanization and its effects on birds. Acta Zoologica Academiae Scientiarum Hungaricae, 61 (4): 373-408. doi: https://dx.doi.org/10.17109/AZH.61.4.373.2015
- Shochat, E. (2004). Credit or debit? Resource input changes population dynamics of cityslicker birds. *Oikos*, 106 (3): 622-626. doi: https://doi.org/10.1111/j.0030-1299.2004.13159.x
- Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E. & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, 21 (4): 186-191. doi: https://doi.org/10.1016/j.tree.2005.11.019
- Smart, S., Bunce, R., Marrs, R., LeDuc, M., Firbank, L., Maskell, L., Scott, W., Thompson, K. & Walker, K. (2005). Large-scale changes in the abundance of common higher plant species across Britain between 1978, 1990 and 1998 as a consequence of human activity: tests of hypothesised changes in trait representation. *Biological Conservation*, 124 (3): 355-371. doi: https://doi.org/10.1016/j.biocon.2004.12.013
- Sol, D., Santos, D. M., Garcia, J. & Cuadrado, M. (1998). Competition for food in urban pigeons: the cost of being juvenile. *The Condor*, 100 (2): 298-304. doi: https://doi.org/10.2307/1370270
- Sol, D., Timmermans, S. & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour*, 63 (3): 495-502. doi: https://doi.org/10.2307/1370270
- Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America*, 102 (15): 5460-5465. doi: 10.1073/pnas.0408145102
- Sol, D., Lapiedra, O. & Gonzalez-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, 85 (5): 1101-1112. doi: 10.1016/j.anbehav.2013.01.023

- Sol, D., González-Lagos, C., Moreira, D., Maspons, J. & Lapiedra, O. (2014). Urbanisation tolerance and the loss of avian diversity. *Ecology letters*, 17 (8): 942-950. doi: https://doi.org/10.1111/ele.12297
- Statistisk sentralbyrå. (2022). *Befolkning, Statistisk sentralbyrå*. Available at: https://www.ssb.no/kommunefakta/oslo (accessed: 21.04.2022).
- Stokke, B. G., Dale, S. J., K.-O., Lislevand, T., Solvang, R. & Strøm, H. (2021). Fugler Aves - Norge. Norsk rødliste for arter. Artsdatabanken. https://artsdatabanken.no/lister/rodlisteforarter/2021/
- Team, R. C. (2021). *R: A Language and Environment for Statistical Computing*. Vienna, Austria. Available at: https://www.R-project.org/
- Thaxter, C. B., Joys, A. C., Gregory, R. D., Baillie, S. R. & Noble, D. G. (2010). Hypotheses to explain patterns of population change among breeding bird species in England. *Biological Conservation*, 143 (9): 2006-2019. doi: https://doi.org/10.1016/j.biocon.2010.05.004
- Thomas, J. A., Telfer, M., Roy, D. B., Preston, C. D., Greenwood, J., Asher, J., Fox, R., Clarke, R. & Lawton, J. (2004). Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, 303 (5665): 1879-1881. doi: 10.1126/science.1095046
- Tucker, G. & Heath, M. (1994). Birds in Europe. Their Conservation Status. *BirdLife International, Cambridge*.
- Turner, W. R., Nakamura, T. & Dinetti, M. (2004). Global urbanization and the separation of humans from nature. *Bioscience*, 54 (6): 585-590. doi: https://doi.org/10.1641/0006-3568(2004)054[0585:GUATSO]2.0.CO;2
- Valtonen, A., Hirka, A., Szőcs, L., Ayres, M. P., Roininen, H. & Csóka, G. (2017). Longterm species loss and homogenization of moth communities in Central Europe. *Journal of Animal Ecology*, 86 (4): 730-738. doi: https://doi.org/10.1111/1365-2656.12687
- Vellend, M., Baeten, L., Myers-Smith, I. H., Elmendorf, S. C., Beauséjour, R., Brown, C. D., De Frenne, P., Verheyen, K. & Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences*, 110 (48): 19456-19459. doi: 10.1073/pnas.1312779110
- Vellend, M., Dornelas, M., Baeten, L., Beauséjour, R., Brown, C. D., De Frenne, P., Elmendorf, S. C., Gotelli, N. J., Moyes, F. & Myers-Smith, I. H. (2017). Estimates of local biodiversity change over time stand up to scrutiny. *Ecology*, 98 (2): 583-590. doi: https://doi.org/10.1002/ecy.1660
- Vercauteren, K. C., Dolbeer, R. A. & Gese, E. M. (2010). Identification and management of wildlife damage. USDA *Wildlife Services - Staff Publications*. 1204. https://digitalcommons.unl.edu/icwdm\_usdanwrc/1204
- Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Škorpilová, J. & Gregory, R. D. (2014). The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis*, 156 (1): 1-22. doi: https://doi.org/10.1111/ibi.12118
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416 (6879): 389-395. doi: 10.1038/416389a
- Ward, M. P., Stodola, K. W., Walk, J. W., Benson, T. J., Deppe, J. L. & Brawn, J. D. (2018). Changes in bird distributions in Illinois, USA, over the 20th century were driven by use of alternative rather than primary habitats. *The Condor: Ornithological Applications*, 120 (3): 622-631. doi: https://doi.org/10.1650/CONDOR-17-153.1

- Wolkovich, E., Cook, B., McLauchlan, K. & Davies, T. (2014). Temporal ecology in the Anthropocene. *Ecology Letters*, 17 (11): 1365-1379. doi: https://doi.org/10.1111/ele.12353
- Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T. & Pärt, T. (2006). Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. *Journal of Applied Ecology*, 43 (6): 1110-1120. doi: https://doi.org/10.1111/j.1365-2664.2006.01216.x

# Appendix

# Appendix 1

Diff. Individual is the percentage change in the number of individuals in Oslo in the last 15 years, and Diff. Occupancy are the percentage change in the number of sites (n=93) a species was observed in Oslo between 2005-07 and 2021. For diet: G= Generalist, S= Specialist. Body and brain weight is measured in grams.

| Species                       | Habitat    | Nest   | Migration<br>strategy | Distance | Diet | Body<br>wt.(g) | Brain<br>wt.(g) | Red-<br>list | Change<br>Occup. | Change<br>Indiv. |
|-------------------------------|------------|--------|-----------------------|----------|------|----------------|-----------------|--------------|------------------|------------------|
| Apus apus                     | Farmland   | Cavity | Migratory             | Long     | S    | 38             | 0,7             | NT           | 12,90            | -55,04           |
| Carduelis cannabina           | Farmland   | Low    | Migratory             | Short    | G    | 18             | 0,67            | LC           | -3,23            | -70,00           |
| Carduelis carduelis           | Farmland   | High   | Resident              |          | G    | 16             | 0,59            | LC           | 5,38             | 64,29            |
| Carduelis spinus              | Coniferous | High   | Migratory             | Short    | G    | 13             | 0,56            | LC           | -18,28           | -92,98           |
| Certhia familiaris            | Mixed      | Cavity | Resident              |          | S    | 10             | 0,55            | LC           | 1,08             | 0,00             |
| Chloris chloris               | Farmland   | High   | Resident              |          | G    | 30             | 0,89            | VU           | -1,08            | 8,43             |
| Coccothraustes coccothraustes | Mixed      | High   | Resident              |          | G    | 55             | 1,63            | LC           | 23,66            | 259,09           |
| Columba livia                 | Urban      | Cavity | Resident              |          | G    | 270            | 2,49            | NA           | 10,75            | -18,53           |
| Columba palumbus              | Farmland   | High   | Migratory             | Short    | G    | 495            | 2,38            | LC           | 1,08             | 22,13            |
| Corvus corone                 | Farmland   | High   | Resident              |          | G    | 543            | 8,14            | LC           | -5,38            | 33,13            |
| Corvus monedula               | Farmland   | Cavity | Resident              |          | G    | 223            | 4,69            | LC           | 6,45             | 108,00           |
| Cyanistes caeruleus           | Mixed      | Cavity | Resident              |          | G    | 11             | 0,65            | LC           | -4,30            | 33,87            |
| Delichon urbica               | Farmland   | Cavity | Migratory             | Long     | S    | 16             | 0,5             | NT           | -5,38            | -82,73           |
| Dendrocopos major             | Mixed      | Cavity | Resident              |          | S    | 87             | 2,51            | LC           | -4,30            | -6,90            |
| Erithacus rubecula            | Mixed      | Ground | Migratory             | Short    | G    | 18             | 0,66            | LC           | 11,83            | 19,25            |
| Ficedula hypoleuca            | Mixed      | Cavity | Migratory             | Long     | S    | 13             | 0,45            | LC           | -16,13           | -59,57           |
| Fringilla coelebs             | Mixed      | High   | Migratory             | Short    | G    | 23             | 0,77            | LC           | 2,15             | -7,75            |
| Hippolais icterina            | Mixed      | Low    | Migratory             | Long     | S    | 13             | 0,54            | LC           | 6,45             | 113,04           |
| Hirundo rustica               | Farmland   | Cavity | Migratory             | Long     | S    | 20             | 0,58            | LC           | -4,30            | -62,50           |
| Motacilla alba                | Farmland   | Cavity | Migratory             | Long     | S    | 22             | 0,58            | LC           | -11,83           | -33,33           |
| Muscicapa striata             | Mixed      | Low    | Migratory             | Long     | S    | 16             | 0,53            | LC           | -8,60            | -13,89           |
| Parus major                   | Mixed      | Cavity | Resident              |          | G    | 18             | 0,85            | LC           | -1,08            | 25,44            |
| Passer domesticus             | Urban      | Cavity | Resident              |          | G    | 30             | 0,92            | NT           | 8,60             | 47,26            |
| Passer montanus               | Farmland   | Cavity | Resident              |          | G    | 24             | 0,79            | LC           | 4,30             | 21,23            |
| Periparus ater                | Coniferous | Cavity | Resident              |          | G    | 9              | 0,51            | LC           | -1,08            | 9,09             |
| Phylloscopus collybita        | Mixed      | Low    | Migratory             | Long     | S    | 8              | 0,38            | LC           | 32,26            | 1275,0           |
| Phylloscopus sibilatrix       | Mixed      | Ground | Migratory             | Long     | S    | 10             | 0,37            | LC           | 9,68             | 188,89           |
| Phylloscopus trochilus        | Mixed      | Ground | Migratory             | Long     | S    | 9              | 0,31            | LC           | -3,23            | 46,39            |
| Pica pica                     | Farmland   | High   | Resident              |          | S    | 223            | 5,34            | LC           | -9,68            | -23,13           |
| Picus viridis                 | Mixed      | Cavity | Resident              |          | S    | 199            | 4,35            | LC           | 2,15             | 66,67            |
| Prunella modularis            | Mixed      | Low    | Migratory             | Short    | S    | 20             | 0,71            | LC           | 2,15             | 37,50            |
| Pyrrhula pyrrhula             | Coniferous | High   | Resident              |          | G    | 32             | 0,97            | LC           | 4,30             | 400,0            |
| Regulus regulus               | Coniferous | High   | Resident              |          | S    | 6              | 0,38            | LC           | -1,08            | -10,0            |
| Sitta europaea                | Mixed      | Cavity | Resident              |          | G    | 23             | 1,11            | LC           | 1,08             | 11,90            |
| Streptopelia decaocto         | Urban      | High   | Resident              |          | G    | 188            | 1,52            | NT           | -4,30            | -34,62           |
| Sturnus vulgaris              | Farmland   | Cavity | Migratory             | Short    | G    | 80             | 1,7             | NT           | -8,60            | -58,52           |
| Sylvia atricapilla            | Mixed      | Low    | Migratory             | Short    | S    | 20             | 0,67            | LC           | -13,98           | -32,03           |

| Sylvia borin            | Mixed      | Low    | Migratory | Long  | S | 21  | 0,62 | LC | -13,98 | -40,24 |
|-------------------------|------------|--------|-----------|-------|---|-----|------|----|--------|--------|
| Sylvia communis         | Farmland   | Low    | Migratory | Long  | S | 14  | 0,56 | LC | -6,45  | -45,45 |
| Sylvia curruca          | Coniferous | Low    | Migratory | Long  | S | 11  | 0,53 | LC | -9,68  | -31,82 |
| Troglodytes troglodytes | Mixed      | Ground | Migratory | Short | S | 9   | 0,5  | LC | 4,30   | 108,70 |
| Turdus iliacus          | Mixed      | Low    | Migratory | Short | G | 68  | 1,22 | LC | -6,45  | -28,17 |
| Turdus merula           | Mixed      | Low    | Migratory | Short | G | 102 | 1,92 | LC | 6,45   | 12,59  |
| Turdus philomelos       | Coniferous | Low    | Migratory | Short | G | 75  | 1,59 | LC | 8,60   | 600,0  |
| Turdus pilaris          | Farmland   | High   | Migratory | Short | G | 102 | 1,76 | LC | 1,08   | 7,65   |



Norges miljø- og biovitenskapelige universitet Noregs miljø- og biovitskapelege universitet Norwegian University of Life Sciences

Postboks 5003 NO-1432 Ås Norway