Urban Ecosyst
DOI 10.1007/s11252-014-0423-7

Effects of urbanization on breeding birds in European towns: Impacts of species traits

J. Jokimäki · J. Suhonen · M.-L. Jokimäki-Kaisanlahti · P. Carbó-Ramírez

© Springer Science+Business Media New York 2014

Abstract Urbanization acts as a filter on bird species behavioral traits so that only few species can tolerate urban constraints. We analyzed how behavioral traits (nesting, feeding, and migratory habits) of breeding bird species affect their frequency of occurrence in the urban centers of 38 European towns. We used binary logistic regression analysis to predict the bird species traits belonging to each trait group. A total of 108 species (21% of the European breeding bird species) were found to breed in the European town centers. According to our broad-scale analyses the bird species most frequently breeding in town centers nest in buildings and/or buildings have diverse diets, in trees (40%) and are resident omnivores, or relied on seeds or fruits as their sources of food. However, almost all bird species also fed on arthropods (92%) during the breeding season. Only a few urban bird species bred on the ground. Four out of the studied 108 species were non-native and five species were predators. Our broad-scale results from Europe indicate that bird species with different behavioral traits can respond differently to urbanization. Bird species that nest in cavities/buildings have diverse diets, that benefit a resident way-of-life, may have an advantage in living and settling in European town centers. Our results from Europe may provide insights related to the development of bird assemblages in the urban core areas of the New World.

Keywords Urbanization · Urban areas · Birds · Occurrence · Traits · Biogeography

Electronic supplementary material The online version of this article (doi:10.1007/s11252-014-0423-7) contains supplementary material, which is available to authorized users.

J. Jokimäki (✉) · M.-L. Jokimäki-Kaisanlahti · P. Carbó-Ramírez
Arctic Centre, University of Lapland, P.O.Box 122, FI-96101 Rovaniemi, Finland
e-mail: jukka.jokimaki@ulapland.fi

J. Suhonen
Department of Biology, Section of Ecology, University of Turku, FI-20014 Turku, Finland

Present Address:
P. Carbó-Ramírez
Lapland University of Applied Sciences, Viirinkangas Campus, Viirinkankaantie 1,
96300 Rovaniemi, Finland

Published online: 24 October 2014

Introduction

According to the general theory of macro-ecology, the distribution and frequency of occurrence of species varies between communities (Magurran 1988; Jenkins 2011). Some species may occur on all sites, while others may occur on a few or even on just a single site. Species' frequency of occurrence may depend on environmental conditions such as the level of urbanization, species traits, and species-specific distribution ranges (see reviews in Collins and Glenn 1997; McGeoch and Gaston 2002). Urban ecosystems differ from pristine areas in many respects. For example, urban areas are characterized by high levels of human-induced disturbance; they provide more anthropogenic food resources, and they contain only small and fragmented remnants of original habitats (Gilbert 1989; Rebele 1994; Shochat et al. 2006; Adams and Lindsey 2010). In addition, the microclimatic conditions differ between urban centers and their surroundings (Francis and Chadwick 2013). Therefore, bird species in urban environments may exhibit different behavioral traits compared to their rural counterparts (Anderies et al. 2007; Adams and Lindsey 2010).

Urbanization has created a number of new ecological niches (e.g. nest-boxes; Erz 1966; Diamond 1986), which benefit some bird species possessing specific traits (e.g. feeding-table species; Kark et al. 2007; Croci et al. 2008). Behavioral adaptations may allow these species to utilize novel resources in urban areas that are absent from natural habitats (Partecke et al. 2006). In Europe, where towns have existed for thousands of years, many species of birds have become human commensals (Diamond 1986). Rock doves (*Columba livia domestica*), starlings (*Sturnus vulgaris*) and House sparrows (*Passer domesticus*) thrive in concrete habitats, and the latter species is now so closely associated with man that its original niche is unknown (Diamond 1986). Such shifts in behavior do not occur instantly and newly acquired behaviors take time to spread (Diamond 1986). Urban areas are open to invasion and colonization by any bird species that can reach them, utilize urban resources, and survive in urban environments (Erz 1966). With increasing urbanization being a world-wide phenomenon, large-scale analyses in particular are needed to provide information on the species occurring frequently in urban environments (Clergeau et al. 2006a, b; Croci et al. 2008; McDonald 2008; Pautasso et al. 2011). Europe has a long history of urbanization compared to other continents; therefore, our results may provide some insights into the future structure of urban bird communities in areas with a shorter urbanization history (Clergeau et al. 2006a, b).

According to O'Connell et al. (2000) and Kennedy et al. (2010), traits can affect dispersal ability, resource acquisition, and/or population growth potential. Analyses of species' ecological traits have demonstrated links to environmental diversity also in urban environments as these ecological traits are closely related to environmental factors (Croci et al. 2008). Urban studies related to species traits can offer crucial information on the factors affecting the guild structure within a community and/or the role of traits in the functioning of ecosystems (Irnai and Nakashizuka 2010). Because urbanization may act as a filter on species' traits, urbanized bird species may share a suite of biological traits that explain their success in tolerating the impact of humans (Kark et al. 2007; Croci et al. 2008). Indeed, the use of species' traits may permit greater generality and predictability in the matter of how bird species respond to land use and urbanization (Leveau 2013). Previous studies focusing on species' traits have been done on a relatively small scale, and therefore our understanding of the kinds of traits that are required for species to tolerate urban environments on a large scale is inadequate (Marzluff et al. 2001; Kark et al. 2007; Møller 2009; Pautasso et al. 2011).

Because small-scale studies may fail to detect the relationship between traits and their response to the matrix type (Kennedy et al. 2010), large-scale analyses of the characteristics of species that can predict their responses to urbanization have been proposed (Kark et al. 2007;

Møller 2009; Evans et al. 2011). Bird species have been shown to have wider environmental niches and greater tolerance of disturbance factors in urban centers than in non-urban areas, which support a generalist way of life (Blair 1996; Bonier et al. 2007; Diaz et al. 2013; but see Jokimäki and Kaisanlahti-Jokimäki 2012). Earlier local-or regional-scale studies have reported that urbanization increases the frequency of occurrence of non-native bird species, generalist bird species, birds nesting in buildings, omnivores, and nest predators, whereas specialists, forest interior-nesting species, and ground-nesting species decrease as a consequence of urbanization (Kark et al. 2007; Croci et al. 2008; Caula et al. 2010; Evans et al. 2011; Ikin et al. 2012; Leveau 2013; see review by Marzluff 2001; Chace and Walsh 2006; Adams and Lindsey 2010).

In this study, we investigated whether the probability of a species having a particular trait (nesting, feeding, and migratory habits) was related to the number of European town centers in which it was found to occur. Based on the results of earlier local-and regional-level studies, we expected most of the species breeding in town centers to nest in buildings, be omnivores, and to be resident species (e.g. Marzluff 2001). We hypothesized that because of the lack of vegetation and suitable nest sites, most bird species living within the town centers will nest in man-made structures (Erz 1966). We also suggested that urbanization may favor the omnivorous and resident way of life because urban areas are characterized by large and predictable anthropogenic food resources (Jokimäki and Kaisanlahti-Jokimäki 2012). To our knowledge, the present study is the first up-to-date large-scale evaluation of the impacts of bird species' traits on their probability of occurring in European town centers.

Study areas, methods, and statistical analyses

Study areas and data

The data include frequency of occurrence of breeding bird species in 38 European historical town centers (i.e. the most urbanized areas of the each study town; Electronic Appendix 1). These areas are dominated by multi-storied residential buildings, commercial buildings, as well as sealed surfaces such as roads and parking areas (per cent of the built-up area>65 %, and residential human density>10/ha; see e.g. Marzluff et al. 2001) (Electronic Appendix 1). Our data include both our unpublished data as well as literature survey data from European town centers. In most cases, our data were collected by atlas-type surveys with breeding species' occurrence being determined in conjunction with several visits (Electronic Appendix 1). In this study, we used only urban breeding bird atlas data collected using either a scale of 1 × 1 km or 0.5 × 0.5 km. Degree of breeding evidence within a given grid has been expressed in these European or national atlases using various codes summarized by the classical breeding indices (breeding unlikely, possible breeding, probable breeding, confirmed breeding). In some cases, our data were collected by means of multiple-visit mapping or by using the point-count method (Bibby et al. 1992; Electronic Appendix 1). Because the results of the mapping method are mainly based on observations of singing males on the same site during different surveys (corresponding to the atlas index of probable breeding), we used only data on probable or confirmed breeders from our atlas data sets. Therefore, observations of unlikely and possible breeding species were excluded from our data. Because the survey methods were mainly based on multiple visits and because we used only presence/absence data of bird species, we supposed that the bird survey method did not affect our results. For more detailed information about the bird census techniques, see Bibby et al. 1992. Indeed, we repeated all statistical analyses without point count data to see if our results showed a similar pattern. The results showed similar patterns without and with the point-count survey data (see also Mönkkönen et al. 2006). In addition, we tested if the results of atlas and mapping methods yield similar patterns, and this was the case.

We determined the urban structure (e.g. wooded area, open vegetation, asphalted roads, parking area, open water area, and area with buildings) of 38 town centers from Europe, for assess variability among habitat features of study sites. To obtain the characteristics of the town centers, we used 500×500 m area from satellite images from Google Earth 7.1 (Google, Inc. Mountain View, CA, and USA). Every image from Google Earth was geo-referenced in ArcView (ver. 3.2, ESRI), this allowed digitize the habitat features and calculate the percentage of each variables before mentioned.

Statistical methods

We estimated the frequency of occurrence of the species in all of the studied European town centers. We classified the traits of each species into groups based on breeding site, migratory status, and their main food items according to the data of Hagemeier and Blair (1997); see Electronic Appendix 2). Because of large scale of our study (Europe), several species were included in several subgroups and consequently the sum of the proportions in each subgroup was greater than 100%. For example, some bird species belong to both migratory and sedentary species in different parts of Europe, and consequently some species can belong to both groups. The main diets of the bird species vary between seasons, but we used only breeding season diet. We divided the bird species in regard to their migratory status (migratory 1; non-migratory 0) or whether they were sedentary (sedentary 1; non-sedentary 0) in Europe. As regards nesting place, we divided the birds into four groups: species which breed (i) in cavities, nest-boxes or buildings, (1 is given for the species breeding in these places; other places 0) (ii) open nest in trees (1; or other places 0), (iii) open nest in bushes (1; or other places 0) or (iv) breed on the ground (1; or other places 0). We classified the bird species into four groups on the basis on their food requirements during the breeding season: (i) omnivorous and scavengers (1; other food items 0), (ii) species eating arthropods during breeding season (1; or other food items 0) (iii) species eating seeds and fruits (1; or other food items 0), and (iv) predators (1; or other food items 0).

We used binary logistic regression analysis to model the probability that traits of urban birds are influenced by the frequency of species occurrence in European town centers. Each species trait was treated as the dependent variable in separate logistic regressions. The frequency of occurrence of each bird species (number of towns centers in which the species was observed to breed) was used as an independent covariate. The binary logistic regressions were computed using IPM SPSS Statistics version 20. Because we carried out multiple tests, there was a probability that some tests would give a significant result by chance alone, therefore we used the Bonferroni correction.

To test differences in the habitat structures between of the European town centers we grouped our data in three categories related on their urbanization level based on the number of inhabitants (large towns>1 mill. inhabitants, n=11; medium-sized towns >200 000 inhabitants, but<1 mill. inhabitants, n=12; and small towns<200 000 inhabitants, n=15). The urban centers were divided among three geographical groups (geographical locations) related on their locations (Northern Europe>59° N latitude, n=9; Central Europe 47–53° N latitude, n=16; and Southern Europe <45° N latitude, n=13). We used analysis of variance (ANOVA) to test differences in the habitat structure variables ((*i*) urban areas, which included buildings, roads or parking areas, (*ii*) wooded areas and (*iii*) open green areas) between urbanization level (three levels) and geographical locations (three levels).

Results

Habitat structure of the European town centers was very similar: 90% (*SD*=9, min 61%, *max*= 99%, *n*=38) of the area was covered by buildings, roads or parking areas, and only 9% (*SD*=9) was covered by wooded or green open areas (Electronic Appendix 1; no statistical differences were noted between the location or size categories in relation to the town center habitat structure, $P>0.05$, results not shown).

A total of 108 species were found to occur in European town centers (Electronic Appendix 2; average 23.2; *SD*=10.3, *n*=38). Four non-native bird species (*Streptopelia decaocto* [occupied in 25 study towns], *Alopochen aegyptiaca* [occupied in 2 study towns],

Psittacula krameri [occupied in 2 study towns] and *Phasianus colchicus* [occupied in 1 study town) were detected in European town centers.

Most of the bird species occurring in European town centers nest in buildings and/or tree cavities (40%, Electronic Appendix 2). About one third of the bird species nested on the ground (35%), 30% nested in trees, and 25% nested in bushes above the ground. The more towns in which a species is found, the greater was the probability it bred in buildings or cavities (Fig. 1, Table 1). However, this relationship did not occur if we used Bonferroni corrected *p*-values. The species occurring in urban town centers seldom bred on the ground (Fig. 1, Table 1).

Most of the species feed on arthropods (92%; Electronic Appendix 2). Almost half of the species feed on seeds or fruits (46%). The proportion of omnivorous species was found to be 14%, and only five of the 108 species were true predators (*Falco tinnunculus*, *F. peregrinus*, *Tyto alba*, *Athene noctua*, and *Lanius collurio*). The more towns in which a species is found, the greater is the probability of that bird species being an omnivore or feeding on seeds or fruits as a part of its diet (Fig. 2, Table 1).

Migratory or resident habits did not affect the occurrence of species in European town centers (Table 1). However, because several bird species are resident in some parts of their geographical distribution range and migratory in other parts in Europe, we constructed two

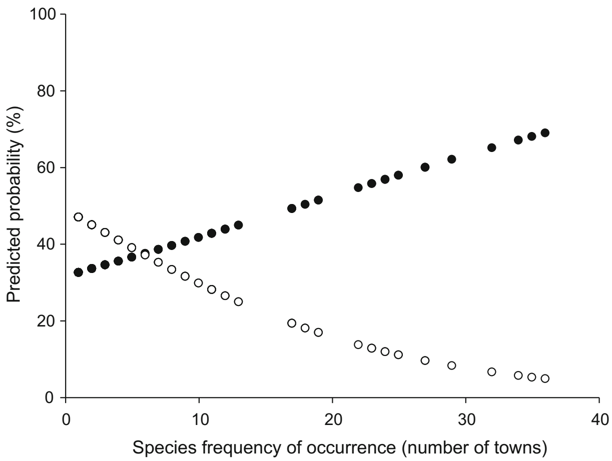

Fig. 1 The frequency of occurrence of breeding bird species in European town centers in relation to the predicted probability (%) that the bird species nests in buildings and/or tree cavities (filled dot) or on the ground (open dot)

Table 1 The results obtained when conducting a binary logistic regression analysis to predict breeding bird species traits in European town centers. Each trait in migratory status groups, nesting habit groups, and feeding guilds was used as a dependent variable and the frequency occurrence (number of towns centers in which the species was observed to breed) was used as the independent covariate. Statistical tests using the logistic regression model (Model), estimated logistic regression coefficient for the constant, and the species frequency of occurrence (B), and standard errors (S.E.). Wald-statistics and P values indicate the statistical significance of each trait in the model. *P2*=Bonferroni corrected *P*-value for the 10 multiple tests

Trait	Model		Constant				Frequency of occurrence				
	Wald	P	B	S.E.	Wald	P	B	S.E.	Wald	P	P2
Breeding habits:											
Buildings	4.00	0.045	−0.78	0.27	8.06	0.005	0.04	0.02	3.85	0.050	0.450
Trees	1.87	0.171	−1.13	0.29	14.92	0.001	0.03	0.02	1.90	0.168	0.171
Bushes	0.27	0.601	−1.20	0.30	15.82	0.001	0.01	0.02	0.28	0.597	0.601
Ground	9.08	0.003	−0.41	0.28	0.02	0.882	−0.08	0.03	6.76	0.009	0.030
Feeding habits:											
Omnivores	11.54	0.001	−2.83	0.48	35.44	0.001	0.09	0.03	11.12	0.001	0.010
Insectivores	2.43	0.119	1.90	0.46	17.43	0.001	0.08	0.07	1.62	0.203	0.119
Seeds	11.16	0.001	−0.76	0.28	7.62	0.006	0.08	0.03	9.25	0.002	0.010
Predators	0.90	0.344	−2.63	0.59	19.75	0.001	−0.06	0.08	0.66	0.416	0.344
Migratory habits:											
Resident	0.01	0.954	0.72	0.28	6.86	0.001	0.01	0.02	0.01	0.954	0.954
Migratory	1.11	0.293	1.07	0.29	13.55	0.001	−0.02	0.02	1.13	0.288	0.293

more detailed analyses incorporating residence status and diet (omnivorous). The more towns in which a species is found (Wald=11.08, *df*=1, *P*=0.001; Fig. 3), the more likely that the bird species is a resident omnivore rather than a migratory omnivore (Wald=4.36, *df*=1, *P*=0.037; Fig. 3).

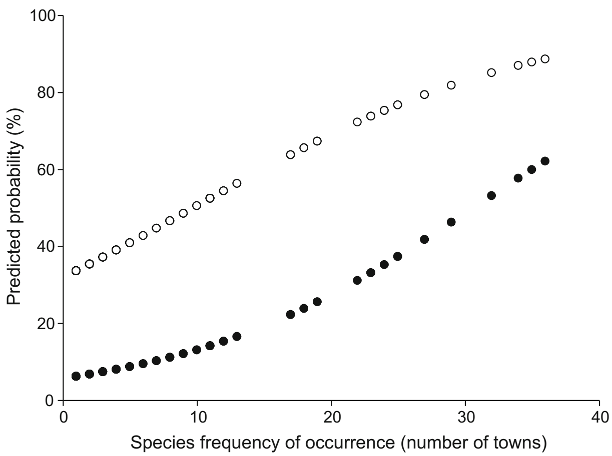

Fig. 2 The frequency of occurrence of breeding bird species in town centers in relation to the predicted probability (%) that the bird species is omnivorous (filled dot) or uses seeds as food (open dot). It should be noted that several omnivorous species also used seeds as food and for that reason the sum of the predicted probability is greater than one

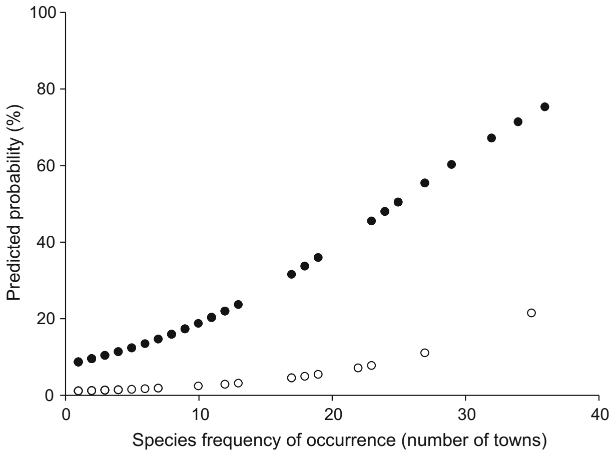

Fig. 3 The frequency of occurrence of breeding bird species in town centers in relation to the predicted probability (%) that the bird species is a resident omnivorous (filled dot) or migratory omnivorous species (open dot)

Discussion

We found 108 bird species living in town centers in Europe, and these represent about 21% of the total number of breeding bird species in Europe (the total number is 513 species; Hagemeier and Blair 1997). Thus, about one fifth of the species recorded in non-urban environments also occupied town centers in Europe. This was a large proportion and it was at least partly explained by the long history of urbanization in Europe. Our data collected in European town centers contained only four non-native bird species (4% of all of the species). This number and proportion corresponded well with the number and proportion of non-native bird species in Europe in general (17 non-native bird species, i.e. 3%; Hagemeier and Blair 1997). However, most of the earlier studies have indicated that the number of non-native bird species increases with urbanization (Marzluff 2001). Thus, the non-native species have a lesser role in the bird assemblages of town centers in Europe than in other continental regions of the world.

Several bird species usually found in forests are absent or rare in urban areas (Morneau et al. 1999; Kaisanlahti-Jokimäki et al. 2012). This is probably related to the harmful effects of wooded green area fragmentation, which increases the amount of edge habitat: the abundance of nest predators favoring edges (e.g. Corvids) is higher than in more contiguous, unfragmented areas (Wilcove 1985; Askins et al. 1990; Askins 1993). The probability of a species having a particular trait was related to the number of town centers in which the particular bird species was found in Europe. Building-nesters or cavity-nesters and resident omnivorous bird species were common breeding bird species in European town centers. Also, ground nesters avoided to avoid breed in European town centers. In addition, most urban bird species included seeds and fruits in their diets. Only a few avian predatory species were encountered in European towns.

Nesting habits

In Europe, urbanization benefitted species that nest in buildings and cavities but not those that nest on the ground. The results of local-level studies have also shown that urbanization favors birds nesting in cavities, whereas ground-nesters may suffer from urbanization (Tomialojc

1970; Emlen 1974; Lancaster and Rees 1979; Luniak 1981; Suhonen and Jokimäki 1988; Jokimäki and Huhta 2000; Ikin et al. 2012; Kaisanlahti et al. 2012; Leveau 2013).

Bird species nesting in tree cavities in more natural areas appear to adapt easily to using buildings with different kinds of chimneys, roofs, and other cavities, as well as nest-boxes (Marzluff 2001). Urbanization benefits species nesting in cavities, partly because suitable nest cavities are available, e.g. in buildings, and nests in cavities are safe from avian nest predators (Jokimäki and Huhta 2000; Kaisanlahti-Jokimäki et al. 2012). Primary and secondary cavity nesters appear to show different responses to urbanization, because primary cavity nesters require deadwood for nesting and foraging, and deadwood may be rare in developed environments (Blewett and Marzluff 2005). However, our data from European town centers included only a few primary cavity nesters (only four woodpecker species). In addition, many old European town centers have many old trees usable for cavity nesters (e.g. Francis and Chadwick 2013). However, this topic needs more detailed further studies, especially since the application of the Bonferroni correction produced a non-significant result for the role of cavity-nesting.

Earlier studies have found that the abundance of ground-nesting bird species is lower in towns than in their surrounding areas (Suhonen and Jokimäki 1988; Jokimäki 1996, 1999; Rottenborn 1999; Jokimäki and Huhta 2000; Jokimäki et al. 2005; Kaisanlahti-Jokimäki et al. 2012; Pellissier et al. 2012). We suggest that the reduction in ground cover and shrub layers in town centers may reduce the suitability of the urban core area for ground-nesters (Kaisanlahti-Jokimäki et al. 2012). Unfortunately, our data did not allow more detailed analyses. In addition to habitat structure, the regional nest predator assemblage might have a large impact on nest predation rates in urban environments (Jokimäki and Huhta 2000; Kaisanlahti-Jokimäki et al. 2012). Earlier results have shown that, possibly due to the increased number of ground mammalian nest predators (e.g. stray cats (*Felis domesticus*) and foxes (*Vulpes vulpes*)), the nesting success of ground-nesting birds in towns is lower than in more natural areas (Gilbert 1989; Rottenborn 1999). Because of these ground-dwelling predators, ground-nesters appear to be at a disadvantage when compared to species nesting higher up (Luniak 1981; Jokimäki 1999; Clergeau et al. 2006a; Sorace and Gustin 2010). However, at northern latitudes, the role of avian nest predators (i.e. Corvids) is more important than in more southern areas. For example, free-ranging cats have poor survival during harsh northern winters (Jokimäki and Huhta 2000; Kaisanlahti-Jokimäki et al. 2012). At the local and regional level, the community of nest predators may differ, and therefore the role of different nest predators in molding the breeding bird community structure may also differ between town centers (Jokimäki and Huhta 2000; Kaisanlahti-Jokimäki et al. 2012).

Feeding habits

Urbanization favor omnivores and seed-eaters both in breeding (see also Gilbert 1989; Jokimäki 1999; Atchinson and Rodewald 2006; Chace and Walsh 2006; Croci et al. 2008) and in wintering seasons (Lancaster and Rees 1979; Tilghman 1987; Jokimäki et al 2002; Smith 2003), despite the remarkably different feeding strategies and behavioral mechanisms applied between the seasons (Telleria and Santos 1995, 1997; Boonstra 2004). Granivorous and omnivorous species are known to adapt well to urban environments (Jokimäki and Suhonen 1998; Lim and Sodhi 2004; Chace and Walsh 2006; Croci et al. 2008). Pellissier et al. (2012) found that omnivorous and granivorous bird species abundance was positively influenced by buildings (height and heterogeneity). Provision of food in winter by humans may be one reason for the urbanization of bird species, as is the case for the Mallard (*Anas platyrhynchos*; Pulliainen 1963), Greenfinch (*Cardulies chloris*) and Blue Tit (*Parus* *cauruleus*) in Finland (Jokimäki et al. 1996, 2002; Jokimäki and Suhonen 1998). The large quantity of food provided by humans and the predictability of food availability favors omnivorous and resident birds in urbanized areas (Lancaster and Rees 1979; Bessinger and Osborne 1982; Clergeau et al. 1998; Jokimäki and Suhonen 1998; Jokimäki and Kaisanlahti-Jokimäki 2012). However, Sorace and Gustin (2010) and Bolger (2011) found that the spread of urban areas constitutes a threat to many granivorous bird species that are diminishing in numbers and belong to the families *Alaudidae*, *Passeridae*, *Fringillidae*, and *Emberizidae* in Italy. These families are sensitive to habitat fragmentation (Henle et al. 2004; Ewers and Didham 2006), loss and degradation (Sorace and Gustin 2010). In order to limit the negative impact of urbanization on these declining families, careful management of open green areas, especially at the urban-rural interface, should be prioritized (Donald et al. 2001; Sorace 2001; Newton 2004; Vickery et al. 2004.2004.

The small number of predator species in urban areas could reduce predation pressure, which could in turn make it more likely that species would colonize urban areas. Only five out of the 108 species detected in European town centers were predators. Historically, *Accipiter nisus*, *Falco peregrinus*, *Falco subbuteo*, *Falco tinnunculus*, *Strix aluco*, *Tyto alba*, *Athene noctua*, *Pica pica*, *Corvus corone*, *Corvus monedula*, *Dendrocopus major*, and *Larus spp* (Village 1990; Sorace 2002; Gregoire et al. 2003; Seress et al. 2011) have been considered to be urban avian predators in Europe. As a consequence, the predator community may be reduced in some towns (Gregoire et al. 2003). However, lack of persecution and adequate food supplies may attract an increasing number of raptors to settle also in urban areas (Chace and Walsh 2006). Some studies report that the density of predators (e.g. kestrels *Falco tinnunculus*, nocturnal raptors, rats *Rattus norvegicus*, cats and foxes) may be even higher in urban parks than in the nearby countryside (Sorace 2002), indicating that urban habitats can no longer be deemed to be “safe nesting zones” (e.g. Jokimäki et al. 2005). In addition, many members of the Falco genus respond well to urban areas because of the large and predictable food sources in the form of small birds and doves (Chace and Walsh 2006). The variation in predator responses to urbanization may also be linked to habitats (Marzluff 2001). For example, in some habitats mammalian predators are more abundant than avian predators, and therefore predation pressure might differ between habitats.

Migratory habits

Migratory status was not an important factor affecting the occurrence of bird species in European town centers. However, the more towns a species was found to occur in, the greater was the probability that it was a resident omnivore rather than a migratory omnivore. Wintering birds in urban areas find improved food resources (Brittingham and Temple 1988), and due to the heat island effect of urban areas they may also encounter warmer temperatures than birds in rural areas (Gilbert 1989; Botkin and Beveridge 1997; Taha 1997). Additionally, urban landscapes may experience lower wind speeds due to the frictional drag of buildings (Gilbert 1989). Thus, the combination of supplemental food and altered microclimate may create habitats that are beneficial to wintering birds, at least in climates with harsh winters (Atchinson and Rodewald 2006). Atchinson and Rodewald (2006) also found that urban development has a positive influence on omnivorous winter birds. Resident birds have an advantage over migratory birds in nest site selection in towns as resident birds are able to select suitable nest sites before the migratory birds arrive from their wintering areas to the towns (von Haartman 1968; Jokimäki and Suhonen 1998). Therefore, we suggest that urbanization favors a resident way of life (Møller 2009).

Conclusions

Our results indicated that bird species traits have an important role in determining whether a particular species occurs in European town centers, and that bird species with specific kinds of traits may be more likely to occur in town centers. The long history of European towns may provide indications of future patterns of bird community composition in urbanization taking place elsewhere in the world. In our study, we considered only the breeding occurrence of species and how often they occur in the centers of certain European towns. However to get a more holistic understanding of the composition of urban bird communities, future studies should consider the abundance of species and also the winter season. Considering species-specific traits is an important tool for understanding global-level of bird communities living in urban environments.

The long history of European towns may provide indications of future patterns of bird community composition in urbanization taking place elsewhere in the world. In our study, we considered only the occurrence of species and how often they occur in the centers of certain European towns. Considering species-specific traits is an important tool for understanding global-level of bird communities living in urban environments.

Acknowledgments JJ and MLKJ were supported by the EU Regional Development Foundation for the project "Rovaniemen kaupunkilintuatlas" (A31026). We wish to thank two anonymous reviewers for their constructive comments on the manuscript. In addition, we wish to thank Drs. G. Baeynes and A. Weiserbs for the data they provided for this manuscript. P.C.-R. acknowledges the scholarship by the Centre for International Mobility (CIMO). We also wish to thank Erkki Pekkinen, M.Sc.(for.), for checking the English of this manuscript.

References

Adams CE, Lindsey KL (2010) Urban wildlife management. CRC Press, London & New York

Anderies JM, Katti M, Shochat E (2007) Living in the city: Resource availability, predation, and bird population dynamics in urban areas. J Theor Biol 247:36–49

Askins RA (1993) Population trends in grassland, shrubland, and forest birds in eastern North America. In: Power DM (ed) Current ornithology, vol 11. Plenum Press, New York, pp 1–34

Askins RA, Lynch JF, Greenberg R (1990) Population declines in migratory birds in Eastern North America. In: Power DM (ed) Current ornithology, vol 7. Plenum Press, New York, pp 1–57

Atchinson KA, Rodewald AD (2006) The value of urban forests to wintering birds. Nat Area J 26:280–288

Bessinger SR, Osborne DR (1982) Effects of urbanisation on avian community organization. Condor 84:75–83

Bibby JC, Burgess DN, Hill AD (1992) Bird census techniques. Academic, London

Blair RB (1996) Land use and avian species diversity along an urban gradient. Ecol Appl 6:506–519

Blewett CM, Marzluff JM (2005) Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. Condor 107:678–693

Bolger DT (2011) Urban birds: population, community, and landscape approaches. In: Marzluff JM, Bowman R, Donelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Dordrecht, pp 155–177

Bonier F, Martin PR, Wingfield JC (2007) Urban birds have a broader environmental tolerance. Biol Lett 3:670–673

Boonstra R (2004) Coping with changing northern environments: The role of the stress axis in birds and mammals. Integr Comp Biol 44:95–108

Botkin DB, Beveridge CE (1997) Cities as environments. Urban Ecosyst 1:3–19

Brittingham MC, Temple SA (1988) Impacts of supplemental feeding on survival rates of black-capped Chickadees. Ecology 69:581–589

Caula SA, Sirami C, Marty P, Martin J-L (2010) Value of an urban habitat for the native Mediterranean avifauna. Urban Ecosyst 13:73–89

Chace J, Walsh J (2006) Urban effects on native avifauna: A review. Landsc Urban Plan 74:46–69

Clergeau P, Savard J-P, Mennechez GL, Falardeau G (1998) Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. Condor 100:413–425

Clergeau P, Croci S, Jokimäki J, Kaisanlahti-Jokimäki ML, Dinetti M (2006a) Avifauna homogenisation by urbanisation: Analysis at different European latitudes. Biol Conserv 127:336–344
Clergeau P, Jokimäki J, Snep R (2006b) Using hierarchical levels for utban ecology. Trends Ecol Evol 21:660–661
Collins S, Glenn SM (1997) Effects of organismal and distance scaling on analysis of species distribution and abundance. Ecol Appl 7:543.551
Croci S, Butet A, Clergeau P (2008) Does urbanization filter birds on the basis of their biological traits? Condor 110:223–240
Diamond JM (1986) Rapid evolution of urban birds. Nature 324:107–108
Diaz M, Møller AP, Felnsted-Jensen E, Grim T, Ibánez-Àlamo JG, Jokimäki J, Marko G, Tryjanowski P (2013) The geography of fear: A latitudinal gradient in antipredator escape distance of bird across Europe. PLoS ONE 8:e64634, Open Access
Donald PF, Green RE, Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. Proc R Soc Lond B 268:25–29
Emlen JT (1974) An urban bird community in Tucson, Arizona: Derivation, structure, regulation. Condor 76: 184–197
Erz W (1966) Ecological principles in the urbanization of birds. Ostrich Suppl 6:357–363
Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ (2011) What makes an urban bird. Glob Chang Biol 17:32–44
Ewers RM, Didham RK (2006) Confounding factors in detection of species responses to habitat fragmentation. Biol Rev 81:117
Francis RA, Chadwick MA (2013) Urban ecosystems. Understanding the human environment. Routledge, London
Gilbert OL (1989) The ecology of urban habitats. Chapman and Hall, London
Gregoire A, Garnier S, Dreano N, Faivre B (2003) Nest predation in Blackbirds (Turdus merula) and the influence of nest characteristics. Ornis Fennica 80:1–10
Hagemeier EJ, Blair MJ (1997) The EBCC atlas of European breeding birds: Their distribution and abundance. T&AD Poyser, London
Henle K, Davies KF, Kleyer M, Margules C, Settele J (2004) Predictors of species sensitivity to fragmentation. Biodivers Conserv 13:207–251
Ikin K, Knight E, Lindenmayer DB, Fischer J, Manning AD (2012) Linkuing bird species traits to vegetation charachteristics in a future urban devcelopment zone: Implications for urban planning. Urban Ecosyst 15: 961–977
Irnai H, Nakashizuka T (2010) Environmental factors affecting the composition and diversity of avian community in mid-to late breeding season in urban parks and green spaces. Landsc Urban Plan 96:183–194
Jenkins DG (2011) Ranked species occupancy curves reveal common patterns among diverse metacommunities. Glob Ecol Biogeogr 20:486–497
Jokimäki J (1996) Patterns of bird communities in urban environments. University of Lapland, Dissertation
Jokimäki J (1999) Occupancy of breeding bird species in urban parks: Effects of park structure and broadscale variables. Urban Ecosyst 3:21–34
Jokimäki J, Huhta E (2000) Artificial nest predation and abundance of birds along an urban gradient. Condor 102:838–847
Jokimäki J, Kaisanlahti-Jokimäki ML (2012) Residential areas support overwintering possibilities of most species. Ann Zool Fenn 49:240–256
Jokimäki J, Suhonen J (1998) Distribution and habitat selection of wintering birds in urban environments. Landsc Urban Plan 39:253–263
Jokimäki J, Suhonen J, Inki K, Jokinen S (1996) Biogeographical comparison of winter bird communities in urban environments in Finland. J Biogeogr 23:379–386
Jokimäki J, Clergeau P, Kaisanlahti-Jokimäki M (2002) Winter bird communities in urban habitats: A comparative study between central and northern Europe. J Biogeogr 29:69–79
Jokimäki J, Kaisanlahti-Jokimäki M-L, Sorace A, Fernandez-Juricic E, Rodriguez-Prieto I, Jimenez MD (2005) Evaluation of the "safe nesting zone" hypothesis across an urban gradient: A multi-scale study. Ecography 28:59–70
Kaisanlahti-Jokimäki M-L, Jokimäki J, Huhta E, Siikamäki P (2012) Impacts of seasonal small-scale urbanization on nest predation and bird assemblages at tourist destinations. In: Lepczyk A, Warren PS (eds) Urban bird ecology and conservation, studies in avian biology, 45th edn. Unversity of California Press, Oakland, pp 93–111
Kark S, Iwaniuk A, Schalimtzek A, Banker E (2007) Living in the city: Can anyone become an 'urban exloiter'? J Biogeogr 34:638–651
Kennedy CM, Marra PP, Fagan WF, Neel MC (2010) Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. Ecol Monogr 80:651–669

Lancaster RK, Rees WE (1979) Bird communities and the structure of urban habitats. Can J Zool 57:2358–2368
Leveau LM (2013) Bird traits in urban-rural gradients: How many functional groups are there. J Ornithol 153: 655–662. doi:10.1007/s10336012-0928-x
Lim HC, Sodhi NS (2004) Responses of avian guilds to urbanisation in a tropical city. Landsc Urban Plan 66: 199–215
Luniak M (1981) The birds of the park habitats in Warsaw. Acta Ornithol 18:335–370
Magurran AE (1988) Ecological diversity and its measurements. Princeton University, Princeton Press, Princeton, NJ
Marzluff JM (2001) Worldwide urbanization and its effects on birds. In: Marzluff JM, Bowman R, Donelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston, pp 19–47
Marzluff JM, Bowman R, Donelly R (2001) A historical perspective on urban bird research: trends, terms, and approaches. In: Marzluff JM, Bowman R, Donelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer Academic publishers, Boston, pp 2–17
McDonald RI (2008) Global urbanization: Can ecologist identify a sustainable way forward? Front Ecol Environ 6:99–104
McGeoch MA, Gaston KJ (2002) Occupancy frequency distributions: patterns, artefacts and mechanisms. Biol Rev 77:311–331
Møller AP (2009) Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. Oecologica 159:849–858
Mönkkönen M, Forsman JT, Bokman F (2006) Energy availability, abundance, energy-use and species richness in forest bird communities: A test of the species-energy theory. Glob Ecol Biogeogr 15:290–302
Morneau F, Décarie R, Pelletier R, Lambert D, DesGranges J-L, Savard J-P (1999) Changes in breeding bird richness and abundance in Montreal parks over a period of 15 years. Landsc Urban Plan 44:111–121
Newton I (2004) The recent declines of farmland bird populations in Britain: An appraisal of causal factors and conservation actions. Ibis 146:579–600
O'Connell TJ, Jackson LE, Brooks RP (2000) Bird guilds as indicators of ecological condition in the central Appalachians. Ecol Appl 10:1706–1721
Pautasso M, Böhning-Gaese CP, Cueto VR, Dinetti M, Fernández-Juricic E, Kaisanlahti-Jokimäki M-L, Jokimäki J, McKinney ML, Sodhi NS, Storch D, Tomialojc L, Weisberg PJ, Woinarski J, Fuller RA, Cantarello E (2011) Global macroecology of bird communities in urbanized and semi-natural ecosystems. Glob Ecol Biogeogr 20:426–436
Partecke J, Schwabl I, Gwinner E (2006) Stress and the city: Urbanization and its effects on the stress phisiology in European blackbirds. Ecology 87:1945–1952
Pellissier V, Cohen M, Boulay A, Clergeau P (2012) Birds are also sensitive to landscape composition and configuration within the city centre. Landsc Urban Plan 104:181–188
Pulliainen E (1963) On the history, ecology and ethology of the Mallards (Anas platyrhynchos L.) overwintering in Finland. Ornis Fennica 40:45–66
Rebele F (1994) Urban ecology and special features of urban ecosystems. Glob Ecol Biogeogr 4:173–187
Rottenborn SC (1999) Predicting the impacts of urbanization on riparian bird communities. Biol Conserv 88: 289–299
Seress G, Bókony V, Heszberger J, András L (2011) Response to predation risk in urban and rural house sparrows. Ethology 117:896–907
Shochat E, Warren PS, Raeth SH, McIntyre ME, Hope D (2006) From pattern to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21:186–191
Smith P (2003) Winter bird use of urban and rural habitats in Ontario. Can Field Nat 117:173–183
Sorace A (2001) Value to wildlife of urban-agricultural parks: A case study from Rome urban area. Environ Manag 28:547–560
Sorace A (2002) High density of bird and nest species in urban habitats and the role of predator abundance. Ornis Fenn 79:60–71
Sorace A, Gustin M (2010) Bird species of conservation concern along urban gradients in Italy. Biodivers Conserv 19:205–221
Suhonen J, Jokimäki J (1988) A biogeographical comparison of the breeding bird species assemblages in twenty Finnish urban parks. Ornis Fennica 65:76–83
Taha H (1997) Urban climates and heat islands: Albedo, evapotranspiration, and anthropogenic heat. Energy Build 25:99–103
Telleria J, Santos T (1995) Effects of forest fragmentation on a guild of wintering passerines: The role of habitat selection. Biol Conserv 71:61–67
Telleria J, Santos T (1997) Seasonal and interannual occupation of a forest archipelago by insectivorous passerines. Oikos 78:239–244

Tilghman N (1987) Characteristics of urban woodlands affecting winter bird diversity and abundance. For Ecol Manag 21:163–175
Tomialojc L (1970) Quantitative studies on the synanthropic avifauna of Lenica and its environs. Acta Ornithologica 12:293–392
Vickery JA, Bradbury RA, Henderson IG (2004) The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. Biol Conserv 119:19–39
Village A (1990) The Kestrel. T. & A.D. Poyser, London
von Haartman L (1968) The evolution of resident versus migratory habit in birds. Some considerations. Ornis Fennica 45:1–6
Wilcove DS (1985) Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66: 1212–1214