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University of South Bohemia in České Budějovice
Faculty of Science

The breeding and foraging ecology of the House Sparrow in rural and urban environments

Ph.D. Thesis

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Annotation

This study describes the effect of farming practices, farmland utilization, and habitat composition in farmland settlements on the distribution and population density of the House Sparrow. Another goal of this study was to describe food availability for offspring and habitat use in rural and urban settlements. The results imply the importance of farms, their surroundings, small-scale farming, and the presence of natural habitats (shrubs, trees, ruderal vegetation) for the local House Sparrow populations. Increased home range size and flight distance were found in urban breeding pairs, implying the absence or lower availability of critical food sources in the urban environment. Future perspectives, threats, and management recommendations to prevent negative factors affecting House Sparrows and the entire bird community inhabiting similar habitats are discussed in this study.

Declaration

I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references.

České Budějovice, 9. 8. 2021

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Jan Havlíček

This thesis originated at the Faculty of Science, University of South Bohemia, in the study programme Zoology.

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I'm deeply grateful to my parents and my entire family for the opportunity to choose my hobby as my future work and lifestyle, trust, and endless support during my whole life and study.

I also cannot forget my many friends for all the “deep” talks 😊 during coffee breaks and drinking beer (thanks to Nezmar and KMP for safe harbor for us), and making all my “university years” tremendous and unforgettable.

List of papers and author’s contribution

The thesis is based on the following papers (listed chronologically):

I. Šálek, M., Havlíček, J., Riegert, J., Nešpor, M., Fuchs, R. & Kipson, M. (2015) Winter density and habitat preferences of three declining granivorous farmland birds: the importance of the keeping of poultry and dairy farms. Journal for Nature Conservation, 24, 10–16.
doi: 10.1016/j.jnc.2015.01.004 (IF = 2.220).
Jan Havlíček participated in the experiment preparation, data collection (including leading volunteer participants), evaluation of data, analysis of landscape characteristics, and the revisions of the manuscript. His contribution was 35 %.

II. Havlíček, J., Riegert, J., Bandhauerová, J., Fuchs, R. & Šálek, M. (2021) Species-specific breeding habitat association of declining farmland birds within urban environment: conservation implications. Urban Ecosystems, 1–12.
doi: 10.1007/s11252-021-01111-9 (IF = 3,005)
Jan Havlíček participated in the experiment preparation, data collection (including leading volunteer participants), evaluation of data, analysis of landscape characteristics, and writing the manuscript, together with other coauthors. His contribution was 55 %.

III. Havlíček, J., Riegert, J. & Fuchs, R. (submitted manuscript) Home-range size, flight distance and preferences for foraging habitats in House sparrow (*Passer domesticus*): A comparison of city and rural population.
Jan Havlíček participated in the experiment preparation, collected and evaluated data, analyzed landscape characteristics and wrote the manuscript with the help of coauthors. His contribution was 75 %.

Co-author agreement

Ing. Šálek Martin, Ph.D., the co-supervisor of this Ph.D. thesis, lead author of paper “*Winter density and habitat preferences of three declining granivorous farmland birds: the importance of the keeping of poultry and dairy farms*”, and corresponding author of paper “*Species-specific breeding habitat association of declining farmland birds within urban environment: conservation implications*” fully acknowledges the stated contribution of Jan Havlíček to this manuscript.

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Ing. Šálek Martin, Ph.D.

doc. RNDr. Fuchs Roman, CSc., the supervisor of this Ph.D. thesis and senior author of paper “*Home-range size, flight distance and preferences for foraging habitats in House sparrow (*Passer domesticus*): A comparison of city and rural population*”, fully acknowledges the stated contribution of Jan Havlíček to this manuscript.

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doc. RNDr. Fuchs Roman, CSc.

Contents

Introduction

Recent global biodiversity loss is considered a major environmental problem (Buchart et al. 2010, Barnosky et al. 2011). Biodiversity loss is mainly caused by habitat loss and the transformation of landscape structure, which significantly influences the number and abundance of animal species (Reidsma et al. 2006, Walz & Syrbe 2013, Šálek et al. 2018a, Horváth et al. 2019). In Europe, the landscape has been shaped and maintained by the human population for millennia (e.g., Antrop 2004, Pinhasi et al. 2005, Elis 2015). The human impact on global ecosystems has significantly increased during the 20th and 21st century, with higher intensity during recent decades (Antrop 2004, Walz & Syrbe 2013, Skokanová et al. 2016). The factors contributing most to habitat loss and decreased landscape heterogeneity have been demonstrated to be agricultural intensification and increasing urbanization due to the higher demands of the growing human population (Tilman et al. 2001, Antrop 2004, Hesperger & Bürgi 2009).

Agriculture in Europe underwent significant modification in the past few decades, mainly due to socio-political changes (e.g., Donald et al. 2001, 2002, Robinson & Sutherland 2002, Wretenberg et al. 2007). This includes former collectivization in recent post-socialistic countries or latter application of Common Agricultural Policy under the European Union (EU) (e.g., Bignal & McCracken 2000, Donald et al. 2002, Reif & Hanzelka 2016, Reif & Vermouzek 2019, Šumrada et al. 2021). These changes have resulted in the intensification of farming practices and homogenization of farmland structure at multiple spatial scales (see, e.g., Krebs et al. 1999, Donald et al. 2001, 2002, Benton et al. 2003, Chrenková 2021, and below for details), or, abandonment of less productive land (MacDonald et al. 2000, Robinson & Sutherland 2002, Mikulić et a. 2014).

Moreover, some changes in agriculture also relate to the depopulation of smaller settlements in rural areas and inhabitants moving to urban and suburban areas (e.g., Antrop 2004, Pinilla et al. 2008). During the 2010s, the worldwide human population living in urban areas reached 50%, and this number is expected to increase in future decades (Eurostat 2016). This process has resulted in growing cities and suburban areas at the expense of natural habitats and further increased the proportion of built-up areas within settlements (e.g., Antrop 2000, Murgui & Macias 2010).

There is enormous scientific interest in how bird communities are changing and in the ecology, biology, and evolution of individual species in agricultural landscapes (see, e.g., Stephens et al. 2003, Bas et al. 2009, Liu et al. 2013, and below), and urban environments (e. g., Fernández-Juricic & Jokimäki 2001, Maklakov et al. 2011, Ferenc et al. 2014, Murgui & Hedblom 2017, Salmón et al. 2021). Despite this, the ongoing and expected changes bring new challenges for scientific research and conservation (Tryjanowski et al. 2011, Wright et al. 2012, Murgui & Hedblom 2017, Mohring et al. 2021).

The House Sparrow (*Passer domesticus*) is an example of a bird species inhabiting a wide range of diverse habitats, including farmland, rural settlements, and highly urbanized environments (Anderson 2006, Kark et al. 2007, De Laet & Summers-Smith 2007). It is a well-known species due to being widespread and closely associated with humans for hundreds of years (Anderson 2006, Sætre et al. 2012, Ravinet et al. 2018). Recently, the House Sparrow has become a species of conservation priority due to its dramatic population decline and range contractions across most of its European distribution range since the second half of the 20th century (Summers–Smith 1999, Hole et al. 2002, De Laet & Summers–Smith 2007, Hanson et al. 2020, PECBMS 2021). Due to massive population reduction across contrasting habitats, the House Sparrow may be considered an indicator bird species showing the negative effects of agricultural intensification and urbanization on bird communities (Hanson et al. 2020, Jokimäki et al. 2021, Mohring et al. 2021, see below). The widespread population decline of House Sparrow has attracted significant scientific interest as demonstrated by the increasing number of publications focused on understanding the key factors affecting its sharp decline in recent decades (Hanson et al. 2020). Similarly, the financial prize offered for a "*proper scientific explanation of the House Sparrow's widespread disappearance from many of our towns and cities, the biggest bird mystery of modern times*" (Independent 2008), represents unprecedented evidence of universal interest. Despite long-term and intensive scientific efforts to understand crucial reasons for House Sparrow population changes, especially in urbanized landscapes in Northern and Western Europe (e.g., De Laet &Summers-Smith 2007, Shaw et al. 2008, De Coster et al. 2015), an unequivocal reason has not been found. The most probable causes influencing House Sparrow population decline include a tangle of factors such as massive reduction in availability of suitable foraging and breeding habitats and the effect of predators (Vincet 2005, De Laet &Summers-Smith 2007). The impact of different factors and their combinations may be specific for regions and types of settlements (De Laet &Summers-Smith 2007).

This doctoral study aims to shed light on the conundrum of the breeding and foraging ecology of the House Sparrow from Central European rural and urban environments. This study primarily describes the effect of farming practices, such as the importance of farm infrastructure (e.g., farmsteads) and typical small-scale farming (e.g., poultry holdings) presence, farmland utilization, and habitat composition in farmland settlements on the distribution and population density of the House Sparrow. Since the importance of individual habitats may vary between breeding (when most extant studies were made) and non-breeding seasons, I focused on comparing the habitat preference and distribution of House Sparrow during the spring and winter seasons. Additionally, the protentional impact of recent increased development and modernization of buildings, that reduces nesting opportunities, was examined using the comparison of House Sparrow density and utilization rate of old and newly built buildings and parts of settlements. Another goal of this study was to describe food availability for offspring and habitat use in rural and urban settlements. Previously, it was clarified that offspring survival rate and condition is significantly decreased in the urban environment due to food limitation. Therefore, a comparison based on fine-scale habitat preference can indicate crucial foraging habitats and the impact of current and future changes in their availability, including reduction of artificial food sources, green space, etc.

So far, most studies have been conducted in highly urbanized settlements in Northern and Western Europe, and detailed studies from other parts of Europe are still largely missing. From this perspective, results from a Central European post-totalitarian country, which underwent a different history of land-use changes in farmland and the urban environment, can provide important information for applied conservation measures for bird populations in human settlements in this region. To fulfil these aims, the future perspectives, threats, and management recommendations to prevent negative factors affecting House Sparrows and the entire bird community inhabiting similar habitats are discussed in this study.

House Sparrow population changes in different environments

It has been suggested that the House Sparrow began its close association with human agricultural societies in the Middle East about 10 000 years ago (Sætre et al. 2012, Ravinet et al. 2018). Due to this close association, the House Sparrow's distribution area increased following the expansion of agriculture. (Sætre et al. 2012, Ravinet et al. 2018; see also Anderson 2006). Later, the House Sparrow population probably profited from the expansions of urban environments (i.e., towns and cities) with poor street hygiene and horse transport (Summers-Smith 2005, De Laet & Summers-Smith 2007). During the 20th century, the House Sparrow completed colonization of the northern and southern parts of the European continent (Cramp et al. 1994). Furthermore, over 250 House Sparrow introduction or translocation events have been recorded worldwide (Lever 2005, Hanson et al. 2020). This includes, for example, the colonization of the Faroe Islands in the 1930s (Bengtson et al. 2004), Iceland in 1959 (Cramp et al. 1994), Israel (Cramp et al. 1994, Hatzofe & Yom–Tov 2002), and Egypt (Cramp et al. 1994). Since 1858, the House Sparrow has been deliberately introduced to North America (first in New York City), where it rapidly spread to new territories and became one of the most common bird species (Barrows 1889). In Australia, where it occupies the eastern part of the continent, it was introduced in 1862 (there is an earlier but unconfirmed record from 1850) in Victoria (Lever 2005). To New Zealand, it was introduced in 1859. From there, it has colonized many of the Pacific islands, including Hawaii, etc. (see Lever 2005, Anderson 2006).

During its long historical coexistence with humans, the House Sparrow was mainly considered a pest, and steps to eradicate this species were taken (e.g., Dearborn 1910, Havlín 1974, Anderson 2006, De Laet & Summers-Smith 2007, Seitz 2007). For example, in Western Europe during the 18th and 19th centuries, money was paid for dead birds and eggs, whereas locally, this practice continued into the 20th century (De Laet & Summers-

Smith 2007, Seitz 2007). In other cases, farmers had to pay fines if they didn't reach the given target for number of sparrows killed based on farm size (Seitz 2007). There was a similar situation in Central Europe, where a reward was paid for the killing of House Sparrows, for example, during the reign of Maria Theresa (1740–1780). Later, during World War II, the eradication was later given a command (see e.g., Brejšková 2003). Still, in his handbook for the conservation of birds, famous Czech ornithologist Klůz (1947) recommends catching and killing adults and post-fledged individuals or destroying the eggs and nest. This was in concordance with other leaders in ornithological research and bird protection in past times (see Seitz 2007). Finally, the Czechoslovak Academy of Sciences tested the possibility of mass poisoning of House Sparrows in the 1950s (Bouchner 1956). Poisoning was previously "successfully" applied in Germany after World War II (Seitz 2007). The "sparrow war" in Europe was ended chiefly in the second half of the 20th century, e.g., in the 1970s in Germany (Seitz 2007).

This information, together with anecdotal notes, e.g., about abundant flocks destroying crops, hunting of House Sparrows for food (e.g., Havlín 1974, Brejšková 2003), or unpublished information from elderly former farmers (practicing farming before and during the second half of the 20th century), can indicate very high abundances of this species. For instance, in the middle of the 1930s, one Czech ornithologist notes: "We *once caught 2 500 sparrows for a taxidermist. The Švanda theater in Smíchov* (Prague – note of author) *is introducing the operetta "Sparrow," and the whole theatre should be decorated, so they also wanted some stuffed sparrows. Additionally, each tenth visitor was given a stuffed sparrow as a present… We were bringing them to the taxidermist in bags containing fifty, or hundreds and were paid one Czech crown for each"* (Brejšková 2003). In contrast, the population in Prague was estimated to be more than 5 200 pairs in 1985–1989 and ca. 1 800 pairs in 2002–2004 (Fuchs et al. 2002, Fuchs in. litt.), whereas the current population is probably much smaller and fragmented.

Modern ornithological systematic monitoring of common bird species began in the 1980s and 1990s (e.g., PECBC 2021). Previous historical population changes were not fully (if at all) covered (Summers-Smith 2005, see also Reif et al. 2021 for more information on this topic).

Despite historically high abundances, colonization of large areas and different habitats, especially in the second half of the 20th century, the House Sparrow has been reported to be declining across several parts of the globe, including most of Europe (e.g., Anderson 2006, De Laet & Summers-Smith 2007, PECBC 2021), North America (Erskine 2006, Lowther & Cink 2020, Berigan et al. 2021), Australia (Olsen et al. 2003) and India (Sharma & Binner 2020).

Cities and urban areas

The first reports of the population decline of the House Sparrow were from the 1920s and 1930s from the centres of large cities, such as Prague, (Baum 1955) and London (see Summers–Smith 2003) in Europe and Chicago in North America (Rand 1956). At Kensington Gardens in London, long-term changes in House Sparrows numbers are well documented. Since monitoring began in 1925, their abundance decreased from 2 603 individuals to 885 in 1948, 624 in 1966, 544 in 1975, 81 in 1995, to just eight in 2000 (Sanderson 1996, Baker 2001, Moss 2001). Since the 1950s, a moderate population decline in urban centres in Northern and Western Europe (Chamberlain et al. 2005, Robinson et al. 2005, Summers-Smith 2005, De Laet & Summers–Smith 2007), and later also from cities in other parts of the continent (e.g., Węgrzynowicz 2013), has been noted (Table 1). For example, in Great Britain, a decline of 60% since the mid-1970s was reported from urban and suburban areas (Robinson et al. 2005). The most significant changes were recorded in London, where the population decreased by 67 % between 1995–2018 (Harris et al. 2020). In Paris the population decreased by 89 % between 2003–2017 (Mohring et al. 2021), and in Prague, complete city mapping showed a loss of 82 % of the House Sparrow population between 1985–1989 and 2002–2006 (Fuchs et al. 2002, Fuchs in litt.). A list of cities where House Sparrow population changes have been studied was compiled by Shaw et al. (2008). Besides these studies, House Sparrow population changes have been published from other cities in more recent years (Table 1). Similarly, population changes were detected in smaller towns (e.g., De Laet & Summers-Smith 2007, Węgrzynowicz 2013, De Coster et al. 2015). For example, the average House Sparrow population density decreased in 34 surveyed Polish cities and towns. The results indicate that the sharpest decline began at the turn of the 20th and 21st centuries (Węgrzynowicz 2013). In concordance, a recent decline in House Sparrow populations was reported from Northern and Western Europe (see De Coster et al. 2015), as well as from Southern Europe, for example, from Spain (Bernat-Ponce et al.

2020). Likewise, in towns and cities in northern Italy, the decline of the Italian Sparrow *Passer* (*domesticus*) *italiae* was recorded (Brichetti et al. 2008).

Table 1: The population changes of the House Sparrow in selected European cities. See Shaw et al. (2008) and above cited literature for other records.

City	Period	Long-term change (%)	Source
Berlin	1990s –2011	stable	Böhner 2014
Livorno	1992/93–2007/08	-53	Dinetti 2009
London	1977–2018	-67	Harris et al. 2020
Lublin	1982–2007	decline	Biaduń & Źmihorski 2011
Lvov	unknown	decline	Bokotey & Gorban 2005
Manchester	unknown	>-80	Summers–Smith 1999
Paris	1960s–2002	-36	Galinet 2003
Paris	2003 – 2017	-89	Mohring et al. 2021
Prague	1985/89–2002/06	-82	Fuchs in litt.
Sofia	1990–2004	increase	Iankov 2005
Valencia	1998–2008	-70	Murgui & Macias 2010
Warsaw	1971/85–2005/06	-48	Węgrzynowicz 2012a

Villages and rural areas

In addition to the most urbanized areas, House Sparrow population decline has been reported from less urbanized settlements, such as villages and farms (Krebs et al. 1999, Hole et al. 2002, De Laet & Summers-Smith 2007). In contrast to the urban environment, the decline was generally slower and less dramatic in this environment compared to large cities (Crick et al. 2002). On the other hand, Summers-Smith (2003) found that the decline began first in the agricultural landscape and after this change (ca. -60%) it stabilised around 1995. Whereas in cities (both small and large – see above), most negative population changes occurred later.

Villages and farms are generally considered crucial habitat for the House Sparrow and farmland birds in otherwise intensively used farmland (Jokimäki & Kaisanlahti-Jokimäki 2012a, b, Hiron et al. 2013, Šálek et al. 2015a, 2018b, Rosin et al. 2016).

For example, Summers-Smith (2003) demonstrated that in comparison to urban areas with gradual decline, the House Sparrow population in small rural settlements had remained stable before ca. 2000 (after the previous massive decline – see above). This is in concordance with Chamberlain et al. (2005), who demonstrated that the House Sparrow population decline started earlier in suburban gardens than rural gardens. Similarly, Robinson et al. (2005) reported that populations in rural areas declined by 47% since the mid-1970s, however, they dropped by 60 % in more urbanized areas. Also, in the USA, House Sparrow populations wintering in more developed areas declined, but rural populations remained stable (Berigan et al. 2021). Nevertheless, decline and local extinction on farms has been witnessed in southern England (Hole et al. 2002) and Norway (Ringsby et al. 2006). In Flanders (Belgium), a decline was reported from urban and rural areas, with no effect of urbanization rate on the declining trend (De Coster et al. 2015). It should be noted, the authors of the study argue that this could be caused by relatively higher urbanization of the whole country (including the "rural" areas) than other parts of Europe. In contrast to the above-cited studies, Vincent (2005) documented a decline of 25 % of territorial males in rural villages, 16% decline in suburban areas, and a tiny increase (4%) in urban centres. However, this study was conducted for just three seasons, and therefore the results should be interpreted with caution. Just a few notes are available about the population changes of this species in villages in Central Europe, and the data is mostly from villages situated at higher elevations. In two villages in the Tyrolean Alps (Austria), the population declined by about 50 % from 1982 to 1991 and did not increase until 2000 (Landmann & Danzl 2020). Similarly, a decline of 25 % was recorded in small-size rural town in the Šumava mountains (Czech Republic) when detailed monitoring was performed in 1984, 2014, 2019, and 2020 (Havlíček et al. in prep.). Finally, in the Krkonoše mountains (the Czech Republic and Poland), local extinction was reported in several villages (Flousek et a. 2015). Already, during mapping in 2006–2011, the species was missing in 11 out of 45 settlements (Vodnárek et al. 2006) and later became extinct in some of the other settlements (Flousek et al. 2015). Generally, House Sparrow density and presence decreases with higher altitudes (Archaux 2007, Šálek et al. 2015a, Keller et al. 2020, Havlíček et al. 2021). A probable reason is the lower proportion of preferred habitats (Havlíček et al. 2021, but see Robinson et al. 2005). Also, colder climatical conditions, especially during the winter, can play a role. This is in concordance with the information mentioned above from the Krkonoše mountains, where the altitudinal limit of House Sparrow presence dropped from 1040 m a.s.l. in the second half of the 20th century (Miles 1986) to 561 m a.s.l. at the beginning of the 21st century (Flousek et al. 2015). Besides the lower proportion of suitable habitats, building repair and the proportion of newly built houses (see below) is higher in mountain areas (e.g., Cuříková 2016). This is most likely due to the high tourism rate and increasing socio-economic status (Havlíček et al. 2021, in prep.). In agreement with this claim, Landmann & Danzl (2020) blame the 40 % change in land use and vegetation cover observed in the examined Alpine villages for the House Sparrow's decline. Unfortunately, evidence and detailed research on long-term population changes in village settlements are missing from Central Europe, making this issue challenging for future work.

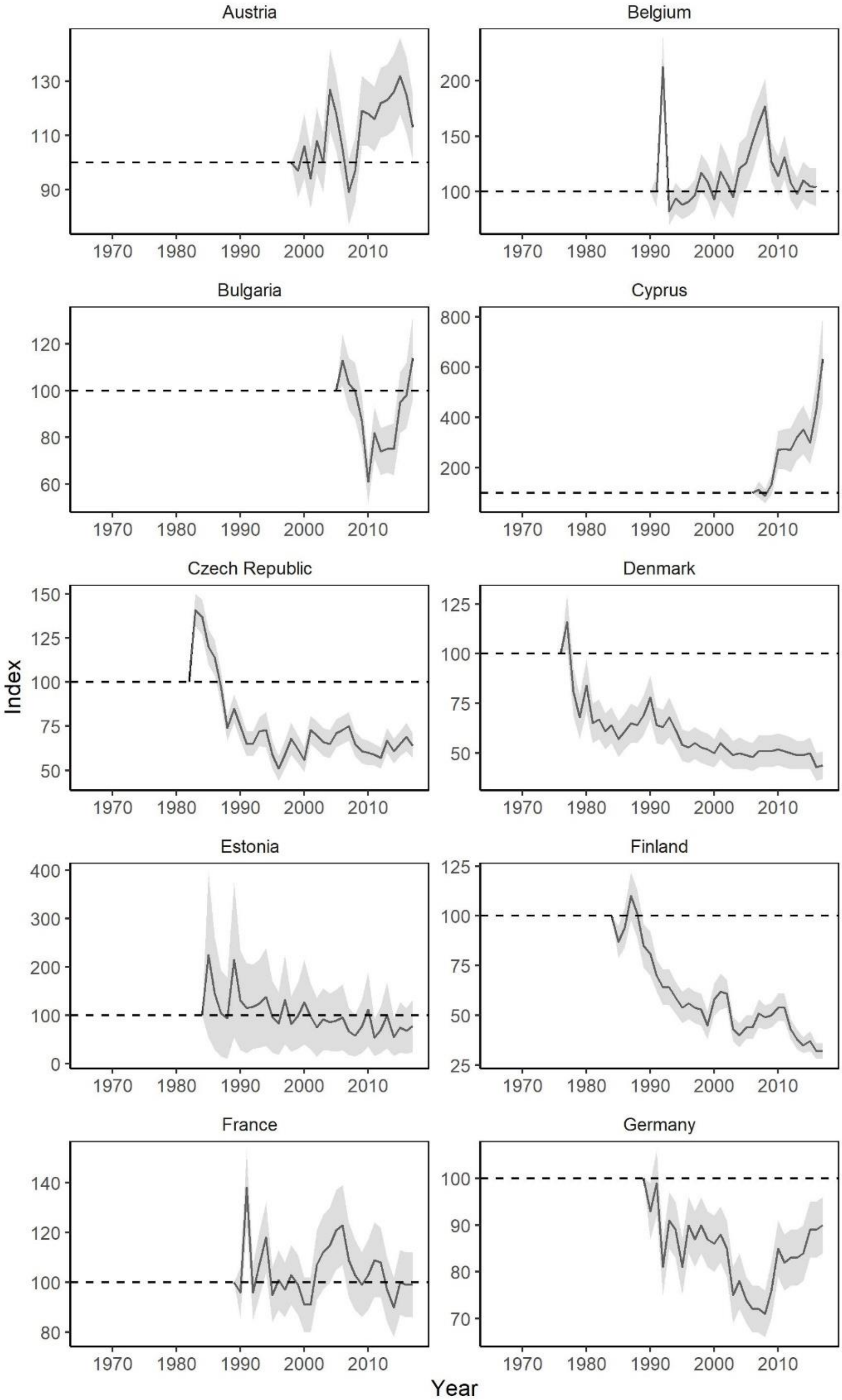
European regions and countries

Based on long-term systematic common bird monitoring incorporated into the Pan European Common Bird Monitoring Scheme (PECBMS 2021), House Sparrow population changes on a national level across Europe can be detected (Tab. 2, Fig. 1). The most extensive dataset comes from the United Kingdom, where the population increased from 1966 to a peak in 1979 but then dropped sharply (Summers-Smith 2003, PECBMS 2021). The recent population trend seems to be stable (Woodward et al. 2020, PECBMS 2021). Based on a winter census, evidence of similar long-term changes was obtained in Finland, where the population increased from the beginning of systematic counting in winter 1956/1957 to winter 1973/1974 when it started to decrease (Väisänen & Hildén 1993). In recent years, numbers of this species in Finland are approximately 50 % less than the peak in the mid-1970s and 10–15 % less than original frequency at the beginning of the project (Laji.fi 2021). A more detailed analysis of Great Britain at a regional level is possible due to sufficient data, and shows considerable differences across regions. During a comparable period from 1995 to 2018, the House Sparrow population decreased by 16 % in England, whereas it increased by 51 and 92 % in Scotland and Wales. The overall population trend for the whole United Kingdom was -1 % in this period (Woodward et al. 2020). Similarly, in England, where the population dropped by 69 % between 1977–2018 (Woodward et al. 2020), differences were observed across (sub)regions – from a decrease of 26 and 28 % in the Southeast and Northeast to an increase of 15 % in the East Midlands (Harris et al. 2020). Similarly, despite the stable long-term trend reported from the Belgian common bird census (see Table 2, Fig. 1), a detailed study focused on House Sparrow population changes in Flanders (44 % of the area of Belgium) shows a significant decline by approximately one third during the period 2002–2011 (De Coster et al. 2015).

On a national level, the most dramatic declines have been observed in Sweden, the Netherlands, Finland, Romania, and Denmark. Still, a strong population decrease has also been reported from Norway, Italy, and the Czech Republic. In contrast, the House Sparrow population increased in other countries, such as Austria, Switzerland, and Ireland, the strongest increase has been documented in Cyprus (Table 2, Fig. 1).

Table 2: National trends for House Sparrow (*Passer domesticus*) in European countries. Data provided by PECBMS. For trend classification method, see Brlík et al. (2021).

Country	Slope	Slope SE	Trend Classification
Austria	1,0125	0,004	Moderate increase (p<0.01)
Belgium	1,0053	0,0036	Stable
Bulgaria	0,9931	0,0092	Stable
Cyprus	1,1765	0,0193	Strong increase (p<0.01)
Czech Republic	0,9859	0,0026	Moderate decline (p<0.01)
Denmark	0,9854	0,0021	Moderate decline (p<0.01)
Estonia	0,9722	0,0093	Moderate decline (p<0.01)
Finland	0,9703	0,0027	Moderate decline (p<0.01)
France	0,9987	0,0046	Stable
Germany	0,9959	0,0019	Moderate decline (p<0.05)
Greece	1,0342	0,0214	Uncertain
Italy	0,9795	0,0024	Moderate decline (p<0.01)
Latvia	1,0317	0,0332	Uncertain
Lithuania	1,0329	0,0428	Uncertain
Luxembourg	1,0265	0,0319	Uncertain
Netherlands	0,9523	0,0047	Moderate decline (p<0.01)
Norway	0,9614	0,0147	Moderate decline (p<0.01)
Poland	0,9937	0,0023	Moderate decline (p<0.01)
Rep. of Ireland	1,0339	0,004	Moderate increase (p<0.01)
Romania	0,9574	0,018	Moderate decline (p<0.05)
Slovakia	0,9816	0,0133	Stable
Slovenia	1,009	0,0056	Stable
Spain	0,9899	0,0017	Moderate decline (p<0.01)
Sweden	0,9562	0,0028	Moderate decline (p<0.01)
Switzerland	1,0087	0,0018	Moderate increase (p<0.01)
United Kingdom	0,9883	0,0102	Stable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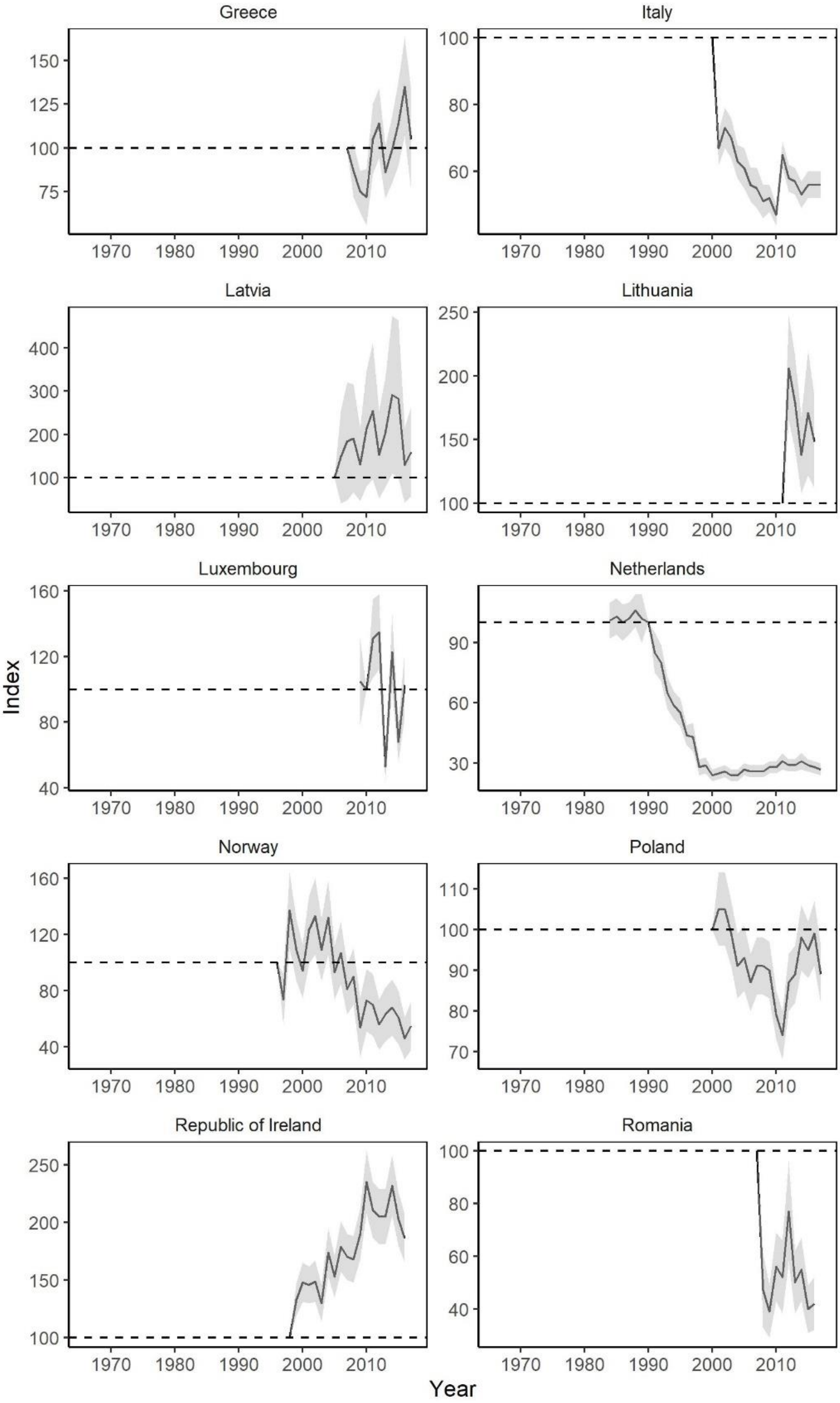
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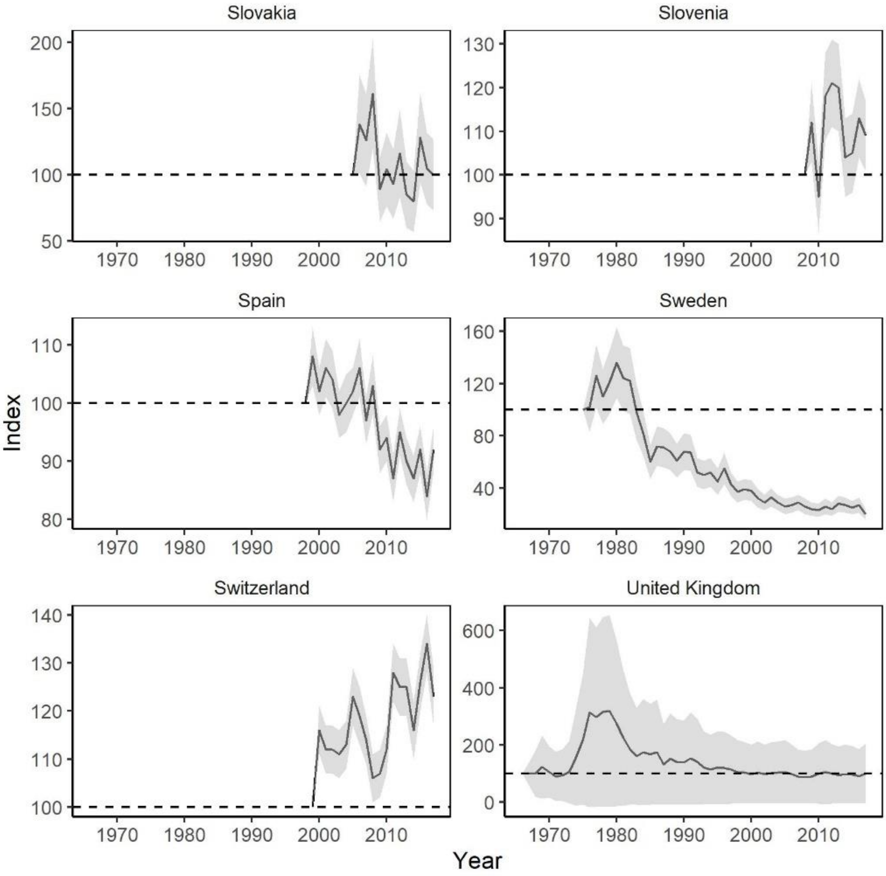

Figure 1: National indices for House Sparrow (*Passer domesticus*) with 95% confidence limits in European countries based on data provided by PECBMS. The dashed lines indicate index = 100.

On a regional level, there are significant differences in the population changes across Europe (Tab. 3, Fig. 2). Surprisingly, Western and Eastern Europe seem to show similar long-term population changes. Long-term (since the 1980s) the House Sparrow population has declined, whereas there is an increasing trend in the past decade (mid-term), and a stable trend in the five years before 2017 (short-term). However, there is a difference in the impact on the overall population size. Nowadays (2017), the population exhibits 60 and 37 % of the original abundance from 1982 and

1980 for Eastern Europe, and Western Europe, respectively. In Northern Europe, the long- (since 1980), mid- (since 2008), as well as a short-term trend (since 2013), exhibits a moderate decrease, and the population in 2017 is just 17 % of the original size (1980). In contrast, the southern parts of Europe have had a stable trend since 1989, with a noticeable decrease in the mid-term period. In the last five years (before 2017), the trend was stable again.

When comparing the "old" and "new" EU member countries, there are differences in the House Sparrow population trends. In the “old” countries that were EU members before 2004, a substantial decline was documented that continued for a longer period. In contrast, in the countries that joined the EU in 2004 or later, a decline was recorded only for the long-term period, whereas there is a slight increase in the mid- and short-term periods (see Table 4, Fig. 3).

Finally, a significant decline has been observed on a pan-European level since 1980 (Table 3., Fig. 4). Moreover, the mid- and short-term trend is stable.

Similarly, the House Sparrow population density differs across regions. They are more abundant in heavily urbanized Western Europe or urban areas in other parts of Europe, and less abundant in mountainous and coniferous areas (Keller et al. 2020). Additionally, based on comparing the 1st and 2nd European breeding bird atlas (Keller et al. 2020), there is a noticeable reduction in occurrence in Scandinavian countries. On the other hand, a range extension was also reported from several parts of Northern Fennoscandia and Eastern Europe (note that this can be affected by lower fieldwork coverage during the 1st atlas mapping) (Keller et al. 2020).

Table 3: Trends for House Sparrow (*Passer domesticus*) in different geographical European regions and the whole of Europe. For the trend classification method, see Brlík et al. (2021). Data provided by PECBMS.

Region	Start year	Slope	Slope SE	Trend Classification
East Europe	1982	0,9822	0,0021	Moderate decline (p<0.01)
East Europe	2008	1,0076	0,0035	Moderate increase (p<0.05)
East Europe	2013	0,9957	0,0089	Stable
South Europe	1989	0,9963	0,0044	Stable
South Europe	2008	0,989	0,0031	Moderate decline (p<0.01)
South Europe	2013	1,0004	0,0078	Stable
West Europe	1980	0,9749	0,0032	Moderate decline (p<0.01)
West Europe	2008	1,0093	0,0016	Moderate increase (p<0.01)
West Europe	2013	1,0042	0,0038	Stable
North Europe	1980	0,9567	0,0025	Moderate decline (p<0.01)
North Europe	2008	0,9736	0,0062	Moderate decline (p<0.01)
North Europe	2013	0,9431	0,0157	Moderate decline (p<0.01)
Europe – compl.	1980	0,9783	0,003	Moderate decline (p<0.01)
Europe – compl.	2008	0,9964	0,0024	Stable
Europe – compl.	2013	1,0064	0,0062	Stable

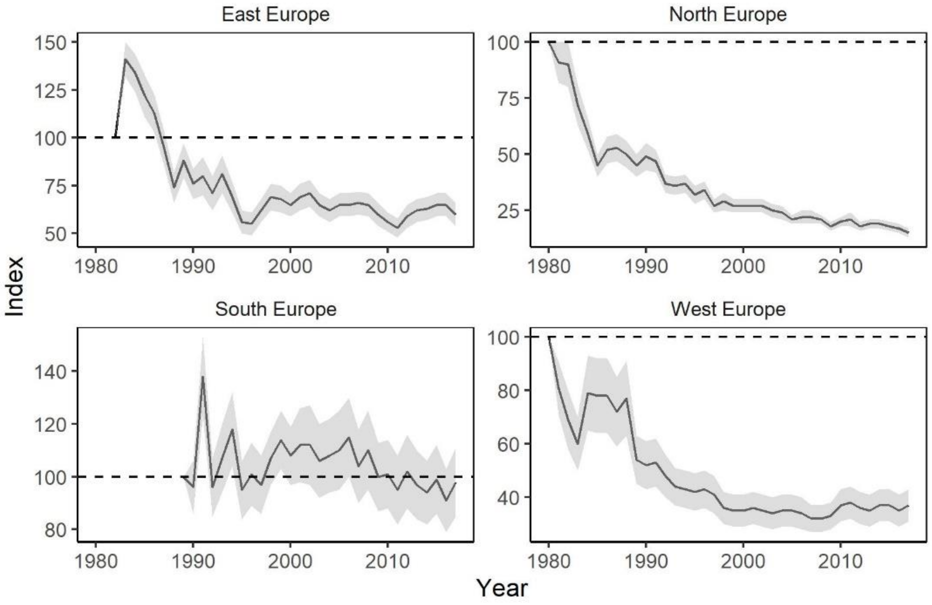

Figure 2: Indices for House Sparrow (*Passer domesticus*) with 95% confidence limits in different geographical European regions based on data provided by PECBMS. The dashed lines indicate index = 100.

Table 4: Trends for House Sparrow (*Passer domesticus*) in different groups of European countries according to their access to the EU. For trend classification method see Brlík et al. (2021). Data provided by PECBMS.

EU country group	Start year	Slope	Slope SE	Trend Classification
Old EU	1980	0,9798	0,0029	Moderate decline (p<0.01)
Old EU	2008	0,9924	0,0029	Moderate decline (p<0.01)
Old EU	2013	1,0029	0,0071	Stable
New EU	1982	0,9838	0,0024	Moderate decline (p<0.01)
New EU	2008	1,016	0,0043	Moderate increase (p<0.01)
New EU	2013	1,0298	0,0125	Moderate increase (p<0.05)

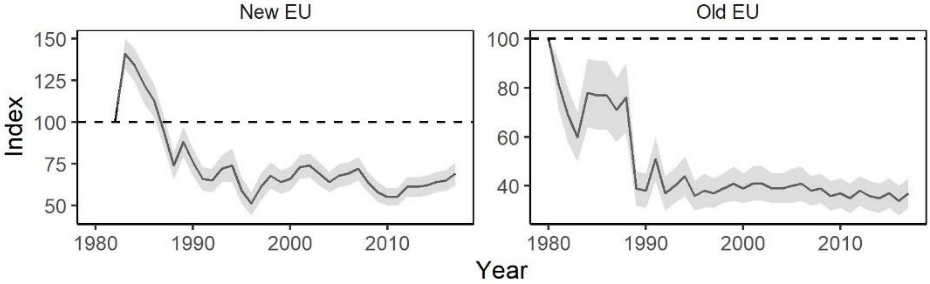

Figure 3: Indices for House Sparrow (*Passer domesticus*) with 95% confidence limits in new and old EU countries based on data provided by PECBMS. The dashed lines indicate index = 100.

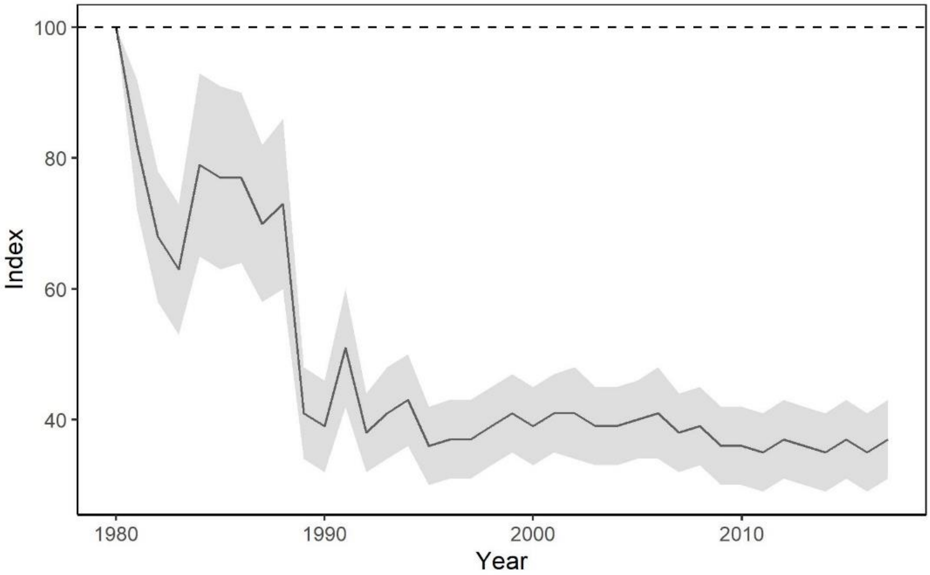

Figure 4: Pan-European indices for House Sparrow (*Passer domesticus*) with 95% confidence limits based on data provided by PECBMS. The dashed lines indicate index = 100.

Reasons for population changes

The most referred to reasons for the rapid population decline of the House Sparrow are lack of food, lack of nesting opportunities, and predation, but diseases and other causes (e.g., environmental pollution) were also cited (e.g., Summers–Smith 1999, 2003, Vincent 2005, Peach et al. 2008, Shaw et al. 2008, Dadam et al. 2019, Bernat-Ponce et al. 2021a). To ascertain which factors influence food availability, or breeding opportunities, several studies focusing on foraging and breeding habitat preferences have been conducted (for details, see Chapters I – III and studies cited). Some of these studies also combined both factors, the habitat composition and age/type of buildings or whole parts of settlements (e.g., Šálek et al. 2015b, Moudrá et al. 2018, Havlíček et al. 2021). Most of the recent studies took place in (sub)urban areas, and detailed work from rural settlements and farms is still scarce. As mentioned above, the “same reasons" (e.g., lack of food or breeding opportunities) are likely to have different origins in urban centres, rural towns, and farmland areas (De Laet & Summers-Smith 2007) and in different regions across the continent, e.g., due to different landscape and settlement structure (see e.g., De Coster et al. 2015). The presented study focuses mainly on the first two factors, food, and breeding site availability.

Lack of food

Food availability is an essential factor limiting birds' survival rate and population size (Martin 1987). Lack of food generally causes smaller clutch size, interruption of breeding, slower growth, and poor condition of offspring, which leads to a decline in population density and size (Newton 1998). Similarly, the timing of the start of breeding and the number of breeding attempts are affected by food availability. Birds at localities with limited food resources start to breed later (Crick et al. 2002) and breed fewer times per season (Newton 1998). On the other hand, in some experimental studies, supplementary feeding had a positive effect on the body mass of offspring (see Newton 1998), which positively affects survival rate in many bird species (see Magrath 1991, Schwagmeyer & Mock 2008).

Already, the first evidence from the 1920s and 1930s linked the decline of House Sparrow populations in urban centres with a reduction in food availability (Baum 1955, Rand 1956, Summers–Smith 2003, De Laet & Summers-Smith 2007). According to the authors of these studies, it was caused by the replacement of horse transport by cars, which led to a lack of food sources represented by spillage of oats from the nosebags of horses and the presence of undigested seeds in droppings. Similarly, recent studies linked the House Sparrow population decline with the reduction of food availability during the breeding and non-breeding (especially winter) season (e.g., Hole et al. 2002, Summers-Smith 2003, Vincent 2005).

Generally, one of the most important factors influencing the survival rates of individuals and local populations of birds is offspring condition and body size, which is influenced by food availability (Magrath 1991, Newton 1998, Schwagmeyer & Mock 2008). This phenomenon was also recorded for the House Sparrow (Ringsby et al. 1998, Schwagmeyer & Mock 2008, Peach et al. 2008, Mock et al. 2009, but see Peach et al. 2018). Larger body mass of House Sparrow offspring was shown to be a predictor of post-fledging survival (Ringsby et al. 1998, Peach et al. 2008, Cleasby et al. 2010). The body mass of House Sparrow offspring can be affected by several factors (Ringsby et al. 1998, Vincent 2005), but generally, the overall amount of food positively influences the condition of offspring (Klvaňová et al. 2011, Seress et al. 2012). Additionally, supplementary feeding led to a better survival rate of offspring (Anderson 1977, Peach et al. 2014, 2015) and decreased time between breeding attempts (Anderson 1977). House Sparrow offspring are predominantly fed with invertebrate prey, and plant food mainly forms a lower proportion of the diet (e.g., Vincent 2005, Anderson 2006, Šťastný & Hudec 2011).

For this reason, the abundance and availability of invertebrate prey within the home ranges of House Sparrows limits survival and body condition of offspring (Vincent 2005, Peach et al. 2015). The ratio between invertebrate and plant components of food was described as a crucial factor. Body mass and condition decreased with increasing proportion of plant components (Vincent 2005, Peach et al. 2008). Similarly, Klvaňová et al. (2011) linked increased offspring condition with a larger amount of invertebrate components in food delivered by parents. On the other hand, the negative effect of plant food proportion was not confirmed. Although the House Sparrow is flexible in using different invertebrate taxa (for details, see Vincent 2005, and Anderson 2006), the proportion of different taxa of invertebrates plays a role in the condition and survival rates of offspring (Vincent 2005). For example, a chick fed more frequently with ants (Formicidae) faces a higher mortality rate compared to those provided more frequently with spiders (Araneae) (Vincent 2005). Similarly, the body size of invertebrate prey brought to offspring was an important factor influencing their condition. The offspring that were more frequently fed larger size prey showed better condition and survival rates (Schwagmeyer & Mock 2008, Seress et al. 2012).

High mortality and low over-winter survival have also been identified as important factors for population declines in several granivorous bird species (Siriwardena et al. 1998, 2000) and House Sparrow in particular (Hole et al. 2002). Due to reduced food availability and high energy demands, winter is a critical period for many sedentary bird species (Fretwell 1972, Gillings et al. 2005). Local extinctions and House Sparrow population declines have been suggested to be caused by reduced winter food supplies (Hole et al. 2002, Jokimäki et al. 2021, but see Von Post et al. 2013). Limitation of winter food sources was also demonstrated by Vangestel et al. (2010). Moreover, the availability of food resources such as cereal grains and weedy seeds may be substantially reduced due to snow cover (Pinowski & Pinowska 1985, Pinowski et al. 2009). Finally, lack of food during the winter season can negatively affect breeding performance in the following year (Summers-Smith 2003).

In this chapter, it is also necessary to mention possible competition for food with other bird species (see e.g., Summers-Smith 2003, Vincent 2005, Skórka et al. 2016).

Food availability in different environments

Recent studies have documented differences in individual body condition in House Sparrow populations across the rural-urban gradient. Generally, House Sparrows with higher nutritional stress, lower reproductive success and body condition were found in populations inhabiting more urbanized areas (Liker et al. 2008, Peach et al. 2008, Seress et al. 2012, Dulisz et al. 2016, Meillère et al. 2017). Compared to larger individuals from less urbanized areas, populations in more urbanized areas show decreased body size (Liker et al. 2008, Peach et al. 2008, Bókony et al. 2010, 2012, Seress et al. 2012, Dulisz et al. 2016, Meillère et al. 2017). It is important to note that decreased body size can be alternatively explained, for example by adaptation to higher predation pressure (see, e.g., Dulisz et al. 2016). On the other hand, there is also evidence of lower quality feather structures in more urbanized environments (Vangestel et al. 2010, Meilléré et al. 2017).

Lower offspring condition and survival rate in urban areas was linked to reduced availability of invertebrate prey in the diet (Vincent 2005, Liker et al. 2008, Bókony et al. 2010, 2012, Seress et al. 2012). Additionally, in a more urbanized environment, parents provided large prey items (e.g., large caterpillars or beetles) less often than rural parents (Seress et al. 2012). Prey size has been described as a predictor of offspring condition (Schwagmeyer & Mock 2008, Seress et al. 2012). Previous studies revealed that some invertebrate taxa are important for House Sparrow offspring, such as beetles and caterpillars (Vincent 2005, Seress et al. 2012), which have decreased diversity, abundance, and size in more urbanized areas (Magura et al. 2004, Niemelä & Kotze 2009, Jones & Leather 2012, Merckx et al. 2018). Woody vegetation such as shrubs and trees represent an important resource habitat for the House Sparrow and other bird species foraging on invertebrate prey (Vincent 2005, Smith et al. 2006, Mackenzie et al. 2014). In concordance shrubs and trees were described as one of the most preferred habitats for House Sparrow (e.g., Vincent 2005, Havlíček et al. 2021, Chapter III). Similarly, other habitats such as wasteland can provide an important proportion of invertebrate prey (Murgui 2009, Murgui & Macias 2010, Chapter III). However, the higher proportion of exotic shrub and tree species, which host fewer invertebrates, reduce this habitat's food availability and attractivity in the urban environment (Vincent 2005, Wilkinson 2006, Mackenzie et al. 2014). There is also a higher risk of degradation and replacement of these habitats (Peach et al. 2008, Murgui & Macias 2010, Bernat-Ponce et al. 2020), as well as more intensive habitat management (see Chapter III). These factors represent a real threat for birds (including the House Sparrow) dependent on this habitat in more urbanized settlements (e.g., Cepák 2011, Bernat-Ponce et al. 2020 Chapter III). Similarly, in highly urbanized areas with dense traffic, air pollution can result in the reduced availability of arthropod prey (e.g., Summers-Smith 2007, Peach et al. 2008, Zvereva &

Kozlov 2010). Previous studies documented that some typical "village" food sources, such as food given to poultry, or food from farms (e.g., grain mixtures for animals, storage cereals), represents an essential driver of House Sparrow abundance during the winter season (Jasso 2003, Šálek et al. 2015a). Lack of these habitats, i.e., farms and poultry yards, can negatively affect urban House Sparrow populations. On the other hand, it is likely, that urban sparrows can compensate for these disadvantages by utilising other resources, e.g., food debris from rubbish containers (see Chapter III and Bernat-Ponce et al. 2021b). The presented study (see Chapter III) shows that in contrast to expectations, some of these habitats are also important during the breeding season.

Small human settlements such as rural villages and towns, especially with the presence of farms, were described as an important habitat in intensively used farmland for several farmland species, including the House Sparrow (Jokimäki & Kaisanlahti-Jokimäki 2012a,b, Šálek et al. 2015a, 2018b, Rosin et al. 2016). Similar to urban environments, the decline of the House Sparrow in agricultural countryside, rural settlements, and farms is often linked to lack of food (e.g., Robinson et al. 2005). In this case, agricultural intensification is to blame (Krebs et al. 1999, Chamberlain et al. 2000, Hole et al. 2002, Robinson et al. 2005, Šálek et al. 2015a). For example, in Sweden, the rate of House Sparrow population changes differs across three periods defined by the application of different agricultural policies. During the period of "intensification," the House Sparrow declined faster in two of three regions than during the period when set-aside policy was applied under EU Common Agricultural Policy. Finally, a slower decline in the House Sparrow population was observed during the period when agri-environment schemes increased rapidly (Wretenberg et al. 2007). Recent shifts in farming practices in Europe, which negatively impact bird communities, have been linked with the application of the EU Common Agricultural Policy (Donald et al. 2001, Reif & Vermouzek 2018, Šumrada et al. 2021). For example, Reif & Vermouzek (2018) showed that agricultural production intensified, and farmland bird populations declined steeply after the accession of the Czech Republic to the EU in 2004. In the case of the House Sparrow, its population declined more dramatically in countries that adopted the EU Common Agricultural Policy sooner. Additionally, the decline continued for a longer period (see above and Table 4, Fig. 4). In contrast, the countries that adopted EU Common Agricultural Policy later show a decline only in the long-term period, whereas there is a slight increase in the mid- and short-term periods (see Table 4, Fig. 4). It is important to note that these results are based on a simple analysis, and a more detailed analysis is a future challenge.

The most significant manifestations of the shift from traditional to modern intensive farming practices are the use of more effective herbicides and insecticides (Siriwardena et al. 1998, Benton et al. 2003), use of lossless agricultural machinery, the building of large capacity farms, reduction in the number of smaller dairy farms (Siriwerdena et al. 1998, Bignal & McCracken 2000, Benton et al. 2003, Šálek et al. 2015a), and general reduction in landscape heterogeneity (Benton et al. 2003, Šálek et al. 2018a). Additionally, some other "smaller" changes in farm infrastructure (e.g., installation of bird-proof grain storages, storage of silage and manure in water-proof containers, often made of plastic and covered with plastic tarps, use of lossless machinery, and changes in sowing patterns) can reduce the availability of food sources (see Šálek et al. 2018b, Havlíček et al. 2021, Chapter III). Most of the changes and factors named above, especially the use of insecticides and herbicides and low farmland heterogeneity, reduce the availability of seed food and abundance of invertebrate prey for birds (Donald et al. 1998, Smith et al. 2008, Ewald et al. 2015). In accordance with these statements, House Sparrow populations declined faster in localities where insecticide applications were more frequent (Mineau et al. 2005). Finally, the negative effect of intensive farming on the abundance of insects, plants, and birds compared to organic farms was confirmed by several studies (Dritschilo & Wanner 1980, Wickramasinghe et al. 2004, Bengtsson et al. 2005, but see e.g., Hole et al. 2005, Piha et al. 2007, Kragten & de Snoo 2008). Additionally, the application of some agri-environment schemes has had a positive effect on some farmland birds, including the House Sparrow (e.g., Bracken & Bolger 2006, Walker et al. 2018). The application of several agri-environmental schemes providing cereal stubbles and seed and invertebrate prey rich habitats may also be important during the winter, which is critical for adult survival (Hole 2002, Robinson & Sutherland 2002), as well as during the breeding season (Walker et al. 2018).

Recently, there have been noticeable socio-economical changes in rural areas, accompanied by higher aesthetical and hygiene needs of inhabitants, (see Chapter III for more details). This includes the abandonment of traditional farming and keeping of poultry (see Jasso 2003, Šálek et al. 2015a, Havlíček et al. 2021), cultivation of formerly derelict sites such as ruderals and native unmanaged shrubs, or planting of exotic plants, and more intensive management of gardens and other green spaces (for details see Chapter III). This trend can result in the subsequent decrease of food availability during the entire year in rural villages and small towns.

The lack of breeding opportunities

Lack of breeding opportunities is, like food availability, a crucial factor affecting population size in cavity-breeding birds (Brawn & Balda 1988, Newton 1994). Despite the ability of the House Sparrow to build nests on green walls and in coniferous and deciduous trees (e.g., Šťastný & Hudec 2011), it primarily breeds in various types of holes and cavities in buildings (Anderson 2006; Summers-Smith 2009, Šťastný & Hudec 2011, Šálek et al. 2015b). A lack of breeding opportunities, mostly due to repairing old houses, or their replacement by modern birdproof buildings, has also been frequently referred to as a potential reason for the House Sparrow's widespread decline (e.g., Summers-Smith 2005, Vincent 2005, Shaw et al. 2008). This factor is probably more severe in urban centres (Summers-Smith 2003) and was reported, for example, from Berlin (Witt 2005), Lviv (Bokotey & Gorban 2005), and Prague (Cepák 2011). Additional evidence for this theory are data showing different population sizes across localities characterized by various buildings and urban architecture (Siriwardena et al. 2002, Vincent 2005, Brichetti et al. 2008, Summers-Smith 2009, Šálek et al. 2015b). Generally, the House Sparrow is less abundant in newly built areas. In a central-European city, Šálek et al. (2015b) documented five times smaller population densities of House Sparrow in new residential locations than in residential areas older than 30 years. The density in urban centres and panel-housing estates was approximately three times smaller, whereas, in garden colonies, the House Sparrow was approximately ten times less abundant. Other previous studies have confirmed the same trend in occupancy of older and newly built areas for House Sparrows (Siriwardena et al. 2002; Vincent 2005; Mason 2006, Brichetti et al. 2008; Summers-Smith 2009; Moudrá et al. 2018). The accepted explanation for this result is that the older houses can offer more diverse and abundant nesting opportunities (Mason 2006; Shaw et al. 2008; Węgrzynowicz 2012a; Šálek et al. 2015b). For example, Von Post & Smith (2015) suggested a preference for nest-sites under tiles when available. The same result was obtained from a Central-European city by Šálek et al. (2015b), who found 79.9 % of all nests in the roof tiles and declared that older buildings offer more potential breeding sites. In contrast, modern facilities, such as shopping centres with glass facades, do not provide much space for nest placement (Nath et al. 2016, see also Skórka et al 2009). House Sparrow density in industrial and commercial areas (including large shopping centres) was approximately ten times smaller than in old residential areas in a Central-European city (Šálek et al. 2015b). In contrast, our findings (Havlíček et al. 2021) imply no effect of building age on House Sparrow population density and habitat selectivity in typical Central-European rural settlements. Additionally, Dulisz & Zasitko (2008) described that the population decreased in other parts of the city, whereas it increased in the newest part. Other studies indicate that House Sparrows prefer sites with a balanced proportion of buildings and other habitats (Šálek et al. 2015b, Havlíček et al. 2021), and avoid areas where urbanization (primarily measured as a proportion of buildings – see De Coster et al. 2015) reached its peak (Murgui 2009; Evans et al. 2009, Węgrzynowicz 2012a, Nath et al. 2019). In contrast to declarations about the lack of breeding opportunities as a limiting factor for House Sparrow occurrence and density, there was no strong (if any at all) evidence for this statement when experiments with the addition of nest boxes as potential breeding opportunities in the urban environment were conducted (Węgrzynowicz 2012a, b, Angelier & Brischoux 2019). This is in concordance with the claim of Murgui & Macias (2010). Surprisingly, Angelier & Brischoux (2019) suggest that cavity availability is probably more constraining in rural areas than in urban ones in France. On my rural study sites (see Chapter III for description), the House Sparrow occupied all of the nest boxes erected on the farm (unpublished data). Nest boxes were also regularly used by House Sparrows on the farm where Klvaňová et al. (2012) conducted their study. In contrast, Von Post & Smith (2015) claimed that House Sparrow populations are mainly limited by another mechanism than nest-site availability on Swedish farms.

Recently, the increasing rate of reconstructions and insulations of buildings, causing a loss of breeding sites, was discussed as a threat for the House Sparrow and other cavity breeding birds (see Havlíček & De Laet 2016, Rosin et al. 2020). For instance, Wotton et al. (2002) found that sparrows only use buildings for breeding before reconstruction. The modernization of buildings was mentioned by Cepák (2011), as one of the reasons for the local extinction of the House Sparrow population in the central part of Prague. In Warsaw, local populations substantially decreased following the renovation of housing estates. In contrast, the decline was much less intensive in urban areas with a lower rate of modernization, and it increased simultaneously in a district with no renovation of buildings (Węgrzynowicz 2012a). In contrast to this study, the results from another Polish city do not indicate modernization as the main factor affecting population changes (Dulisz & Zasitko 2008). Landmann & Danzl (2020) found that House Sparrows prefer older buildings. They speculate that new ways of constructing houses and especially roofs are responsible for decreasing local populations in mountain villages in the Alps. On the other hand, our data do not support this finding (Havlíček et al. 2021), and House Sparrows were regularly observed to occupy recently reconstructed houses and roofs (unpublished data). The increasing rate of modernization and renovation is mainly caused by changes in socio-economics status (Shaw et al. 2008, Rosin et al. 2016, Żmihorski et al. 2020) and to reduce energy consumption (see, e.g., Rosin et al. 2020 for details). For instance, in the Czech Republic, one of the highest (besides large city suburbs) rates of newly built and reconstructed buildings is evident in some mountain settlements in recreation areas, such as in the Šumava National Park (e.g., Cuříková 2016, Havlíček et al. in prep.). Together with other factors influencing House Sparrow populations at higher elevations (Havlíček et al. 2021 and above), this is a threat to the future existence of local populations (Havlíček et al. in prep.). In the rural environment, old farms and buildings associated with traditional farming offer important breeding sites for many farmland species, including the House Sparrow (Rosin et al. 2016, 2020, Żmihorski et al. 2020). Renovations or replacement of old farm buildings with new ones supported by EU Common Agricultural Policy funds (for details see, e.g., Šálek et al. 2018b), or abandonment of traditional small-scale farming represents an actual threat for several bird species inhabiting urban and farmland landscapes (e.g., Šálek et al. 2015a, 2018b, Rosin et al. 2016. Żmihorski et al. 2020).

On the other hand, in some countries (including the Czech Republic, Germany, etc.), compensation for selected breeding species, such as Common Swift (*Apus apus*) and bats (Chiroptera), must be applied during the process of building insulation and renovation, especially when financed from public funds (ČSO et al. 2008, Schaub et al. 2016). The most common compensation solution is the erection of special swift and bat nest boxes. The House Sparrow has been reported to occupy some types of these nest boxes and thus profit from "swift protection." For example, in Mecklenburg, a middle-sized city in Germany, House Sparrow occupied 21.4 % of observed swift boxes (Schaub et al. 2016).

In this chapter, it is also necessary to mention possible competition for breeding sites with other bird species such as Common Swift – see above, Black Redstart (*Phoenicurus ochruros*), House Martin (*Delichon urbicum*), and Barn Swallow (*Hirundo rustica*) (Bokotey & Gobanov 2005). Similarly, in North America, interspecific competition with Tree Swallow (*Tachycineta bicolor*) was described by Robillard et al. (2013). On the other hand, House Sparrows relatively frequently use old nests of some other species – in Europe, often House Martin and Barn Swallow (Šťastný & Hudec 2011). The recent decline of House Martin and Barn Swallow (e.g., PECBMS 2021) can also potentially lead to a shortage of breeding opportunities for House Sparrows.

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Chapter I

Winter density and habitat preferences of three declining granivorous farmland birds: the importance of the keeping of poultry and dairy farms

Martin Šálek, Jan Havlíček, Jan Riegert, Marek Nešpor, Roman Fuchs, Marina Kipson

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Winter density and habitat preferences of three declining granivorous farmland birds: The importance of the keeping of poultry and dairy farms

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Abstract

Populations of granivorous farmland birds have dramatically declined during recent decades in many European countries. Winter conditions and consequently, survival rates of farmland bird species during this critical period, are considered as one of the main causes of this negative trend. However, the importance of different habitat structures and connected food sources for successful overwintering in bird species has gained little attention so far in the Czech Republic. In this study we aimed to examine the role of habitat composition and food availability on winter distribution and abundance of three declining sedentary and granivorous bird species. During the winters 2009–2014, 149 villages in the Czech Republic were monitored for distribution and density of three farmland seed-eaters. House Sparrow was the most dominant species (88.6% of villages occupied; 4.32 ± 4.67 ind./100 m of transect), followed by Tree Sparrow (67.1% villages occupied; 1.83 ± 3.53 ind./100 m of transect) and Collared Dove (65.8% villages occupied; 0.72 ± 1.51 ind./100 m of transect). Occurrence of House and Tree Sparrow was significantly affected by the number of instances of poultry keeping. In both species, occupied villages showed a higher number of instances of poultry keeping. We did not find any such significant relationship for Collared Dove. Density of House Sparrow was significantly higher in villages with dairy farms, but we failed to find this relationship for Tree Sparrow and Collared Dove. Habitat preferences were similar for all three studied species. They positively responded to the proportion of shrubs/trees, the keeping of poultry, dairy farms and they avoided houses, arable land and grasslands. We conclude that poultry keepings and dairy farms can be important for studied species during the winter since they offer high food availability and good protection against predators. This suggestion is supported by the fact that long-term population decline has coincided with a long-term reduction in the keeping of poultry and dairy farms in the Czech Republic during the last 50 years.

Keywords: Central Europe; Dairy farms; Granivorous birds; Habitat preferences; Poultry keeping; Winter period

Introduction

Large-scale population declines and range contractions in many birds inhabiting farmland have been reported from various parts of Central and Western Europe (Fuller et al., 1995, Pain and Pienkowski, 1997Donald et al., 2001, Reif et al., 2008). Between 1970 and 1990, 86% of farmland bird species had reduced ranges and 83% showed significant decline (Fuller et al. 1995). In particular, populations of granivorous farmland birds have declined dramatically during recent decades, which resulted in conservation concern in many European countries (Gregory et al., 2002, Robinson et al., 2005). Within Europe, the most dramatic declines and range contractions of farmland species have occurred in the countries with the most intensive agriculture, especially in those countries which have been influenced by EU farmland policy for the longest period (Donald et al. 2001). This supports the hypothesis that rates of decline in farmland bird populations are primarily caused by increases in agricultural intensification.

Among various reasons for this widespread population decline within intensively used agricultural land, winter survival rate seems to be crucial for changes in population size. Winter is a critical period for sedentary, small-sized granivorous farmland birds due to reduced food availability and the high energy demands of surviving long nights with low ambient temperatures (Fretwell, 1972, Witter and Cuthill, 1993). Moreover, the availability of food resources such as cereal grains and weedy seeds may be substantially reduced due to snow cover (Pinowski & Pinowska 1985; Pinowski et al. 2009). High mortality and over-winter survival have been identified as the main factor for breeding population declines in several granivorous bird species (Siriwardena et al., 1998, Siriwardena et al., 2000). For example, Hole et al. (2002) demonstrated that reduced House Sparrow survival in the rural landscape is connected with winter starvation risk and could be the principal explanation for its recent widespread population decline. Reduced winter survival of granivorous birds inhabiting farmland is thought to be connected with widespread changes in agricultural management and intensity. In particular, the switch from spring to autumn sowing and loss of non-cropped habitats result in decreases of food availability of cereal grain and weed seeds during the winter (Chamberlain et al., 2000, Hole et al., 2002, Robinson and Sutherland, 2002). In agreement, breeding population declines of many farmland UK birds, especially sedentary granivorous species, are connected to reduction in area of key foraging habitats–stubbles (Gillings et al. 2005).

Residential areas such as rural villages, small towns and suburban areas have been described as a primary habitat for many resident granivorous farmland species in intensively used agricultural landscapes (Coombs et al., 1981, Hengeveld, 1988, Summers-Smith, 1988, Hancock and Wilson, 2003, Summers-Smith, 2003, Vepsäläinen et al., 2005, Fujisaki et al., 2010, Jokimäki and Kaisanlahti-Jokimäki, 2012). In contrast to the intensively used agricultural landscape with its marked loss of non-agricultural habitats and dominance of homogeneous arable habitats, human settlements may offer continuous availability of food sources during winter. The food availability may, however, significantly differ with the structure and composition of individual human settlements due to various proportions of anthropogenic and “natural” habitats. Moreover, the local farming management such as number of instances of poultry keeping or large scale dairy farms may have significant influence on distribution and abundance of seed-eating birds (Hole et al., 2002, Ringsby et al., 2006). Thus, habitat preferences of granivorous birds during winter are important indicators of habitat quality and resource availability that in turn determine their survival rates (Fuller et al., 1995, Evans, 1997, Chamberlain et al., 2010).

The primary aim of this study was to examine the effects of habitat composition and food availability on winter habitat distribution and population density of three declining granivorous and sedentary farmland birds (House Sparrow *Passer domesticus*, Tree Sparrow *Passer montanus* and Collared Dove *Streptopelia decaocto*) using a volunteer-based nationwide survey in the Czech Republic. In particular, we tested the effect of farming intensity on occurrence and density of the studied species inhabiting rural landscapes and we also evaluated their winter habitat preferences. Our study presents large-scale research of winter habitat preferences, which could help conservationists to better evaluate the importance of individual habitats and farming management for birds inhabiting rural landscapes. In general, the results of our study may also indicate future changes of vulnerable synanthropic farmland populations related to habitat changes in Central European farmland.

Methods

Data collection and study design

Data on distribution and density of the studied synanthropic farmland birds (House Sparrow, Tree Sparrow and Collared Dove) were obtained from the nationwide volunteer-based survey program "Monitoring of synanthropic birds in the Czech Republic" undertaken between the years 2009–2014, covering 149 villages (descriptive characteristics in Table 1). The monitoring of study localities was carried out during winter periods (15th December–28th February) using a transect method (Vincent, 2005, Chamberlain et al., 2007). Each locality was visited once. At each locality (village), the observers were asked to walk slowly (<3 km/h) and count the birds along transects (>50 m) that included all available local roads, streets, pavements and pathways as well as local dairy farms and other agricultural infrastructure. The study localities were chosen prior to field work, based on digital aerial orthophotograph maps (1:5000) using a geographical information system (GIS, ArcView 3.2a—Environmental Systems Research Institute, Inc. 2000). The route comprised a variety of different habitats including various artificial (houses, dairy farms) and green (grasslands, arable land, shrub and tree vegetation) habitats. The monitoring was carried out during favourable meteorological conditions (without strong wind, precipitation or heavy snowfall), from 06:00 to 11:00 CEST. The position, number of seen or heard individuals and habitat use of monitored birds were recorded onto detailed aerial maps (1:5000, Google Maps 2013).

Table 1. Descriptive characteristics of studied villages and habitat characteristics around transects (n = 149).

	Mean ± s.d.	**Range**
Altitude (m a.s.l.)	465.9 ± 125.0	184.0–998.0
Transect length (m)	1833.2 ± 1582.1	224.0–9270.0
Number of poultry keepings	4.5 ± 4.6	0.0–33.0
% Of shrubs around transects	15.6 ± 4.9	4.9–32.0
% Of houses around transects	26.2 ± 8.0	5.0–45.0
% Of dairy farms around transects	2.4 ± 5.2	0.0–50.0
% Of poultry around transects	2.6 ± 2.0	0.0–11.2
% Arable areas around transects	6.8 ± 7.5	0.0–30.6
% Of grasslands around transects	46.3 ± 9.8	14.5–84.2

Monitored characteristics

In order to reveal factors which affect the distribution and abundance of the studied birds, we investigated main habitat, topographical and human-related characteristics within 30 m buffers around the route of monitored transects. In particular, we recorded the percentage of each habitat cover by shrub and tree vegetation, grasslands, arable area and houses (i.e. family houses, multi-story houses). Similarly, because food availability may affect bird distribution, we also recorded the numbers of small scale farming (including poultry, sheep and cattle with less than 10 individuals or bird-feeding stations) and occurrence of dairy farms (0/1) with cattle. The elevations of individual localities were derived from local tourist maps. The selected characteristics have been recorded as important predictors of density and distribution for selected granivorous birds in the rural environment (Coombs et al., 1981, Vincent, 2005, Chamberlain et al., 2007, Murgui, 2009, Shaw et al., 2011). The length of the individual transect within each study locality was calculated in Seznam Maps Route Measurement (http://www.mapy.cz/). The percentage cover of individual habitats was estimated from the most recent aerial maps (http://www.mapy.cz, http://www.google.cz) in the GIS environment (GIS, ArcView 3.2a—Environmental Systems Research Institute, Inc. 2000).

Statistical analyses

The effect of variables on House and Tree Sparrow and Collared Dove occurrences in the village (0/1) and densities (individuals per 100 m of transect) were analysed using generalized linear mixed models (GLMM) in R v. 2.8.1 (2008) with relevant link function (logit and inverse, respectively) and altitude as a random factor. In the analyses on densities, we included only villages with occurrence of tested species (House Sparrow n = 132, Tree Sparrow n = 100, Collared Dove n = 98). We used the occurrence of dairy farms (0/1) and the keeping of poultry (number of fowl farms) as well as their interaction as independent variables. Before each analysis, we performed a null model without independent variables. Factors were included into the model based on AIC criterion. Only variables with significant effects ($P < 0.05$) are shown. The effect of altitude (independent variable) on species density (dependent variable) was tested using simple regression (STATISTICA software v. 9.1, StatSoft, Inc. 2010).

Habitat preferences were assessed only for occupied villages. The R statistical software (R Development Core Team 2009) with the package Adehabitat (Calenge 2006) was used to compute compositional analysis of habitat selection. We used a randomization test with 500 repetitions. Habitat that was not found within the particular category (zero values in entry data matrix) was replaced by 0.01 (Aebischer et al. 1993). A village represented a data unit. For each village, we computed percentages of each habitat category available (proportion of area surrounding transect) and the percentages used by the study species (proportion of individuals recorded in particular habitat). Compositional analysis was performed for all three bird species separately. This analysis was carried out in two steps: first the significance of habitat use was tested (using a Wilks lambda). Then, a ranking matrix was built, indicating whether the habitat category in the rows is used significantly more or less than the habitat type in the columns. Further, habitats were assorted from most preferred to non-preferred (Aebischer et al. 1993). The relationships between the overall proportion of habitat available (proportion of habitat area) and habitat used (proportion of individuals recorded in particular habitat) were expressed by log2 (used/available) after Sunde et al. (2001). Statistical significance was obtained using the chi-square test (StatSoft, Inc. 2010).

Results

In total, we recorded 15,159 individuals in 273.2 km of surveyed transects. House Sparrow was the most dominant species (88.6% of villages occupied; mean density ± s.d., 4.32 ± 4.67 ind./100 m of transect), followed by Tree Sparrow (67.1% villages occupied; mean density ± s.d., 1.83 ± 3.53 ind./100 m of transect) and Collared Dove (65.8% villages occupied; mean density ± s.d., 0.72 ± 1.51 ind./100 m of transect). Occurrence of House and Tree Sparrow was significantly affected by the number of instances of poultry keeping (GLMM, Table 2). In both species, occupied villages showed higher number of such instances of poultry keeping (Fig. 1). We did not find any such significant relationship for Collared Dove. Simultaneously, density of House Sparrow was significantly higher in villages with dairy farms (GLMM, Table 2 and Fig. 2). We did not find any significant effect on density of Tree Sparrow and Collared Dove. We also found an indicative negative relationship between House Sparrow density and altitude (regression, beta = −0.14, F = 2.80, P = 0.097). This relationship was not significant in Tree Sparrow and Collared Dove (regressions, P at least 0.27).

In all the studied species we found significant differences between habitat availability and habitat use (Compositional analyses, House Sparrow: Wilk's lambda λ = 0.08, P = 0.002; Tree Sparrow: Wilk's lambda λ = 0.10, P = 0.002; Collared Dove: Wilk's lambda λ = 0.09, P = 0.002, for detailed comparisons see Appendix 1). In House and Tree Sparrow, we found the highest preference for areas where poultry was kept and the least for grasslands (habitat ranking; House Sparrow: instances of poultry keeping > shrubs/trees > dairy farms > houses > arable land > grasslands; Tree Sparrow: poultry keeping > shrubs/trees > dairy farms > arable land > houses > grasslands). In Collared Dove, the most preferred habitat was shrubs/trees (habitat ranking: shrubs/trees > poultry keeping > dairy farms > houses > arable land > grasslands).

Table 2. Factors that significantly affect winter occurrence and density of House and Tree Sparrow in monitored rural areas in the Czech Republic (GLMM analyses, random factor—altitude, n = 149). We show only best and significant models based on AIC criteria.

Species	Dependent variable	Model	Independent variable	d.f.	% Of explained variability	χ	*P*
House Sparrow	Occurrence (0/1)	Binomial	Number of instances of poultry keeping	3	30.5	32.35	<0.001
Tree Sparrow	Occurrence (0/1)	Binomial	Number of instances of poultry keeping	3	3.0	5.73	0.017
House Sparrow	Density (inds./100 m transect)	Gamma	Dairy farm occurrence (0/1)	5	2.3	19.93	<0.001

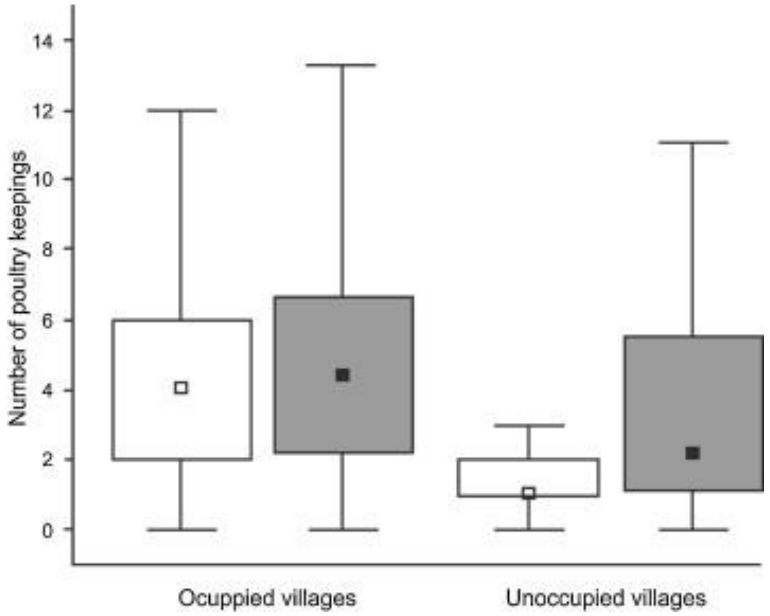

Fig. 1. Numbers of instances of poultry keeping in villages occupied and unoccupied by House Sparrow (white boxes, GLMM, n1 = 132, n2 = 17 villages, P < 0.001) and Tree Sparrow (grey boxes, GLMM, n1 = 49, n2 = 100 villages, P = 0.017). Squares—medians, boxes—25–75% of data, whiskers—non outlier ranges.

Overall habitat use differed from habitat availability (Chi square tests, House Sparrow: χ = 56,329.9, d.f. = 4, P < 0.001; Tree Sparrow: χ = 12,875.9, d.f. = 4, P < 0.001; Collared Dove: χ = 10,816.9, d.f. = 4, P < 0.001). Habitat preferences were similar for all three studied species. They positively responded to the proportion of shrubs/trees, poultry keeping, dairy farms and avoided houses, arable land and grasslands. The strongest preference for dairy farms was recorded in Collared Dove, both sparrows showed similar values (Fig. 3).

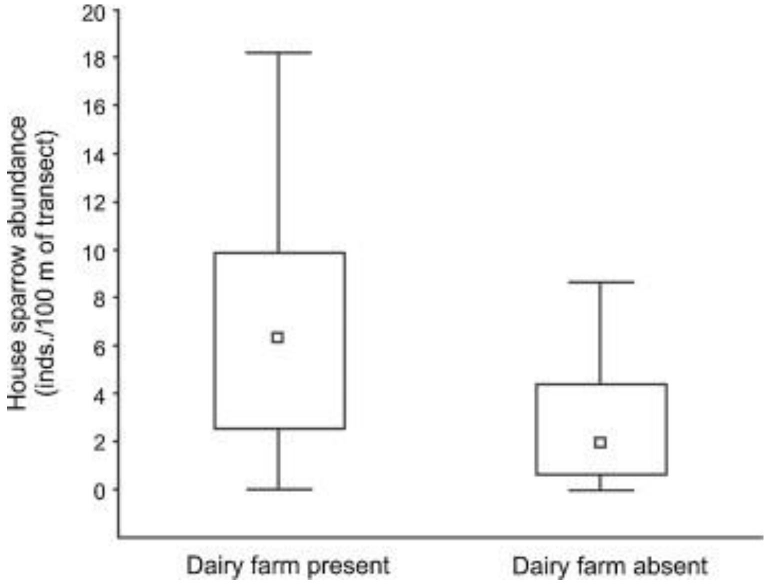

Fig. 2. Winter density of House Sparrow for villages with and without dairy farm occurrence (GLMM, n1 = 44, n2 = 105 villages, P < 0.001).

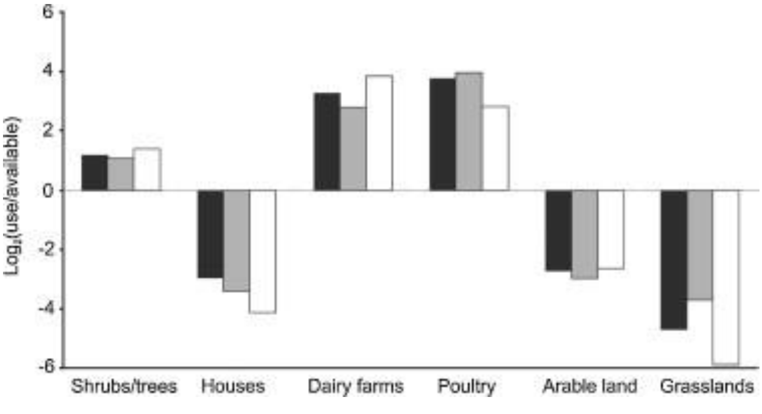

Fig. 3. Habitat preferences of House Sparrow (black columns), Tree Sparrow (grey columns) and Collared Dove (white columns) for each habitat category expressed by $\log_2$ (used/available).

Discussion

Massive and widespread changes in farming practices and agricultural intensification of Western and Central European farmland, combined with the switch from spring to autumn sowing and substantial loss of over-winter stubbles, has led to a substantial reduction in the availability of winter food for farmland birds (Summers-Smith, 1989, Summers-Smith, 1995, Evans, 1997, Siriwardena et al., 2006, Wretenberg et al., 2007, Kasprzykowski and Goławski, 2012). Previous experimental research demonstrated that winter food supplementation has a positive effect on over-winter survival (e.g. Smith et al., 1980, Jansson et al., 1981, Hole et al., 2002), body condition (Rogers & Heath-Coss 2003) and abundance (Källander, 1981, Siriwardena et al., 2007) of farmland birds. It has been demonstrated that loss of the winter stubble fields as a food source has had a negative impact on winter mortality of farmland birds (Evans and Smith, 1994, Donald and Forrest, 1995; Gillings et al. 2005). On the other hand good winter food availability positively affects farmland bird survival which, in turn, determines local and landscape-scale abundance (Newton, 1994, Peach et al., 2001, Hole et al., 2002) and hence may explain some of the variation in population trends (Siriwardena et al., 1999, Hole, 2001). Therefore, assessing key foraging winter habitats and understanding factors that determine their utilization are of crucial importance for ecology and population dynamics of farmland species, enabling the setting of efficient conservation measures to support farmland bird populations. Our results show that farming management such as poultry keeping and cattle-breeding dairy farms are valuable habitats for a selected population of granivorous birds inhabiting rural habitats in Central Europe (Pinowska et al., 1976, Ringsby et al., 2006, Saether et al., 1999).

The positive effect of poultry keeping and dairy farms for occurrence, population density and habitat selection is mainly attributed to abundant food supply in these habitats (see also Hudec, 1983, Jasso, 2003, Šťastný et al., 2006, Griesser et al., 2011, Liu et al., 2013). In particular, the keeping of poultry provides high quality food resources such as energy rich cereal grains and food debris given to poultry or other domestic animals. Dairy farms contain grain spillage, silage holes or grain storehouses that also provide a high availability of important food resources. The cereal grains are the most important food for all the studied species during winter, accounting for up to 82% of the diet of the House Sparrow, 50% for Tree Sparrow and 67% for Collared Dove (House and Tree Sparrows—Keil, 1972, Hudec, 1983, Szlivka, 1983, Sanchez-Aguado, 1986, Summers-Smith, 1988, Anderson, 2006, Collared Dove—Hudec & Černý 1977Helešic, 1981, Snow and Perrins, 1998; Varga 2008), however, compared to the House Sparrow the diet of the Tree Sparrow consists of more weed seeds (Keil, 1972, Hudec, 1983, Summers-Smith, 1988, Anderson, 2006).

All studied species showed habitat preferences for shrub and tree vegetation within rural settlements. In agreement with previous studies (Coombs et al., 1981, Hengeveld, 1988), the Collared Dove occurrence was mainly associated with gardens and orchards with a mixture of shrub and tree cover providing safe roosting sites. Similarly, a preference for native shrub vegetation by both sparrow species during the breeding season was reported from previous studies (Pinowska and Pinowski, 1999, Zhang and Zheng, 2010Vincent, 2005, Wilkinson, 2006, Chamberlain et al., 2007). However, its utilization during breeding could be, apart from roosting, connected with foraging on arthropod prey, which is the dominant prey of adults and nestlings (Hudec, 1983, Pinowska and Pinowski, 1999Wilson et al., 1999, Field and Anderson, 2004; Vincent 2005). In contrast, shrubs and tree vegetation do not offer suitable prey (e.g. arthropods) during the winter and we, therefore, suggest that positive selection of structurally diverse shrub vegetation by all the studied birds during the winter may be a defence against predators (e.g. Tobolka 2011). Structurally diverse canopy may minimize detection and predation risk by avian and mammalian predators, such as Eurasian Sparrowhawk Accipiter nisus and domestic cat Felis catus, which are the main predators of the studied species in Europe (Barnard, 1980, Churcher and Lawton, 1987; Bell et al. 2010). Furthermore, the habitat preference of the House Sparrow for dairy farms could, besides the benefit of high resource availability, also be connected with antipredator behaviour and thermal conditions within the farmsteads. For example, Barnard (1980) found that predation risk was apparently much lower within the farm buildings than in open fields where House Sparrows paid high attention to scanning for predators at the expense of feeding behaviour. Dairy farms may thus provide relatively predator-safe places against avian and mammalian predators. Last but not least, the farm buildings used for cattle breeding may play an important role for House Sparrows when roosting during the winter due to the higher temperature and the constant microclimatic conditions created by livestock (Pinowska et al. 1976). Winter is the most critical season for non-migratory farmland birds in temperate zones and reducing energy demands connected with roosting in farm buildings with higher and stabile microclimatic conditions may result in a higher survival rate. Moreover, it has been demonstrated that House Sparrows in heated farm buildings may also breed during winter (Snow, 1955, Kozák, 1988). The House Sparrow was the only species which frequently occurred inside dairy farms, whereas the Tree Sparrows and Collared Doves were recorded in close vicinity to or at farm buildings. These findings were also confirmed using intensive bird ringing inside and outside dairy farms during the year (Šálek, unpublished data). These preliminary data show a substantial increase of captured Tree Sparrows in the vicinity of dairy farms during autumn and winter months. Only four individuals were caught during the summer period (June–August), but 147 individuals were caught during winter (November–January), which just underlines the importance of dairy farms for Tree Sparrows during the winter period.

Arable and grassland habitats, as well as houses in these habitats, were avoided by all the studied species. A negative association of birds with these habitats could be associated with low food resource availability and higher predation pressure (see above and Tobolka 2007). In particular, most grasslands habitats in our study area are intensively used hayfields which are cut more than twice per year which leads to their homogenization and to low seed availability (Šálek & Lövy 2012). Moreover the unavailability of food is more pronounced during the periods of snow cover. Similarly arable land is mainly used for intensive cultivation of autumn sowing cereals and oilrape, or is composed of ploughed fields with a small proportion of cereal stubbles and weedy patches. Finally, due to the altitudinal gradient of rural settlements across the territory of the Czech Republic we tested the effect of altitude on the abundance of studied granivorous species. Although the centre of distribution of all the studied species is mostly situated in lowland habitats, and their population densities decrease towards higher altitudes (Šťastný et al. 2006), we found a negative correlation between abundance and altitude only in the House Sparrow (see also Bejček et al. 1995). These results are in concordance with the study by Jasso (2003) who found an increasing density of House Sparrow populations in a gradient from submontane (0 ind./10 ha) to lowland (33.2–129.2 ind./10 ha) rural settlements in the Czech Republic and Slovakia.

Conclusions

In conclusion, our results indicate the great value of habitats with high food resource availability as a crucial factor for granivorous birds during winter and, in particular, we highlight the importance of dairy farms and poultry keeping for the occurrence of the study species in the rural environment. The positive influence of animal husbandry and dairy farms was previously reported for the studied species (Bejček et al., 1995, Väisänen and Solonen, 1997Saether et al., 1999, Hole et al., 2002, Jasso, 2003, Ringsby et al., 2006, Šťastný et al., 2006, Griesser et al., 2011, Liu et al., 2013) as well as for other farmland birds which are the subject of conservation concern (Møller, 2001, Wretenberg et al., 2007, Ahnstrom et al., 2008, Hiron et al., 2013). Based on the number of occupied quadrants, the study species slightly decreased between two national atlas mappings in the Czech Republic during 1985–1989 and 2001–2003 (Šťastný et al. 2006). The number of occupied quadrants between the two mappings decreased by 3% in House Sparrow, 4% in Tree Sparrow and 6% in Collared Dove. However, based on these two mappings, greater change was reflected in overall population size resulting in decline of House Sparrow numbers by 7%, Tree Sparrow numbers by 20% and Collared Dove numbers by 15% (Reif et al. 2009). Based on our results, we believe that the population declines could be connected with a decline in the amount of poultry keeping and dairy farming (see also Väisänen and Solonen, 1997, Tiainen and Pakkala, 2001; Ringsby et al. 2006). Changes in farming practices and socioeconomic status in rural landscapes during the last 50 years are characterized by a massive reduction in dairy farming and the amount of animal breeding. For example, long-term data show that during 1961–2012 the number of cattle bred in the Czech Republic decreased by 55.3% and the number of hens kept decreased by 69.2% (Czech Statistical Office, unpublished data). Similarly, during 2000–2010 the number of farming enterprises with cattle decreased by 29%, which is similar to the situation in other parts of Europe (Wretenberg et al., 2007, Hiron et al., 2013). Moreover, increased farmyard cleanliness has led to reduced grain spillage around dairy farms and the implementation of a European Union hygiene law connected with bird-proof grain storage has also had a direct effect on food availability for a number of granivorous species (O’Connor and Shrubb, 1986, Crick and Siriwardena, 2002Hole et al., 2002, Robinson and Sutherland, 2002Vincent, 2005, Anderson, 2006, Vepsäläinen, 2007, Hiron et al., 2013). Similarly, the widespread reduction in the number of poultry keepings with free range chickens and other domestic animals, across rural areas has led to a decreased availability of grain (Vincent 2005). Effective large-scale conservation of granivorous farmland birds in rural areas should thus consider management measures which enhance food availability during the winter.

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Appendix A. Supplementary data

Appendix 1 Multiple preference comparisons among habitat types for the studied species (House Sparrow, Tree Sparrow, Collared Dove). Each mean element in table was replaced by its sign; tripled signs represent significant deviation from random at $P < 0.05$. The signs indicate whether the habitat category in the rows is significantly used more or less than the habitat type in the columns.

House Sparrow	Shrubs	Houses	Dairy farms	Poultry	Arable land	Grasslands
Shrubs	0	+++	+	---	+++	+++
Houses	---	0	---	---	+	+++
Dairy farms	-	+++	0	---	+++	+++
Poultry	+++	+++	+++	0	+++	+++
Arable land	---	-	---	---	0	+++
Grasslands	---	---	---	---	---	0

Tree Sparrow

	Shrubs	Houses	Dairy farms	Poultry	Arable land	Grasslands
Shrubs	0	+++	+	-	+++	+++
Houses	---	0	---	---	-	+
Dairy farms	-	+++	0	---	+++	+++
Poultry	+	+++	+++	0	+++	+++
Arable land	---	+	---	---	0	+++
Grasslands	---	-	---	---	---	0

Collared Dove

	Shrubs	Houses	Dairy farms	Poultry	Arable land	Grasslands
Shrubs	0	+++	+++	+++	+++	+++
Houses	---	0	---	---	---	+++
Dairy farms	---	+++	0	-	+++	+++
Poultry	---	+++	+	0	+++	+++
Arable land	---	+++	---	---	0	+++
Grasslands	---	---	---	---	---	0

Chapter II

Species-specific breeding habitat association of declining farmland birds within urban environment: conservation implications

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Species-specific breeding habitat association of declining farmland birds within urban environments: conservation implications

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Abstract

Human settlements represent important year-round habitats for many declining farmland birds; however, detailed knowledge of species-specific habitat associations is crucial for effective conservation of individual species. In this study, we examined the effect of environmental factors on the occurrence, population density, and habitat associations of three sedentary granivorous farmland bird species (house sparrow *Passer domesticus*, tree sparrow *Passer montanus*, and Eurasian collared dove *Streptopelia decaocto*) during the breeding season within an urban environment and compared the results with a previously published study carried out during winter. To fulfil our aims, we used a comprehensive dataset from a nation-wide monitoring program focused on the studied species in the Czech Republic covering the period 2010–2016 and including a total of 162 human settlements (330.3-km length of transect). House sparrow was the most numerous and common species recorded on the studied transects, followed by tree sparrow and Eurasian collared dove. The population density of house sparrows and Eurasian collared doves was positively correlated with the proportion of farmsteads, and the population density of tree sparrows was positively correlated with proportion of grasslands. The occurrence of house sparrows and Eurasian collared doves increased with higher proportion of buildings and small-scale farms, whereas occurrence of tree sparrows increased with higher proportion of small-scale farms and woody plants. Habitat preference analyses demonstrated that house sparrow and Eurasian collared dove primarily preferred buildings, and tree sparrows preferred small-scale farms. Arable habitats were generally avoided by all studied species. Based on species-specific occurrence and habitat associations, several management measures may be adopted to support declining populations of the studied species, as well as whole bird communities inhabiting urban environments.

Keywords: Habitat selection, Farmsteads, Small-scale farming, Building modernization, Nesting, Urbanization

Introduction

In Europe, there has been an alarming population decline in common bird species reported, with more than 400 million birds lost during the last three decades (Inger et al. 2015). Farmland birds represent the most heavily affected group (Donald et al. 2001; Inger et al. 2015) and show a population decline of 57% during the last 38 years, whereas the population trend for common forest birds is relatively stable (PECBMS 2020). There is growing evidence that substantial proportion of declining farmland birds is now aggregated in urban environment, such as villages or farmsteads, and therefore may represent bird diversity hotspots in rural landscapes, including the species of conservation concern (Rosin et al. 2016; Šálek et al. 2018). For many sedentary farmland birds, such as house *sparrow Passer domesticus* and tree sparrow *Passer montanus* or Eurasian collared dove *Streptopelia decaocto*, human settlements have been described as the most important breeding and overwintering habitats within intensively used agricultural landscapes (Summers-Smith 1988; Hancock and Wilson 2003; Summers-Smith 2003; Jokimäki and Kaisanlahti-Jokimäki 2012; Rosin et al. 2016). However, despite many species adapted to urban environments, urbanization process has profound effect on bird communities due to contrasting availability of crucial foraging and breeding opportunities. For example, habitat structure of urban environment (e.g., representation of urban green areas, Šálek et al. 2015a, 2021), management of individual habitats (e.g., presence of active farming management, Šálek et al. 2015b, 2018) or rural development, and socio-structural changes in human settlements (e.g., level of new housing and modernization of rural properties, Shaw et al. 2008; Rosin et al. 2020; Żmihorski et al. 2020) may have a profound effect on the occurrence, abundance, and species richness of birds within urban ecosystems, and such factors are therefore essential for effective bird conservation and management efforts.

Selection of suitable winter and nesting habitats is crucial for the majority of sedentary birds due to its importance for survival and breeding performance (Siriwardena et al. 2000, 2001; Hinsley and Bellamy 2000; Moorcroft et al. 2002). However, as bird habitat selection may markedly differ across seasons, it is crucial to evaluate its year-round changes in habitat preference (e.g., Šálek et al. 2018). More specifically, in comparison to winter when species occurrence is mainly concentrated in the vicinity of crucial food resources (Vangestel et al. 2010; Šálek et al. 2015b), other factors may influence their fine-scale distribution during the breeding period (Field and Anderson 2004; Wilkinson 2006; Šálek et al. 2015a). For example, distribution and population numbers of house and tree sparrow during the breeding seasons are primarily focused on habitats with the increased availability of invertebrates, which represent the main food source for offspring (Vincent 2005; Šťastný and Hudec 2011). In particular, house sparrows in urban populations prefer localities with higher representation of (semi)natural habitats, such as parks, gardens, patches of derelict land, and horticultural fields (Wilkinson 2006; Chamberlain et al. 2007; Murgui 2009; Šálek et al. 2015a). Moreover, during the breeding period, the distribution of individual species is linked with the availability of suitable nesting opportunities (Newton 1994), and therefore habitat selection by sparrows may be primarily driven by the availability of foraging habitats in close vicinity to nesting structures (Šálek et al. 2015a). For species nesting in cavities within buildings, such as house sparrows, the effect of modernization of buildings may reduce the number of nesting sites (Rosin et al. 2020), which may result in a lower density of house sparrows at localities with a higher proportion of new or modernized settlements or in new residential areas (Summers-Smith 2009; Moudrá et al. 2018). In Central European region, the expansion of newly built residential areas and the increasing rate of modernization of older buildings in recent decades is obvious (Rosin et al. 2020; Moudrá et al. 2018). In combination with other factors linked with increasing human socioeconomic status (such as replacing old farmsteads and homesteads with new ones or abandonment of traditional backyard poultry and small-scale farming), this may have an important impact on the populations of farmland birds in urban environment (Shaw et al. 2008; Rosin et al. 2016).

The main objective of this study was to examine the effect of environmental factors on the occurrence and population density of three sedentary granivorous farmland bird species (house sparrow, tree sparrow, and Eurasian collared dove) during the breeding season within the urban environment and compare the results with a previously published study carried out during winter (Šálek et al. 2015b). The European populations of both sparrows significantly declined by approximately 63% (for house sparrow) and 65% (for tree sparrow), whereas the population of Eurasian collared dove increased by about 83% during 1980–2017 (PECBMS 2020). In general, we expected that the importance of farmsteads and small-scale farming (poultry keeping) on the population numbers of both sparrow species will be lower, and utilization of shrubs and trees will be higher during the breeding season compared to winter. We also examined the effect of new residential areas (we expect preference for older residential areas) and the proportion of shrub and tree coverage (we expect a preference for a higher proportion of this habitat) on the occurrence of both species.

Material and methods

Bird surveys

Data on distribution and population density of the studied bird species (house sparrow, tree sparrow, and Eurasian collared dove) within human settlements were obtained from a nation-wide volunteer survey in the Czech Republic (Central Europe). A total of 162 human settlements (Fig. 1a), especially smaller towns and rural settlements, were surveyed. The surveys were carried out once between 20th of April and 20th of May during the years 2010–2016 to cover the main nesting period of the studied species in Central Europe (Hudec and Šťastný 2005; Šťastný and Hudec 2011), and to avoid the registration of newly fledged individuals (Šálek et al. 2015a). The birds were surveyed using transect walks which is a widely used and effective method for identifying distribution and population numbers of these bird species (Vincent 2005; Chamberlain et al. 2007) and was previously successfully applied within the urban environment (e.g., Šálek et al. 2015a, b). The observers were asked to walk slowly (< 3 km/h) and to census birds within a 40-m buffer on both sides along transects, including all available roads, streets, pavements, and pathways. The study transects led through all available habitats within human settlements, including artificial habitats (e.g., buildings, roads), agriculture infrastructure (e.g., farmsteads), (semi)natural habitats (gardens, orchards), or cultivated habitats (e.g., arable habitats, grasslands). The surveys were conducted during the highest bird activity in the morning hours (06:00 to 11:00 CEST) under favorable weather conditions (without heavy rain, strong wind, or mist). The position, number, and habitat use of seen or heard individuals were recorded on digitalized satellite pictures (1: 5000, Seznam Maps 2018). Furthermore, during the fieldwork, the occurrence of small-scale farms and farmsteads was recorded (see also Šálek et al. 2015b).

Environmental characteristics

To evaluate species-specific environmental factors influencing population density, we monitored habitat composition within a 40-m buffer on both sides along each transect (Fig. 1b, c). The proportion of individual habitats was evaluated using digitalized satellite pictures in the GIS environment (QGIS Development Team 2017). In particular, we recorded the proportion of woody plants (shrubs and trees), grasslands, arable habitats, buildings, artificial surface, small-scale farms (i.e., poultry, sheep, cattle, and horses with < 10 individuals) and farmsteads (Table 1). The representation and proportion of newly built-up areas and newly built houses (e.g., new properties built before 2003) within each settlement/transect was calculated based on a comparison of recent (2016) and older (2003) satellite pictures (Seznam Maps 2018). Both age categories (i.e., built before vs. after 2003) were separated in the GIS environment (QGIS Development Team 2017). Finally, the length of the individual transects, and the altitude of their centroid within each locality was calculated in the GIS environment (QGIS Development Team 2017).

To uncover the fine-scale habitat association of individual species, we evaluated the proportion of different habitats and the age of buildings (see above) within a 25-m buffer around the position of observed birds (Fig. 1b, c). We generated the same number of random points (according to the number of used records for house and tree sparrow, and Eurasian collared dove within individual settlements) using GIS tool Random Point Generator (QGIS Development Team 2017) that were randomly spread over the area of individual transects (Fig. 1c). Within each buffer, we assessed the proportion of the abovementioned habitats using GIS environment (QGIS Development Team 2017).

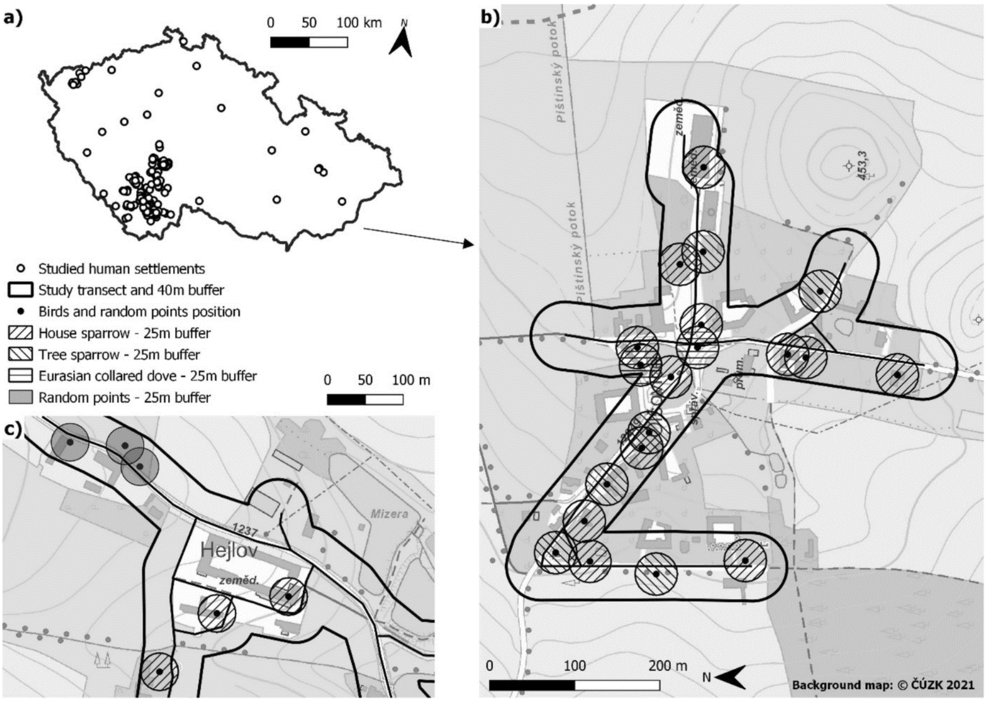

Fig. 1 Map of (a) positions of 162 studied localities across the Czech Republic. (b) Example of small-size human settlement with study transect and 40-m buffer on both sides along the transect and positions with 25-m buffer around recorded individuals of all three studied species. (c) Detail of part of the human settlement with 25 m buffers around house sparrow records and generated random points

Table 1 Descriptive statistics of habitat characteristics around transects within studied human settlements (n = 162 villages)

Variable	**Mean ± s.d.**	**Range**
Altitude (m a.s.l.)	482.58 ± 127.37	177.89–1050.45
Transect length (m)	2038.90 ± 1858.15	259–10,025
Number of small-scale farms (n)	4.38 ± 4.79	0–31
% of buildings	0.15 ± 0.04	0.06–0.32
% of woody plants	0.00 ± 0.02	0.00–0.20
% of small-scale farms	0.01 ± 0.01	0.00–0.15
% of farmsteads	0.01 ± 0.02	0.00–0.08
% of arable habitats	0.09 ± 0.08	0.00–0.39
% of artificial surfaces	0.14 ± 0.04	0.02–0.37
% of grasslands	0.60 ± 0.09	0.38–0.84
% of new buildings	0.03 ± 0.05	0.00–0.40

Statistical analyses

Two datasets (1—settlement-level dataset and 2—species occurrence level dataset) were used to assess the effect of environmental factors on the population densities and occurrence of studied species: (1) settlement level dataset including population density (inds./100 m of transect) of studied species within a human settlement (n = 162) and (2) species occurrence level dataset including locations and random points of studied species within a human settlement: house sparrow (n = 1607 points, mean ± s.d., 3.72 ± 3.98 inds./point), tree sparrow (n = 339 points, 2.85 ± 4.07 inds./point), Eurasian collared dove (n = 268 points, 1.85 ± 1.42 inds./point), and absence of species (n = 2366 random points). The effect of environmental factors was calculated using variance partitioning by principal coordinate analysis of neighbor matrices (PCNM) in Canoco 5 software (ter Braak and Šmilauer 2012), the method recommended by

Marrot et al. (2015). This multivariate analysis enabled us to separate the effect of space predictors (i.e., geographical position) from the effect of primary predictors (Legendre and Legendre 2012). The analysis is suitable for calculating inter-correlated variables since all these variables enter the analysis simultaneously. The analysis included nine steps: (1) primary predictor test (i.e., preliminary test of the overall effect of primary predictors on the dataset), (2) primary predictor selection by partial redundancy analysis (RDA) using forward selection based on partial Monte-Carlo permutation tests, (3) principal coordinate analysis (PCoA) based on Euclidean distances (i.e., finding the main space predictors based on GPS coordinates), (4) PCNM for all predictors (i.e., preliminary test of the overall effect of space predictors on the dataset), (5) PCNM selection (i.e., the choice of space predictors based on coordinates using forward selection and partial Monte-Carlo permutation tests), (6) spatial effects analysis (i.e., assessing the amount of variability explained by space predictors), (7) primary predictor effects analysis (i.e., assessing the amount of variability explained by primary predictors), (8) joint effects analysis (i.e., assessing the amount of variability explained by both predictor types), and (9) removal of spatial effects (Šmilauer and Lepš 2014). The following factors for each point/settlement were used as environmental variables: altitude (m a.s.l.), proportions for the cover of woody plants, grasslands, arable habitats, buildings, new buildings, artificial surface, small-scale farms, and farmsteads. In the case of the settlement-level dataset, we used also the number of poultry yards. The proportion of water area was excluded from the analyses, as this habitat does not represent a suitable environment for the studied species. Statistical significance was obtained by Monte-Carlo permutation tests under 499 permutations. Correlations among proportions of individual habitats within the settlement-level dataset were calculated using Spearman rank correlations in Statistica 13 (TIBCO Software Inc. 2017). Moreover, for chosen settlements, we compared the population densities of each species among study years (2010–2012). However, we did not find significant differences among years (Table S1). Similarly, we did not find differences in species densities between the first and second visit within 1 year for chosen settlements (Table S2).

The R statistical software (R Development Core Team 2009) with the package Adehabitat (Calenge 2006) was used to compute compositional analysis of habitat selection. We used a randomization test with 500 repetitions. Habitat that was not found within the particular category (zero values in the entry data matrix) was replaced by 0.01 (Aebischer et al. 1993). A data unit was represented by each species occurrence/random point. For each point, we computed percentages of each habitat category available (proportion of area surrounding the point). Compositional analysis was performed for all three bird species separately. This analysis was carried out in two steps. First, the significance of habitat use was tested (using a Wilks lambda). Then, a ranking matrix was built, indicating whether the habitat category in the rows is significantly used more or less than the habitat type in the columns. Furthermore, habitats were sorted from most preferred to non-preferred (Aebischer et al. 1993). The relationships between the overall proportion of habitat available (proportion of habitat area) and habitat used (proportion of individuals recorded in particular habitat) were expressed by log2 (used/available) after Sunde et al. (2001).

Results

In total, we recorded 7438 individuals of three studied species, from which house sparrow was the most numerous species (80.4%, n = 5977), followed by tree sparrow (13.0%, n = 965) and Eurasian collared dove (6.7%, n = 496). Consequently, house sparrow had the highest mean population density (± s.d., range) in the studied transects (2.44 ± 1.92/100 m, 0.00–14.39/100 m), followed by tree sparrow (0.55 ± 0.85/100 m, 0.00–5.33/100 m), and the lowest population density was recorded in Eurasian collared dove (0.18 ± 0.27/100 m, 0.00–1.79/100 m).

Based on the settlement level dataset, population densities of studied species were explained mainly by environmental factors (8.8% of variability), less by geographical position (7.8%), and shared fraction was 2.8% (Table 2). The first and second ordination axes together explained 98.3% of variability. Population density of house sparrow and Eurasian collared dove was positively correlated with each other as well as with the first ordination axis (correlation coefficient 0.95 and 0.14, respectively). The population density of tree sparrow was negatively correlated with the second ordination axis (− 0.49). The proportion of farmsteads was positively correlated (0.36) and proportion of grasslands was negatively correlated (− 0.16) with the first ordination axis. The effect of grasslands was indicative (Table 2). Altitude represented an independent gradient that negatively correlated with the first (− 0.30) and positively correlated with the second ordination axis (0.23). Population density of house sparrows and Eurasian collared dove was positively correlated with the proportion of farmsteads (Spearman rank correlations, house sparrow: $r_s = 0.30$, $P < 0.05$, Eurasian collared dove: $r_s = 0.26$, $P < 0.05$). Tree sparrow population density was independent of the other species (Fig. 2a) and was associated with grasslands. Further analyses showed that altitude was negatively correlated with proportion of buildings and artificial surfaces, and positively correlated with proportion of grasslands. We also found that proportion of farmsteads was negatively correlated with proportion of grasslands and positively with proportion of artificial surfaces (Table S3).

Based on the species occurrence level dataset, the occurrence of the studied species was explained by environmental factors (2.3% of variability) as well as by geographical position (0.6%, Table 2) and shared fraction was lower than 0.01%. The first and second ordination axes together explained 95.7% of variability. The proportion of buildings was positively correlated (correlation coefficient 0.84), and the proportion of arable habitats was negatively correlated (− 0.23) with the first ordination axis. The proportion of grasslands and woody plants was negatively correlated with the second ordination axis (− 0.45 and − 0.66 respectively). The proportion of small-scale farms was negatively correlated with the proportion of arable habitats (Spearman rank correlation, $rs = 0.25$, $P < 0.05$, Fig. 2b). Proportions of artificial surfaces and farmsteads were positively correlated with the first (0.47 and 0.42 respectively) and second (0.52 and 0.56 respectively) ordination axis. House sparrows and Eurasian collared dove often occurred at the same points, and they occurred at points with an increased proportion of buildings and small-scale farms. Tree sparrows occurred at points with an increased proportion of small-scale farms and woody plants. Random points were located mainly at points with an increased proportion of arable habitats (Fig. 2b). Comparison of median values and ranges (min-max) showed that the most pronounced differences between buffers for presence and random points were found in proportions of buildings. These values especially differed in house sparrow (Table S4). Medians for other habitats did not differ markedly; however great differences in maximal values were found. The greatest difference between points with presence and random points in maximal values was found for farmsteads in Eurasian collared dove, where the maximal proportion of this habitat was higher by 44.1% within points with species presence compared with random points. Similarly, the greatest maximal value of proportion of small-scale farms was found in house sparrow, i.e., the maximal value within points for species presence was increased by 36.1% compared to random points.

Regarding the tree sparrow, the greatest difference was found for proportions of artificial surfaces and small-scale farms. Proportion of small-scale farms was higher for points with species presence for 23.1%, and proportion of artificial surfaces was increased within random points by 25.9% (Table S4).

Table 2 The effect of environmental and spatial variables on studied species population density (inds./100 m, i.e., settlement level dataset) and occurrence (i.e., species occurrence level dataset). PCNM analyses with forward selection of variables, PCO variables represent spatial predictors based on geographical coordinates

Dataset	**Explanatory variable**	**Pseudo-F**	**P**
Villages	Farmsteads (%)	13.50	0.002
	Altitude (m a.s.l.)	7.60	0.004
	Grasslands (%)	2.30	0.110
	PCO 2	17.40	0.002
	PCO 9	3.50	0.052
Points	Arable habitats (%)	51.40	0.002
	Buildings (%)	23.00	0.002
	Small-scale farms (%)	17.00	0.002
	Artificial surfaces (%)	10.50	0.002
	Farmsteads (%)	6.40	0.002
	Woody plants (%)	3.70	0.012
	Grasslands (%)	2.80	0.036
	PCO 78	12.80	0.002
	PCO 52	6.40	0.004
	PCO 12	5.90	0.004
	PCO 125	5.50	0.002
	PCO 3	5.20	0.004

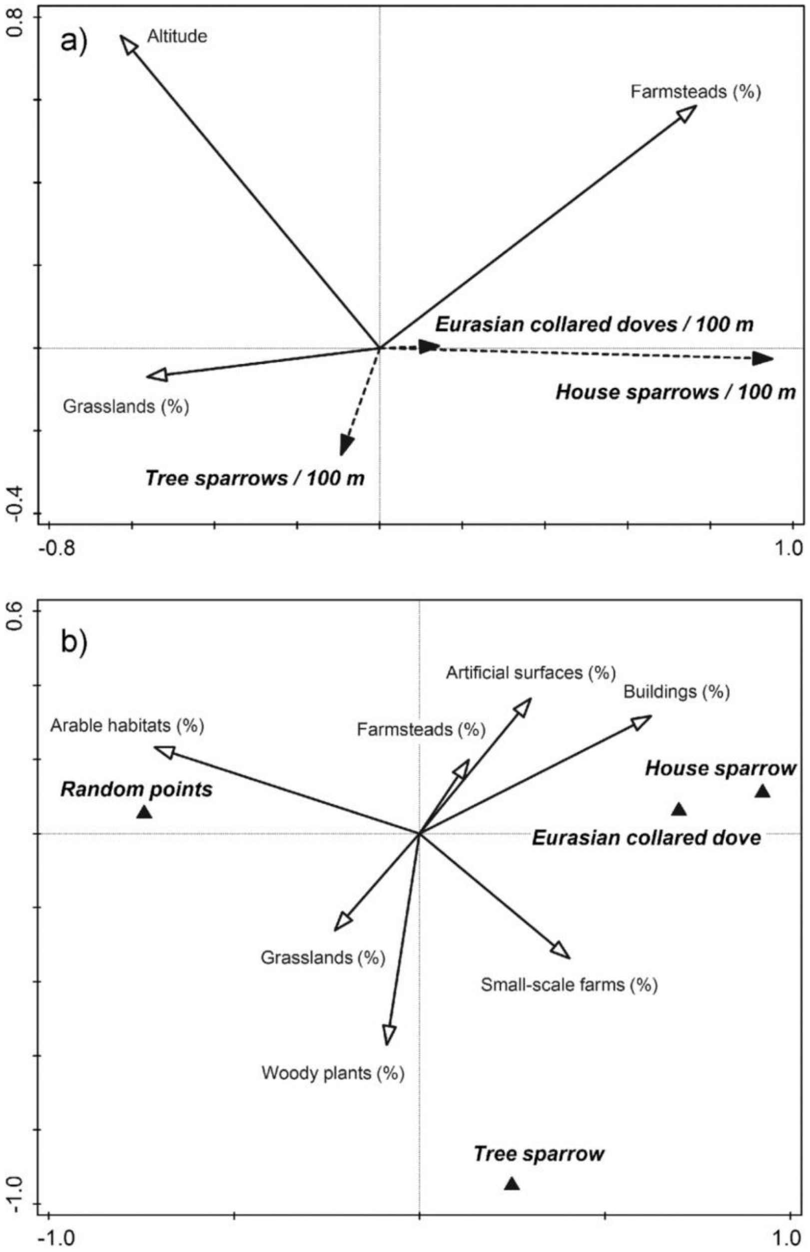

Fig. 2 Projection scores for (a) population densities of studied species per 100 m of transect and (b) occurrence of species and random points in relation to environmental factors. PCNM analyses, I and II ordination axes together explain 98.3% and 95.7% respectively

We found significant differences between the habitat composition of occupied and random points in all studied species (compositional analyses, house sparrow: Wilk's lambda λ = 0.85, P = 0.002; tree sparrow: Wilk's lambda λ = 0.95, P = 0.004; Eurasian collared dove: Wilk's lambda λ = 0.91, P = 0.002). Habitat ranking showed that buildings were the most preferred habitat in house sparrow and Eurasian collared dove. However, these species differ in the order of preferred habitats (habitat ranking, house sparrow: buildings>small-scale farms>artificial surfaces>woody plants>grasslands >farmsteads>arable habitats, Eurasian collared dove: buildings>farmsteads >woody plants>artificial surfaces>grasslands>small-scale farms>arable habitats). Tree sparrows clearly preferred small-scale farms (habitat ranking: small-scale farms>buildings>woody plants>grasslands>farmsteads>artificial surfaces>arable habitats). Based on the index of selectivity, we recorded clear avoidance of arable habitats in all studied species. Simultaneously, small-scale farms were the most preferred habitat by both sparrows and less by Eurasian collared dove. Farmsteads and buildings were preferred by house sparrow and Eurasian collared dove (Fig. 3).

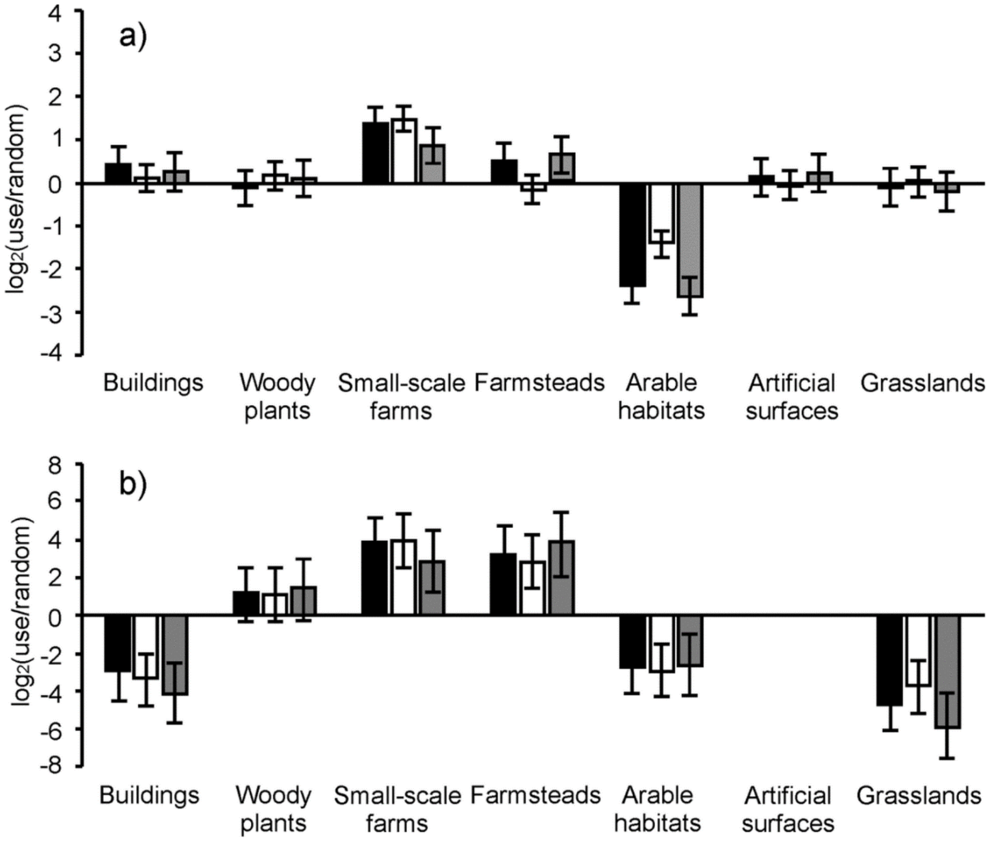

Fig. 3 Habitat selectivity index (± s.d.) of studied species for each habitat type during breeding (a) and winter period (b), see Šálek et al. 2015b. Black columns—house sparrow, white columns—tree sparrow, grey columns—Eurasian collared dove. Artificial surfaces were not investigated during the winter period

Discussion

Our study, which is based on a comprehensive nation-wide research on breeding distribution and population numbers of three sedentary farmland species inhabiting urban environments, demonstrated that (i) house sparrow was the most numerous and common species at studied transects, followed by tree sparrow and Eurasian collared dove, and in comparison with winter, breeding population densities were lower for all studied species, (ii) based on the settlement level dataset, population densities of house sparrows and Eurasian collared doves were positively correlated with proportion of farmsteads, and population density of tree sparrows was positively correlated with proportion of grasslands, (iii) based on the species occurrence level dataset, house sparrows and Eurasian collared doves occurred at points with an increased proportion of buildings and small-scale farms, whereas tree sparrows occurred at points with an increased proportion of small-scale farms and woody plants. Finally, (iv) we found that house sparrow and Eurasian collared dove primarily preferred buildings, and tree sparrow preferred small-scale farms, whereas arable habitats were generally avoided by all studied species.

In comparison with the winter census (Šálek et al. 2015b), the population densities of studied species were lower during the breeding period (cf. population density during breeding and winter season: house sparrow 2.44 ± 1.92/100 m vs. 4.32 ± 4.67 inds./100 m, tree sparrow 0.55 ± 0.85/100 m vs. 1.83 ± 3.53 inds./100 m, and Eurasian collared dove 0.18 ± 0.27/100 m vs. 0.72 ± 1.51 inds./100 m). The most plausible explanations for lower population density during the breeding period may be associated with the more scattered distribution of the studied species during breeding in combination with secretive behavior of individuals during nesting and generally higher concealment during the vegetation period. Firstly, in comparison with winter, when birds are concentrated in larger flocks around crucial feeding resources (Jasso 2003; Vangestel et al. 2010; Šálek et al. 2015b; Ciach and Fröhlich 2017), during the breeding season, individual birds are defending breeding territories and therefore their distribution is mainly situated in the vicinity of nest sites which may lead—in combination with high inter or intra specific competition for nesting—to a more uniform distribution across larger spatial scales. Moreover, the core area of some species distribution (e.g., tree sparrow) during the nesting period may be situated outside the urban environment, especially within (semi)natural habitats in the agricultural landscape (Zhang and Zheng 2010; Šťastný and Hudec 2011). Finally, some birds may already be involved in nesting behavior (e.g., incubation) and due to the progress in the vegetation period shrubs and trees have leaves, thus making it is more difficult to spot birds. All these factors may ultimately lead to underestimation of general population numbers during the breeding period. However, in general, most of the similar studies conducted in the urban environment struggle in the interpretation of results due to various bird detectability across individual habitat types in urban landscape which differ depending on the number of barriers such as buildings, fences, or background noise (see Šálek et al. 2015a). The detection probability of the studied species is generally lower in built-up areas (e.g., backyard spaces, inner blocks, or inaccessible industrial areas) compared to more open parts of settlements with unlimited access (e.g., parks and unfenced gardens, orchards, lawns, and streets). Similarly, farmsteads and small-scale farms belong to habitats with limited accessibility. To reduce potential bias in detectability in individual habitats, we surveyed birds (and habitat composition) only within a 40-m buffer on both sides along each transect (see also Šálek et al. 2015b). Such buffer size also reduces overlap with non-urban habitats (such as arable fields or forests) that are not considered as suitable habitats for the studied species (Šálek et al. 2015b). In conclusion, despite the mentioned limitations, our data are fully comparable with previous studies on studied species in urban environment.

Farmsteads were the most important and preferred habitat for the house sparrow and Eurasian collared dove, which is in line with previous research during the breeding (Saether et al. 1999; Hole et al. 2002; Ringsby et al.

2006; Griesser et al. 2011; Liu et al. 2013) and winter season (Šálek et al. 2015b; Šálek et al. 2018). In particular, human settlements with farmsteads have more abundant populations of house sparrow (Chamberlain et al. 2007) and exhibit a slower declining trend in comparison with localities without farmsteads (Erskine 2006). The slower population decline is probably partially linked with increased survival and breeding productivity due to better conditions for house sparrows and Eurasian collared doves in farmsteads (Hole et al. 2002; Liker et al. 2008; Seress et al. 2012). Recent evidence clearly indicates that farmsteads represent current strongholds of farmland bird distribution within the agricultural landscape, including species of conservation concern (Hiron et al. 2013; Rosin et al. 2016; Šálek et al. 2018). Farmsteads provide high-quality food for granivorous birds, such as a plant remains, cereal grains (grain mixtures for animals), and plant material within silage pits (Jasso 2003; Šálek et al. 2015b). They also offer increased diversity and abundance of invertebrate prey connected with cattle breeding, manure heaps, or silage stores (Møller 2001; Šálek and Żmihorski 2018; Šálek et al. 2018; 2020). Moreover, farm buildings, such as barns, hen houses, or stables provide high diversity of various nesting places for cavity breeding species (Šálek et al. 2016), including house and tree sparrows (Šálek et al. 2018).

We recorded the positive effect of the presence of small-scale farms on the occurrence of tree sparrow, and habitat selection analysis showed that all studied species have a general preference for small-scale farms (see also Jasso 2003; Šálek et al. 2015b; Moudrá et al. 2018). This result is in concordance with the winter census which showed that the occurrence of house and tree sparrow and the habitat selection of all studied species were significantly affected by the number of small-scale farms within the locality (Šálek et al. 2015b, see also Fig. 3). Similarly, Daniels and Kirkpatrick (2006) have suggested that the presence of poultry yards have a positive effect on the abundance of the whole bird community. Poultry yards may represent stable and energy-rich food resources for the adults, especially due to cereal grains and artificial food given to poultry (Šálek et al. 2015b).

Thanks to easy access to this food source, the adults may invest more time in searching for invertebrates for nestlings. Moreover, cereal grains and artificial food can also be delivered to the nest as food for nestlings. An increased proportion of artificial food in the diet of nestlings may indicate a general lack of invertebrate prey and may ultimately result in the starvation of nestlings (Vincent 2005; Peach et al. 2008).

Woody plants, represented by shrubs and trees, were positively selected by the tree sparrows. In contrast to previous studies, we did not find a positive association of the house sparrow with this habitat (e.g., Pinowska et al. 1999; Field and Anderson 2004; Vincent 2005; Wilkinson 2006; Zhang and Zheng 2010). The highest numbers of both sparrow species in Central-European urban environment were found in squares with approximately 50% of green-space cover, including woody plants (Šálek et al. 2015a). Especially during the breeding season, protein-rich insect food is crucial for rising chicks (Vincent 2005; Anderson 2006; Peach et al. 2008) as well as prey for adults (Anderson 2006; Šťastný and Hudec 2011). In comparison with artificial habitats, such as roads or buildings, the insect abundance within woody plants is markedly higher (Summers-Smith 2009). Therefore, a higher representation of woody habitats within an urban environment leads to greater food availability and even a small reduction in natural habitats may have a substantial effect on distribution and abundance of sparrows (Shaw et al. 2008) and other birds (Threlfall et al. 2016). Moreover, woody plants, especially within gardens and parks, may represent the main nesting and roosting place for the Eurasian collared dove (Šálek 2014).

House sparrow and Eurasian collared dove occurrence was linked to an increased proportion of buildings, which was also confirmed by the habitat analysis. The preference for buildings by the house sparrow and Eurasian collared dove is in contrast with the results from the winter census, when all three species avoid this habitat (Šálek et al. 2015b). The change in habitat affinity may be generally linked with nesting of the studied species within buildings. In particular, buildings are the primary nest sites of house sparrows (Anderson 2006; Summers-Smith 2009; Šťastný and Hudec 2011), and they are also frequently used for nesting by the Eurasian collared dove (Hudec and Šťastný 2005). In contrast, previous studies have found that house sparrow numbers did not correlate with the increasing proportion of built-up area (Šálek et al. 2015a), or was lower in human settlements, where urbanization reached its peak (Murgui 2009; Evans et al. 2009; Nath et al. 2019). A similar pattern was found for the Eurasian collared dove (Evans et al. 2009). These contrasting results may be explained by the fact that the localities studied in our research are mainly represented by moderately urbanized areas (i.e., rural settlements and small towns), where the house sparrows may benefit from a balanced combination of nesting (buildings) and foraging habitats. In contrary, the tree sparrow predominantly nests in natural cavities in trees, or in nest boxes (Šťastný and Hudec 2011; von Post and Smith 2015). Furthermore, the tree sparrow is more abundant in urban edges or rural habitats compared to house sparrow, which may explain its lower population densities in places with a higher proportion of buildings.

Surprisingly, we did not find an effect of new residential areas on population numbers of the studied species. This finding is in contrast with the results of Šálek et al. (2015b), who documented between five- and seven-times smaller population densities of house and tree sparrows in new residential areas compared to residential areas older than 30 years. The same trend has been confirmed by other previous studies for house sparrows (Siriwardena et al. 2002; Vincent 2005; Brichetti et al. 2008; Summers-Smith 2009; Moudrá et al. 2018) or the whole bird community (Rosin et al. 2020). The accepted explanation of this result is that the older houses can offer more diverse and abundant nesting opportunities (Mason 2006; Shaw et al. 2008; Węgrzynowicz 2012; Šálek et al. 2015a). However, Angelier and Brischoux (2019) also documented that house sparrow populations are probably not constrained by a lack of nesting sites in medium-sized human settlements. In particular, the house sparrow is very flexible in nest site selection (Anderson 2006; von Post and Smith 2015; Sheldon and Griffith 2017). Therefore, newly developed areas can be used by house sparrows more frequently than is expected; however, this topic needs future detailed research.

General avoidance of arable habitats by all studied species and grasslands in the case of house sparrow and Eurasian collared dove is in accordance with species preference within the winter period (Šálek et al. 2015b). Arable habitats provide low availability of food resources throughout the year, as the number invertebrates and plant food within arable habitats is substantially reduced due to frequent application of agricultural chemicals (i.e., pesticides and insecticides) or mechanical operations (Wilson et al. 1999). Moreover, the relatively high and dense vegetation of crop fields during the breeding period may limit access of the studied species to prey resources. Similarly, grasslands in the study areas are mostly represented by species-poor and homogenous lawns or hayfields, that are intensively managed (usually cut every 1 or 2 weeks) or, at the other extreme extensive grasslands with-tall and dense vegetation (cut once or twice a year), both unsuitable due to low food availability or reduced accessibility to invertebrate prey (Whittingham and Evans 2004; Summers-Smith 2009; Jones and Leather 2013).

Finally, the population density of all three studied species was negatively correlated with increasing altitude (see also Šálek et al. 2015a). We also found a negative correlation between altitude and proportion of buildings and artificial surfaces. Simultaneously, we found a positive correlation between altitude and proportion of grasslands. Therefore, settlements in lower altitudes were characterized by more suitable composition of habitats compared to settlements in higher altitudes. The center of distribution of the studied species is situated within the lowlands, and numbers generally decline towards higher altitudes (Jasso 2003; Hudec et al. 2011; Šálek et al. 2015b). For example, in the settlements situated within higher altitudes, a sharp decrease (Robinson et al. 2005) or local population extinction of house sparrows was documented (Flousek et al. 2015). This may also be connected with a sharp increase in human socioeconomic status and development in these areas (Cuříková 2016).

Based on species-specific occurrence and habitat associations, several management measures may be adopted to support declining populations of the studied species, as well as whole bird communities within urban environments. In particular, we suggest the following recommendations:

i) Farmsteads, especially dairy farms, and small-scale farms represent crucial strongholds for breeding and wintering populations of farmland birds in urban environment and may benefit large numbers of declining species of conservation concern (Hiron et al. 2013; Rosin et al. 2016; Šálek et al. 2015b, 2018). The recent decline in the number of dairy farms and poultry yards (Šálek et al. 2018) is the result of a shift from diverse mixed-farming to crop-based production of a few economically productive crops, partially due to EU agricultural policy and/or higher human socioeconomic status (Donald et al. 2006; Ringsby et al. 2006; Shaw et al. 2008; Rosin et al. 2016). Furthermore, the EU financial support for farmstead modernization under the 2014–2020 Rural Development Programme, including modernization of agricultural buildings, changes in storage of grains (i.e., bird-proof grain storages/containers), manure, and silage (storage in water-proof basins or containers, often made of plastic and covered with plastic tarps), result in further decline of nesting and foraging opportunities for farmland birds (Šálek et al. 2018; 2020). We argue that the long-term decline of actively used farmsteads and small-scale farms may substantially contribute to declines of several farmland species, including the studied species (Chamberlain and Fuller 2000; Ringsby et al. 2006; Šálek et al. 2015a). Moreover, there is an urgent need for legislation changes and financial support for mitigation measures to increase nesting and foraging opportunities within farmsteads (see also below).

ii) Diversified management of grasslands (e.g., patchy mowing), woody vegetation (e.g., age stratification and vertical stratification), and supporting of native vegetation may increase the resource supplies for studied species (see Wilkinson 2006; Summers-Smith 2009), as well as for a variety of bird species in urban environment (Fontana et al. 2011; Šálek and Lövy 2012). Previous evidence suggests that even a small loss or destruction of urban green habitats (e.g., private gardens, inter-block vegetation) may ultimately have serious consequences for urban bird populations (e.g., Chamberlain et al. 2007).

iii) Although we did not find evidence for the negative effect of newly built-up areas on the numbers of studied species (cf. Moudrá et al. 2018; Rosin et al. 2020), provision of extra nesting opportunities (e.g., nest-boxes or special bricks for nesting of cavity breeders) may substantially increase nesting opportunities for both sparrow species, especially in city centers or other habitats with high urbanization intensity (Węgrzynowicz 2012; von Post and Smith 2015).

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Author contribution

JH, MŠ, and RF were responsible for the study conception and design. JH, JB, MŠ, JR, and many volunteers contributed for the data collection. JH and JB performed GIS analysis. JR and JH performed the data analysis. JH, MŠ, and JR wrote the first manuscript draft. All authors commented on previous versions and approved the final manuscript.

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Declarations

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Supplementary material

Table S1. Comparison of species densities among study years (2010-2012) in chosen settlements. Friedman ANOVA and Kendall Concordance.

Species	N	df	Anova Chi square	Coefficient of concordance	Average rank r	p
House sparrow	7	2	0.96	0.07	-0.08	0.618
Tree sparrow	8	2	1.53	0.09	-0.03	0.465
Eurasian collared dove	8	2	1.37	0.08	-0.05	0.504

Table S2. Comparison of species densities between first and second visit within one year for chosen settlements. Wilcoxon matched pairs test.

Species	N	T	Z	p
House sparrow	7	12.00	0.34	0.735
Tree sparrow	5	4.50	0.81	0.418
Eurasian collared dove	4	2.50	0.91	0.361

Table S3. Correlation coefficients among number of poultry yards and proportions of various habitats within the village-level dataset (n = 162 villages). Spearman rank correlations, values lower than p = 0.05 are in bold.

Variable	**Altitude**	**Number of poultry yards**	**Buildings (%)**	**Wooded plants (%)**	**Small-scale farms (%)**	**Farmsteads (%)**	**Arable habitats (%)**	**Artificial surfaces (%)**	**Grasslands (%)**
Number of poultry yards	-0.12								
Buildings (%)	-0.24	-0.05							
Wooded plants (%)	0.13	-0.08	0.11						
Small-scale farms (%)	0.08	0.48	-0.22	-0.10					
Farmsteads (%)	-0.01	0.08	-0.13	-0.05	-0.04				
Arable habitats (%)	0.01	0.04	-0.35	-0.10	0.15	0.11			
Artificial surfaces (%)	-0.21	-0.14	0.37	0.10	-0.43	0.22	-0.27		
Grasslands (%)	0.19	0.12	-0.31	-0.13	0.13	-0.22	-0.51	-0.44	
New buildings (%)	-0.12	0.12	0.03	-0.02	-0.22	-0.04	0.00	0.17	0.05

Table S4. The median and range of percentages for main habitat characteristics within a buffer for points with presence of each species and for random points.

Habitat	***Passer domesticus***		***Passer montanus***		***Streptopelia decaocto***	
	Points with presence	Random points	Points with presence	Random points	Points with presence	Random points
Buildings (%)	21.3 (0.1 - 70.7)	13.2 (0.1 - 96.1)	16.3 (0.1 - 81.1)	13.7 (0.1 - 96.1)	18.7 (0.1 - 68.5)	14.9 (0.1 - 96.1)
Wooded plants (%)	14.9 (0.1 - 74.1)	14.8 (0.1 - 95.7)	18.1 (0.1 - 93.2)	13.3 (0.1 - 88.5)	17.5 (0.1 - 91.1)	15.3 (0.1 - 88.5)
Small-scale farms (%)	0.1 (0.1 - 81.9)	0.1 (0.1 - 45.8)	0.1 (0.1 - 68.9)	0.1 (0.1 - 45.8)	0.1 (0.1 - 75.1)	0.1 (0.1 - 45.8)
Farmsteads (%)	0.1 (0.1 - 99.6)	0.1 (0.1 - 91.4)	0.1 (0.1 - 63.0)	0.1 (0.1 - 44.1)	0.1 (0.1 - 89.7)	0.1 (0.1 - 44.1)
Arable habitats (%)	0.1 (0.1 - 73.5)	0.1 (0.1 - 99.1)	0.1 (0.1 - 81.0)	0.1 (0.1 - 99.1)	0.1 (0.1 - 87.3)	0.1 (0.1 - 99.1)
Artificial surfaces (%)	18.4 (0.1 - 76.1)	16.3 (0.1 - 83.4)	15.9 (0.1 - 57.5)	15.9 (0.1 - 83.4)	19.4 (0.1 - 58.7)	17.7 (0.1 - 83.4)
Grasslands (%)	34.0 (0.1 - 91.8)	36.4 (0.1 - 100.0)	37.0 (0.1 - 91.7)	35.4 (0.1 - 99)	32.2 (1.2 - 78.8)	34.3 (0.1 - 89.1)
Number of points	1607	1607	339	339	268	268

Chapter III

Home-range size, flight distance and preferences for foraging habitats in House Sparrow (*Passer domesticus*): A comparison of city and rural populations

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(submitted manuscript)

Home-range size, flight distance and preferences for foraging habitats in House Sparrow (*Passer domesticus*): A comparison of city and rural populations

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Abstract

Lack of food for nestlings is a crucial factor influencing population size and dynamics in birds. It is one of the most cited reasons for the recent House Sparrow (*Passer domesticus*) population changes in cities and rural settlements. However, a detailed study of habitat utilization by parents delivering food to offspring in different environments is still missing. To obtain the most detailed information on fine-scale habitat selection, home range size, flight distance, and foraging time in a typical Central European city and rural environment, we conducted systematic observations of focal individuals feeding their offspring. We found increased home range size and flight distances in the urban population compared to the rural population. Additionally, some of the preferred habitats, such as ruderal and woody vegetation occurred in the city less frequently and consequently increased flight distance to key sources of invertebrate prey. In both environments, the most selected habitats, bin stages and poultry yards, offer a stable and rich, but low quality "fast food" source. Birds are willing to fly a longer distance to access these sources (c.f. bin stages and poultry yards). Our findings imply that key food sources in the urban environment are lacking and scattered. Due to changes in socioeconomic status, urbanization, and farming, crucial habitats are now under a threat. We discuss the importance of maintaining suitable small and medium-scale farms, and the management of green spaces in human settlements that may support House Sparrow populations and whole bird communities.

Keywords: habitat selection, food sources, small scale farming, ruderal habitats, urbanization, flight distance, home-ranges

Introduction

The House Sparrow (*Passer domesticus*) is well known as an exclusively synanthropic bird species, populations of which have sharply declined in many parts of its range over recent decades (Crick et al. 2002, Hole et al. 2002, De Laet and Summers-Smith 2007, PECBMS 2020). Despite intense public and scientific interest, the reasons for this decline have not been sufficiently uncovered.

In comparison with other potential reasons such as lack of breeding possibilities, predation, parasitism, and illnesses due to environmental pollution (Vincent 2005), lack of food during both the winter and breeding season is the most referred to reason (Summers–Smith 1999, 2003, Vincent 2005, De Laet & Summers-Smith 2007). Studies dealing with data from the 1920s and 1930s linked the decline of House Sparrow populations in the centre of large cities with replacement of horse transport, which led to food shortage (Baum 1955, Rand 1956, Summers–Smith 2003). Recent studies from the urban environment also predominantly link House Sparrow decline with reduced food availability (e.g., Vincent 2005, Peach et al. 2008).

Similar to the urban environment, the decline in rural settlements is often linked to lack of food due to intensification of farming practices (Krebs et al. 1999, Hole et al. 2002, Šálek et al. 2015a). Use of lossless machinery, more efficient pesticides, decreased landscape heterogeneity and reduction of number of farms are the most probable reasons for the alarming decline in common farmland bird populations including the House Sparrow (Siriwardena et al. 1998, Chamberlain et al. 2000, Donald et al. 2001, 2002, Robinson & Sutherland 2002, Inger et al. 2015). The most convincing evidence for the importance of farms for the survival of House Sparrow populations was demonstrated by the extinction of local populations after the closure of a farm on an isolated Norwegian island (Ringsby et al. 2006). Additionally, in settlements with active dairy farms, House Sparrows were more abundant (Chamberlainem et al. 2007, Liu et al. 2013, Robillard et al. 2013, Šálek et al. 2015a, Havlíček et al. 2021) and their population decline slower compared to settlements without farms (Erskine 2006). Additionally, farms have been described as an important source of invertebrate prey for birds (Møller 2001) and as bird biodiversity hotspots (Hiron et al. 2013, Rosin et al. 2016, Šálek et al. 2018a). Moreover, small-scale farming, such as poultry keeping has a positive effect on the local House Sparrow population during both the winter and breeding season (Jasso 2003, Šálek et al. 2015a, Havlíček et al. 2021). However, an increase in the socioeconomic status of the inhabitants of rural settlements may increase negative pressure on local bird populations (Shaw et al. 2008, Rosin et al. 2016, Zmihorski et al. 2020).

Previous studies have shown that survival rates of individuals and local populations of birds are affected by the physical condition and body size of juveniles due to different food availability (Magrath 1991, Newton 1998, Schwagmeyer & Mock 2008, but see Peach et al. 2018). The effect of body size on survival rate of House Sparrow fledglings was demonstrated by several studies (Ringsby et al. 1998, Peach et al. 2008, Cleasby et al. 2010). Recent studies on House Sparrow documented higher nutritional stress, decreased reproductive success and physical condition in urban areas (Liker et al. 2008, Peach et al. 2008, Seress et al. 2012, Meilléré et al. 2017). Additionally, it has been documented that individuals inhabiting more urbanized environments have decreased body size compared to individuals from less urbanized areas (Liker et al. 2008, Meillère et al. 2017). Previous studies on several bird species have shown that decreased body mass and condition of nestlings in urban environments was caused by reduced amount and decreased quality of delivered food (e.g., Richner 1989, Pierotti & Annett 2001, Mennechez & Clergeau 2006), and surplus food led to a better survival rate of House Sparrow juveniles (Anderson 1977, Peach et al. 2014, 2015).

Whereas adult House Sparrows are influenced mainly by the availably of seed and grain food (Hole et al. 2002, Šálek et al. 2015a), the nestlings are dependent on invertebrate food (Anderson 2006, Peach et al. 2008, 2015). Previous studies have demonstrated the differences in House Sparrow nestling diet composition across localities (Simeonov 1964, Encke 1965, Wieloch 1975, Peach et al. 2008). Schwagmeyer & Mock (2008) detected a relationship between the size of food pieces delivered by parents, and the condition and survival rate of House Sparrow nestlings. The nestlings fed more frequently with large sized prey showed better condition (body mass) and survival rate. According to Seress et al. (2012), parents in a suburban area brought to their nests fewer prey of larger size compared to those in a rural area, where they produced more, and bigger fledglings. Apart from prey size, the composition of food is a similarly important factor. Offspring with smaller body sizes and higher mortality were associated with an increased proportion of vegetal food or a decreased proportion of several invertebrate taxa in the diet (Vincent 2005). The plant-based food of the House Sparrow, which comes frequently from human sources (c.f., remains of food) can make up more than half of the nestlings' diet in cities (Bower 1999).

Recently, the planting of exotic plants, and intensive care of urban green areas (including increased use of insecticides and herbicides) has led to a reduction in insect abundance (Burghart et al. 2009), and decreased the attractiveness of these green areas for House Sparrows (Cannon 1999, Wilkinson 2006, Burghart et al. 2009). Additionally, the isolation of suitable food resources in urban environments may be a limiting factor in the local distribution of birds. Vangestel et al. (2010) found, that due to increased fragmentation and scattering among suitable habitats urban House Sparrows used only a limited number of food patches. Thus, local populations are more vulnerable to changes or loss of individual suitable sites (Chamberlain et al. 2007, Bernat-Ponce et al. 2020).

Current studies show that the crucial factor influencing the quality and quantity of food for nestlings is the availably of habitats hosting invertebrate prey in both urban and rural environments. Knowledge of habitat use at a fine scale is important for understanding local House Sparrow population changes. Increased knowledge may lead to more effective future conservation efforts focused on the House Sparrow and also other birds inhabiting human settlements. Therefore, we found it surprising that a detailed study of fine-scale habitat utilization by the House Sparrow during the breeding period is still missing. The present study compares the foraging behavior and fine-scale habitat utilization of both, urban and rural populations of House Sparrow in typical Central-European settlements. We suggest that urban habitats provide decreased food availability in more fragmented food patches compared to rural areas and that this may lead to increased home range sizes in urban areas (but see Vangestel et al. 2010). We also predict increased utilization of low-quality food sources (e.g., remains of human food) in the urban environment.

Material and methods

Study area

The study was conducted in two settlements in South Bohemia, Czech Republic. The settlement Radětice (GPS: 49°19'11"N, 14°26'34"E, 420 m a.s.l., ca. 230 inhabitants) is a typical Central-European rural village with small-scale farming such as poultry holdings, and large-scale farming represented by a former collective farm focused on mixed-farming including dairy, meat, and crop production. Within the village there was a silage pit, manure heaps, grain storages and haylofts. České Budějovice is a medium-sized city (GPS: 48°58'29"N, 14°28'29"E, 390 m a.s.l.) with ca. 90000 inhabitants. The study was conducted in a housing estate comprised of blocks of flats, typical for cities and towns in Central-European post-totalitarian countries. It was built mostly during the 80s and 90s of the 20th Century and modernized (including the green spaces) at the beginning of the 21st Century.

Foraging behaviour

We chose the method of focal individual observation to avoid registration of non-breeding birds and individuals with non-foraging behavior (Frey-Roos et al. 1995, Brickle & Peach 2004, Field & Anderson 2008). Birds were caught before the breeding season using ornithological mist nets. All caught individuals were banded with an ornithological metal ring and a combination of colour rings making up a unique code. During the period of feeding nestlings in the breeding seasons 2010–2015, we observed the parents leaving the nest to collecting food. The observations were carried out from at least 50 m from the nest (according to the behavior of the parents), to avoid disturbing the birds. The position of the observer, with a good view of the nest and potential feeding patches, was changed during the observation to cover the whole surrounding area. We used binoculars (8×42) and a spotting scope (20–60×80) during these observations.

Although most of birds were colour-ringed, identification of feeding individuals was not always possible. Therefore, foraging trips per nests were analysed for both sexes combined rather than separately (Frey-Roos et al. 1995). We recorded the exact time of leaving and arrival at the nest, the exact feeding site location, habitat type, time spent by the individual at the feeding site, behavior (if possible), sex of the individual parent (or unknown if it was not possible due to quick movements), and other details using a voice recorder with continuous recording. We also marked all activities onto the most recent detailed aerial map 1:750 (Seznam maps 2018). The time of flight to and back from the feeding site was included into the "foraging time", because its proportion is generally low (Frey-Roos et al. 1995). Additionally, potential feeding patches were checked for colour-ringed birds with known breeding site and status. We also measured the distance from the nest to each individual feeding patch using QGIS (QGIS Development Team 2020).

Habitat utilization analysis

For analyses of habitat use, we carried out fine scale field monitoring within the 150 m buffer zone (Peach et al. 2014) around observed nests. All habitat (Table 1) patches larger than ca. 2×2 metres were recorded onto a recent aerial map 1:750 (Seznam maps 2018, Google maps 2018) and vectorized using the GIS environment (QGIS Development Team 2020). To obtain detailed information on the use of different vegetation patches, the "green space" was divided into several categories (see Table 1 for details).

The minimal convex polygon (MCP) and 95% and 50% Kernel home-range area (KDE) for pairs with more than 5 records from particular feeding patches (Fig. 1) was calculated and exported to shapefile (adehabitatHR, rgdal, raster, and rgeos packages) in R 4.0.2s software (R Core Team 2020). For further analysis, we selected only the MCP and KDE 50% and 95% based on more than 20 recorded points per breeding pair (Tella et al. 1998, Shaw 2009, Supplementary information Fig. 1). The proportion of individual habitats inside the 150 m buffer around the nest (habitat availability), MCP and KDE 50% and 95% were calculated in QGIS (QGIS Development Team 2020).

Table 1. The composition and description of the habitats within a 150 m radius of the observed nest position.

Habitat	**Mean coverage (%) ± SD**	**Range**	**Description**
Arable land	1.7 ± 2.2	0.0-16.9	Fields for crop production and other cultivated farmland except meadows
Artificial surface	18.9 ± 7.5	8.9-35.4	Paved and unpaved roads, pavements, parking lots and other paved surfaces without vegetation (except sparse ruderals)
Bin stages	0.2 ± 0.3	0.0-0.8	Stages of bins and containers outside buildings
Buildings	16.1 ± 4.7	6.6-24.1	Houses (i.e., family houses, multi-story houses) and other buildings including farm buildings except for crop storage, cowsheds, henhouses etc.
Farm	2.2 ± 2.5	0.0-11.5	Farm buildings (i.e., storage of cereals, and cowsheds), silage and haylage pits (“silage pits” in the text), manure heaps, and stacks of straw

Meadows	8.4 ± 6.6	0.0-26.1	Dense and tall meadow vegetation (Poaceae) for production of hay, haylage and silage, mowed once or twice a year
Poultry holdings	1.9 ± 2.1	0.0-4.9	Poultry, sheep and cattle with less than 10 individuals
Short ruderals	1.6 ± 1.4	0.0-5.7	Sparse vegetation of "ruderal" plant species (e.g., *Poa annua*, *Polygonum aviculare*, *Persicaria* sp., *Chenopodium* sp., *Plantago* sp., *Trifolium* sp.) up to ca. 15 cm, mostly on or by unpaved roads, footpaths, and damaged surfaces, unmanaged, or mowed occasionally
Shrubs and trees	8.1 ± 2.9	1.4-13.5	All types of woody plants (i.e., shrubs and trees in gardens or single individuals in public spaces, hedgerow etc.)
Short grass	32.9 ± 9.7	3.7-47.9	Intensively managed dense grass vegetation in gardens or public spaces, usually cut every few weeks

Tall ruderals	7.7 ± 8.1	0.0-31.8	Dense or less often sparse vegetation of "ruderal" plant species (e.g., *Urtica dioica*, *Chenopodium album*, *Artemisia* sp., *Rumex* sp., single individuals of young woody plants e.g., *Sambucus nigra* can be present) taller than ca. 20 cm, regularly about 100 - 150 cm, mostly on brownfields and derelict land, formerly damaged surfaces, unmanaged edges of crop fields, or in the vicinity of cowsheds, manure heaps and silage pits, unmanaged, or mowed occasionally
Water	0.3 ± 0.4	0.0-2.1	Water bodies

Figure 1. An example of KDE 50 and KDE 95, its overlap with mapped habitats, and feeding site positions for selected breeding pairs in urban (a), and rural (b) environments. The shape of patches was simplified for the visualization, with respect to their area.

Statistical analyses

The effect of city/village location on home-range size was analysed using generalized linear mixed models (GLMM) in R 4.0.2s software (R Core Team 2020) using lmer function (package lme4). We used MCP and KDE 50% and 95% as dependent variables with Gamma distribution. Number of points within a home-range was used as a random factor. Firstly, we performed a null model analysis without the independent variable and then we added city/village as binomial independent variable. Consequently, we compared these models with anova function in R. Similarly, we calculated these GLMM models for distance moved (m) and foraging time (s) as dependent variables with random factor nest ID. We used Gamma distributions of dependent variables. For these models, we used habitat type (artificial surfaces, bin stages, buildings, farms, short grasses, poultry holdings, tall and short ruderals, shrubs and trees) and city/village as independent variables. We also calculated interaction between these two variables. Statistical significance among distances from the nest and time spent within a particular habitat were calculated by post-hoc Tukey tests using lsmeans function in R (package lsmeans).

The effect of habitat representations (including water bodies, see above) in city/village and its connection with home-range size (i.e., primary predictors) were calculated using variance partitioning by principal coordinate analysis of neighbour matrices (PCNM) in Canoco 5 software (ter Braak & Šmilauer 2012) that was recommended by Marrot et al. (2015). This multivariate analysis enabled us to separate the effect of geographical position (i.e., space predictors) from the effect of primary predictors (Legendre & Legendre 2012). The analysis is suitable for calculating inter-correlated variables since all these variables enter the analysis simultaneously. The analysis included nine steps: (1) primary predictor test (i.e. preliminary test of the overall effect of primary predictors on the dataset), (2) primary predictor selection by partial redundancy analysis (RDA) using forward selection based on partial

Monte-Carlo permutation tests, (3) principal coordinate analysis (PCoA) based on Euclidean distances (i.e. finding the main space predictors based on GPS coordinates), (4) PCNM for all predictors (i.e., preliminary test of the overall effect of space predictors on the dataset), (5) PCNM selection (i.e. the choice of space predictors based on coordinates using forward selection and partial Monte-Carlo permutation tests), (6) spatial effects analysis (i.e. assessing the amount of variability explained by space predictors), (7) primary predictor effects analysis (i.e. assessing the amount of variability explained by primary predictors), (8) joint effects analysis (i.e. assessing the amount of variability explained by both predictor types) and, (9) removal of spatial effects (Šmilauer & Lepš 2014). The relationships between KDE size and proportion of artificial surfaces and poultry holdings were fitted using regression in software Statistica 13 (TIBCO Software Inc. 2017).

Habitat preferences were assessed using R statistical software (R Core Team 2020). We used the package Adehabitat (Calenge 2006) to compute compositional analyses of habitat selection. We used a randomization test with 500 repetitions. Habitat that was not found within the particular home-range (zero values in entry data matrix) was replaced by 0.01 (Aebischer et al. 1993). A home-range represented a data unit. We computed percentages of each habitat category available (proportion of area within a radius of 150 m around the nest), used by the study species (proportion of individual records within a particular habitat extracted from home-ranges (KDE 50% and 95%), and directly observed habitat use (see above). These three analyses were carried out in two steps. First the significance of habitat use among all habitats was tested (using a Wilks lambda). Then, a ranking matrix was built, indicating whether the habitat type in rows is used significantly more or less than the habitat type in columns. Further, habitats were sorted from most preferred to non-preferred (Aebischer et al. 1993).

Results

Home-ranges of House Sparrows in the city were significantly larger than those in the village (mean size of MCP, KDE 50% and 95% in the village: 8159 ± 5103 m^2; 7244 ± 8385 m^2; 31007 ± 32700 m^2, and city: 22268 ± 8258 m^2; 13682 ± 6203 m^2; 58038 ± 22708 m^2). This result has been confirmed (Table 2, Fig. 2a-c) using MCP as well as KDEs (50% and 95% of points). Using multivariate analysis, we further found that primary predictors (proportions of available habitats and KDE 50%) explained 22.3% of variability, space predictors (PCO variables) explained 23.7% of variability and the overlap was 10.2%. With the first ordination axis, we found more pronounced negative correlation with proportions of meadows (-0.92), short ruderals (-0.94), tall ruderals (-0.79), farms (-0.70) and positive correlation with artificial surfaces (0.94), buildings (correlation coefficient 0.83) and short grasses (0.71). Some of these habitats were also correlated with the second ordination axis (e.g., tall ruderals: 0.46, artificial surfaces: 0.73 and short grasses: -0.44). The most pronounced negative correlation with the second ordination axis showed proportions of poultry holdings (-0.74), shrubs and trees (-0.63) and arable land areas (-0.44). Independent variables for KDE for 50% of points and location of nest in city/village were significantly linked with proportion of habitats (Table 3). Home-ranges located in the city contained increased proportions of buildings, artificial surfaces and short grasses. In contrast, village home-ranges included increased proportion of meadows and short ruderals. These home-ranges also showed presence of tall ruderals, poultry holdings and farms that were missing in city home-ranges (Fig. 3). We found that KDE 50% was positively affected by the proportion of artificial surfaces. Simultaneously, we found a negative relationship between KDE 50% and proportion of poultry holdings (Fig. 4).

Table 2. The effect of city/village and habitat type on home-range size (MCP - minimum convex polygon, KDE - Kernel home-ranges for 50 and 95% of points), distance moved, and time spent on foraging patches. GLMM analyses (see methods for details).

Dependent variable	**Independent variable**	**d.f.**	**% of explained variability**	**Chi**	**P**
MCP (m^2)	City/village	4	3.8	24.8	< 0.001
KDE 50 (m^2)	City/village	4	0.9	6.0	0.014
KDE 95 (m^2)	City/village	4	1.1	7.7	0.006
Distance moved (m)	Habitat	11	1.6	220.6	< 0.001
	City/village	4	< 0.1	10.5	0.001
	Habitat + city/village	12	0.2	20.9	< 0.001
	Habitat * city/village	16	0.2	26.7	< 0.001
Foraging time (s)	Habitat	13	0.6	29.4	< 0.001
	City/village	5	0.1	6.6	0.010
	Habitat + city/village	14	0.8	4.1	0.043
	Habitat * city/village	18	< 0.1	4.2	0.376

Table 3. The relationship between a habitats’ availability and city/village location and Kernel home-range size defined by 50% of points (KDE 50). PCNM analysis. PCO – space independent variable.

Independent variable	Contribution (%)	Pseudo-F	P
City/village	62.6	22.8	0.002
KDE 50	9.9	4.0	0.050
PCO.2	54.0	28.5	0.002
PCO.1	22.0	19.0	0.002
PCO.5	12.5	17.5	0.002
PCO.3	9.5	25.8	0.002

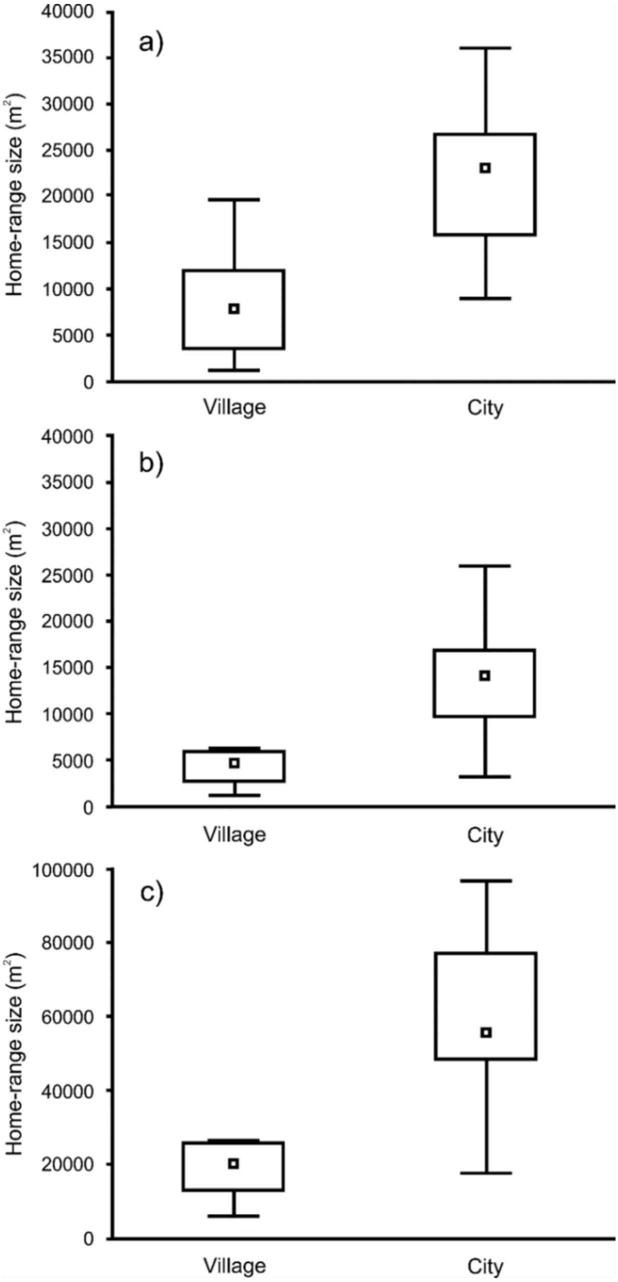

Figure 2. Comparison of home-range sizes of a) MCP, b) KDE 50, c) KDE 95 for pairs breeding in the village (n = 11 home-ranges) and city (n = 20 home-ranges). Square – median, box – 25-75% of data, whiskers – non-outlier range.

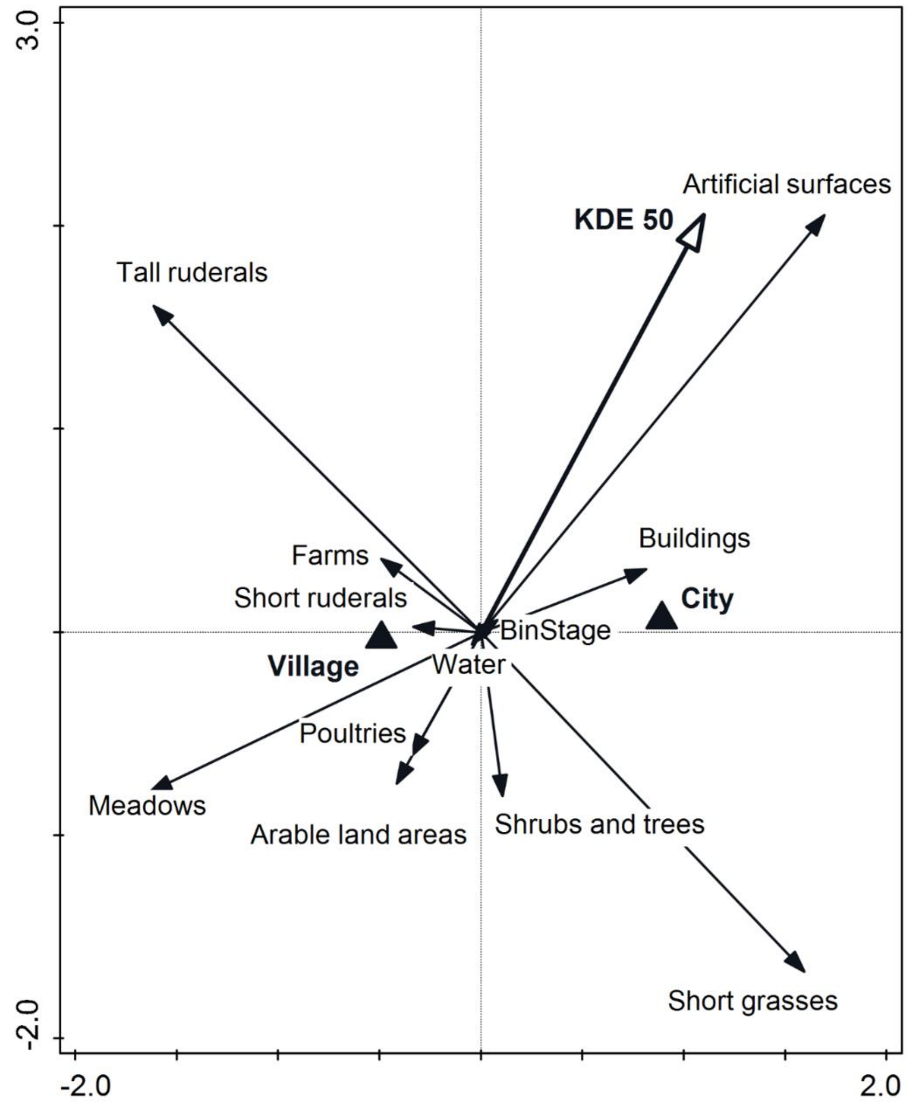

Figure 3. Projection scores of proportions of habitats in city and village with trend of home range size of Kernel for 50% of points (KDE 50) within House sparrow home-ranges. PCNM analysis, I. and II, axes together explain 52.1% of variability (n = 31 home ranges).

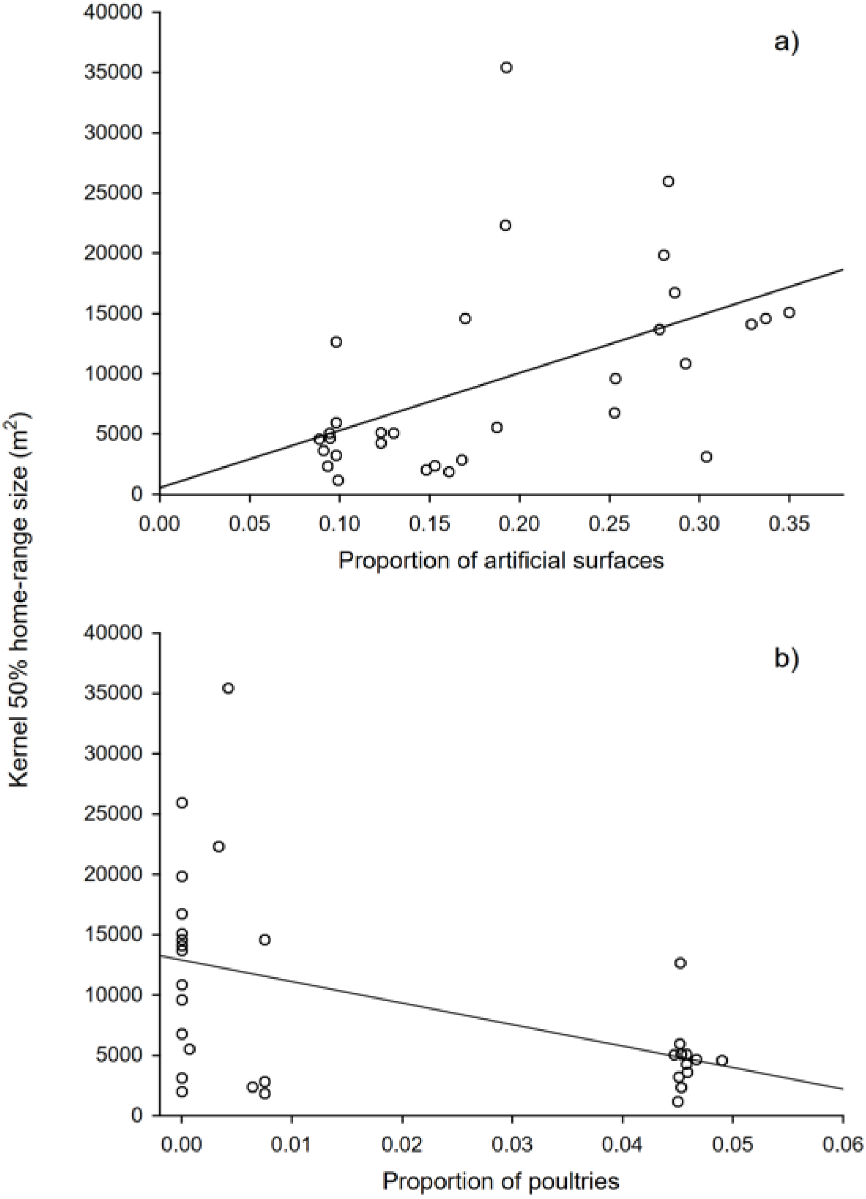

Fig. 4. The effect of proportion of a) artificial surfaces, and b) poultry holdings on Kernel home-range size defined by 50% of points (regression, n = 31 home-ranges, $R^2 = 0.26$, F = 10.1, beta = 0.51, P = 0.003, and r R2 = 0.23, F = 8.5, beta = -0.27, P = 0.007 respectively).

Distance moved by House Sparrows to foraging places was significantly affected by interaction of city/village (mean distance 79.8 ± 42.6 m, range 4–233 m in city vs. 56.9 ± 38.3 m, and range 1–192 m in village) and habitat used (Table 2). Using post-hoc tests, we revealed that differences among many categories were statistically significant (Supplementary information Tables S1). With a single exception, we did not find differences between distances to buildings and other habitats. The most marked differences in the village were found between distances moved to tall ruderals and farms, whereas the median distances moved to tall ruderals were more than twice as long compared to distances moved to farms (Fig. 5). Between distances moved to bin stages and short grasses within the city, the medians of the latter represent approximately half the distances to bin stages (Fig. 5).

Foraging time was significantly affected by habitat used and city/village population (Table 2). We found significant differences among short and tall ruderals, shrubs and trees vs bin stages and poultry holdings, respectively (Supplementary information Table S2). The median foraging times at bin stages and poultry holdings were much lower than those at tall or short ruderals and shrubs and trees (Fig. 6a). Simultaneously, we found that median foraging time was lower in the city compared to the village (Fig. 6b).

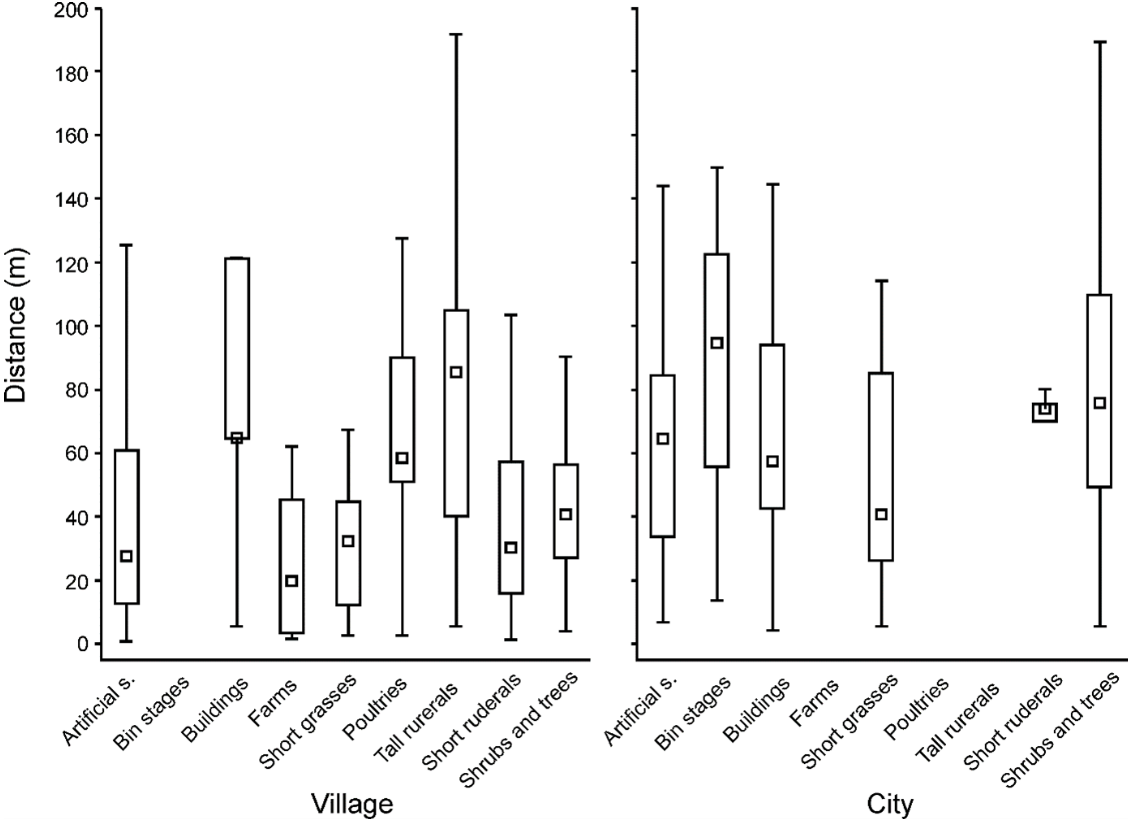

Figure 5. Foraging distances for main habitats within city and village home-ranges (n = 1394 focal observations). Square – median, box – 25-75% of data, whiskers – non-outlier range.

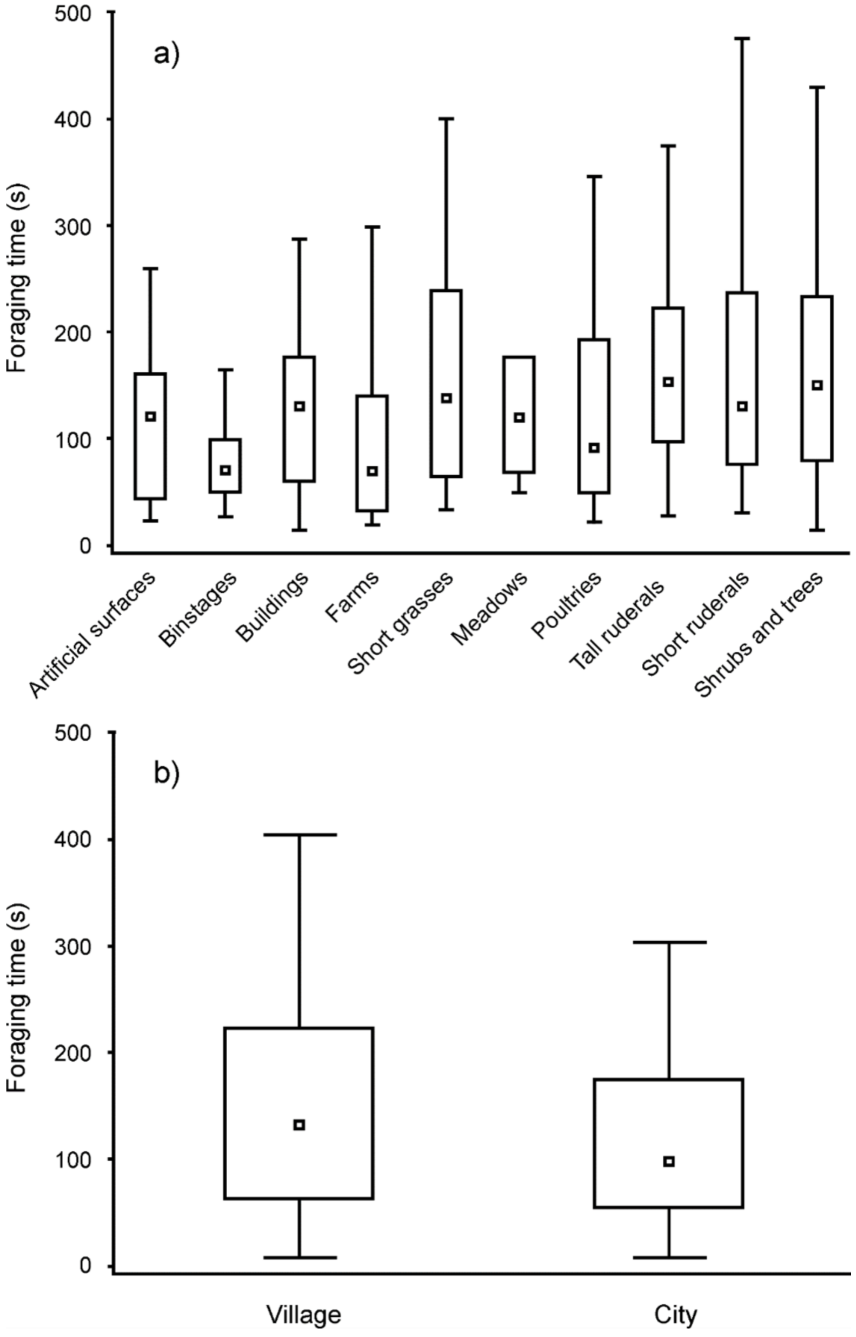

Figure 6. Foraging time for a) main habitats and b) city/village home-ranges (n = 416 focal observations). Square – median, box – 25-75% of data, whiskers – non-outlier range.

The habitat preferences calculated using KDE (50% and 95% of points) and use of habitats showed similar results (Table 4, for detailed results see Supplementary information Table S3-5). The rank of habitats was similar for both KDEs, with most preferred poultry holdings, bin stages, short ruderals and farms. The four main preferred habitats based on their use were also similar, but farms were replaced with shrubs and trees. We also found that tall ruderals were the fifth preferred habitat that was not shown using KDE (Table 4).

Table 4. Ranks for habitats according to habitat preference analyses between Kernel home-ranges for 50% (KDE 50) and 95% (KDE 95) of points, habitat use and habitat availability. The higher value refers to higher rank, i.e. more preferred habitats.

Habitat	**KDE 50 vs availability**	**KDE 95 vs availability**	**Use vs availability**
Poultries	11	9	11
Bin stages	10	10	10
Short ruderals	9	8	8
Farms	8	11	5
Water bodies	7	7	6
Artificial surfaces	6	5	3
Buildings	5	6	0
Shrubs and trees	4	4	9
Tall ruderals	3	3	7
Arable lands	2	2	4
Short grasses	1	1	2
Meadows	0	0	1

Discussion

Our study based on detailed observations of House Sparrow foraging activities during the breeding season confirmed the differences in habitat use between a typical Central-European rural and urban settlement. In the urban population i) the mean home-range size was 1.9–2.7 times larger, ii) birds flew a longer distance for the nestlings' food and iii) spent less time at feeding places compared to the rural population. Finally, the study shows that birds in both populations prefer both artificial food sources and natural habitats (ruderal patches and woody plants).

Home-range size in urban and rural populations

An animal's home-range size is likely to be influenced by multiple factors (McLoughlin & Ferguson 2000, Ronaldo 2002, Rivrud et al. 2010). In birds, the availability of food and presence of suitable foraging habitats are most important. Home-range size generally increases with reduced food availability, and higher fragmentation and distance to feeding sites, it decreases with more abundant prey, and less fragmented feeding sites situated closer to the nest (Ronaldo 2002, Bruun & Smith 2003, Anich et al. 2010, Kouba et al. 2017). A previous telemetry study on House Sparrows showed that home-range sizes differ across the gradient of urbanization (Vangestel et al. 2010). In contrast with our findings, winter home-range size was larger in a rural population compared to those in an urban area, where the key habitats were more scattered and isolated (Vangestel et al. 2010). It also conflicts with most previous studies (see above). There are exceptions of reduced mobility and home-range size during unfavorable weather conditions (Dussalt et al. 2005, Kouba et al. 2017). The House Sparrow is known as a highly sedentary species with limited dispersal and movement (Hole et al. 2002, Anderson 2006, Liu et al. 2012). Thus, higher fragmentation of foraging and shelter sites can lead to the situation where birds occupy only a small area around limited resources, as was observed by Vangestel et al. (2010). Similar to our results, Shaw (2009) recorded only small home-ranges during the breeding season (approximately 200 m^2 and 760 m^2 for KDE 50% and 95%) in a highly urbanized area. Due to methodological differences (e.g., sampling of individuals vs. pairs, telemetry vs. direct observation, software tools etc.) comparison with our study is highly approximate, but there is a diametral difference (we observed ca. 70–80 times larger home-ranges for KDE 50% and 95% within the urban settlement). A potential explanation is that Shaw (2009) conducted their study within a highly urbanized and homogenous environment without potential rich feeding sites within the exploration radius of observed individuals. Habitat cover around the nest was previously described as a factor influencing home-range size (Tella et al. 1998, Bruun & Smith 2003, Anich et al. 2010). In our study increased home-range size was related to a higher proportion of artificial surfaces. These habitats were not preferred by House Sparrows (see below) and exhibited, on average, at least twice as much land cover in urban sites. In contrast, the proportion of poultry holdings decreased the home-range size and has been recognized as an important food resource for House Sparrows (e.g., Šálek et al. 2015a, Havlíček et al. 2021, this study), representing typical habitat for the village. This result can partly explain the difference in home-range size between both environments.

Foraging distance and foraging time within habitats and foraging opportunities

The distance of suitable feeding habitats from the nest is considered an important driver of home-range size (Bruun & Smith 2003, Tella et al. 2008, Evens et al. 2018). In a study on House Sparrows in different environments, Vincent (2005) and Bower (1999) found that 70 and 60 percent of foraging flights were within 70 m from the nest. Others concluded that the distance between nest and foraging site does not exceed 50 m for most individuals (Heij & Molieker 1990, Mitschke et al. 2000). In an experimental study with mealworm feeders, 97% were taken by sparrows nesting within 26 m from feeders with maximum distance of 165 m (Peach et al. 2014). In contrast to these studies and our results, Shaw (2009) observed that in 95% of cases birds moved only within 760 m^2 (~16 m radius if the home-range has an approximately circular shape) and none were observed beyond 100 m from the site at which they were tagged. Other bird species of similar body size were reported to fly up to 100 m, longer distances were scarce when delivering invertebrate food for nestlings (Frey-Roos et al. 1995, Naef-Daenzer & Keller 1999, Brickle et al. 2000, Brickle & Peach 2004, Britschgi et al. 2006). In the closely related Tree Sparrow (*Passer montanus*), with the similar foraging ecology (Šťastný & Hudec 2011), 98% of foraging flights were closer than 300 m from the nest (Field & Anderson 2008).

Generally, birds fly longer distances to feeding patches when suitable food-rich sites in the nest vicinity are limited (Frey-Roos et al. 1995, Brickle et al. 2000, Bruun & Smith 2003, Evens et al. 2018). Therefore, the longer distances to feeding patches in the urban compared to the rural environment found in our study were probably caused by low availability and scattered distribution of key habitats (e.g., Vangestel et al. 2010, Jarrett et al. 2020) and the generally lower quality of the urban environment (Stauss et al. 2005, Britschgi et al. 2006, Jarrett et al. 2020). Longer distances flown to feeding habitat were also probably linked with better quality (e.g., size of invertebrate prey) of delivered food (Frey-Roos et al. 1995). We assume that for this reason, the tall ruderals, poultry holdings, and buildings exhibited longer median distances within the rural environment. On the other hand, the farm habitats were visited only when they were situated in the nest vicinity. In the case of buildings, the result is most probably an artefact given by low utilization of this habitat. The tall ruderals, formed mainly by native plants, were mostly scattered within the area surrounding the nest (except several nests located on the farm) and probably offered an increased amount of vertebrate prey. Additionally, within this habitat birds searched for prey for a significantly longer time compared to other habitats. Breeding Water Pipits (*Anthus spinoletta*) brought a larger amount of food to the nest collected in remote patches and therefore spent increased time on food collection (Frey-Roos et al. 1995). Similarly, Evens et al. (2018) demonstrated that birds occupying sub-optimal areas compensate for travelling longer distances by increasing time spent on foraging sites. The opposite trend, i.e., a short time spent (in comparison to other habitats) on further sites, was demonstrated for the poultry holdings and bin stages. In comparison with “natural” habitats both offer mainly plant based food or remains of human food. A mix of cereal meal and food scraps was observed to be delivered from poultry holdings and bin stages respectively, whereas invertebrate prey was never observed to be delivered (unpublished data). Thus, we suppose that poultry holdings and bin stages represent stable, predictable, and rich food sources. Birds can profit from visiting known and numerous resources by reducing searching time as confirmed by a study on Great and Blue Tits (*Parus major*, *Cyanistes caeruleus*) (Naef-Daenzer & Keller 1999). On the other hand, the mainly plant-based food from this source has decreased nutritional quality compared to invertebrate components of diet (Douglas et al. 2012, Vincent et al. 2005, McHough et al. 2016). The lack of invertebrate prey from the poultry holdings may be caused by competition with hens. Additionally, hens can prey on smaller birds, which makes longer searching and handling of prey disadvantageous. On the other hand, the birds can partly compensate for the disadvantage of low quality vegetal food by its quantity (Klvaňová et al. 2011). The shrub and tree habitats that were present, especially in the urban environment, were located farther than other habitats. When comparing both populations, the mean distance was approximately twice as long in the urban population compared to the rural site. This finding supports the previous suggestions that this important habitat is less available, more scattered, and of less quality in the urban environment compared to rural sites (Mackenzie et al. 2014, de Satgé et al. 2019). Despite the benefits of visiting remote sites (see above), there are some disadvantages of long flights, e.g., increased energy costs (Daan et al. 1996, Hinsley 2000, Evens et al. 2018), increased predation pressure (e.g., Tsurim et al. 2010, Villén-Pérez 2013), and probably also increased risk of collisions with traffic or human-made constructions. Similarly, the increased distance, and searching time reduce the time spent by adults on their nests, leaving nestlings unprotected (Eybert et al. 1995).

Habitat selection

There was not a big difference in the preference score for the most preferred habitats revealed by KDE 50% and 95% and direct observations. Although, we identified irregularity in some less preferred habitats. In comparison with habitat availability, in both KDEs home-ranges the proportion of farms, buildings, and artificial surfaces were more abundant, than their real usage. There was an opposite trend for shrub and trees, and tall ruderals, which were less represented in both KDEs compared to their availability in the nest vicinity. Although, they were frequently visited by feeding parents. Here we argue that using only KDE for estimating preferences for feeding sites may bring some biases into the results compared to direct observations.

In accordance with the theory that birds are willing to fly a longer distance to better foraging habitats (see above), we found that poultry holdings, bin stages, shrubs and trees, and tall and short ruderals were the most preferred habitats. The bin stages and containers with garbage and scraps provide a year-round rich supply of food in the urban environment, especially for adults (Summers-Smith 1956, Bokotey & Gorban 2005, Erskine 2006, Bernat-Ponce et al. 2018). Utilization of trash bins and containers by House Sparrow may be affected by several factors. For example, technical protection against pests such as rats, feral pigeons etc., or a shift to underground systems can dramatically reduce this food resource. These changes arise due to modernization and increasing urbanization of settlements (Bokotey & Goban 2005). Similarly, in the rural environment, food sources of human origin, represented by food given to poultry was preferred (see also Summers-Smith 1956, Bokotey & Goban 2005). This evidence is in concordance with previous findings that showed this habitat to be a key food resource during the breeding and winter period (Jasso 2003, Šálek et al. 2015a, Havlíček et al. 2021). With the modernization of settlements, numbers of poultry holdings have declined rapidly (Bokotey & Goban 2005, Šálek et al. 2015a).

In addition to bin stages and poultry holdings, “green” habitats were represented mainly by natural vegetation or a mix of natural and non-native plants (especially in the urban settlement). We confirmed the preference for shrubs and trees as was described by previous studies on the House Sparrow (Vincent 2005, Wilkinson 2006, Murgui 2009, Bernat-Ponce et al. 2018). In comparison with the rural settlement, this habitat was used more frequently in the city, even though its availability was similar for both populations. In the urban environment, shrub and tree vegetation are an important source of invertebrate prey (Vincent 2005, Mackenzie et al. 2014, Ješovnik & Bujan 2021). This is because other suitable “natural” habitats compensating for the loss of this habitat are scarce (e.g., ruderals in our study were much less abundant in the city compared to the rural site). Moreover, patches of woody plants at the rural site were generally larger, denser, and often formed by natural plant species (unpublished data) making them more suitable for hunting invertebrates (Pithon et al. 2021). Additionally, we observed, that the shrub vegetation in the urban settlement was more intensively managed (mostly at least once a year) compared to an increased proportion of unmanaged shrubs in the rural settlement, especially in the vicinity of the farms. Destruction or changes in vegetation structure (e.g., eradication of dense native shrubs, their replacement by non-native, smaller and sparser shrubs, single trees, or artificial surfaces; unpublished data) currently represent a real threat for House Sparrow populations in human settlements (Chamberlain et al. 2007, Shaw et al. 2008, Bernat-Ponce et al. 2020, Landmann & Danzl 2020).

Similarly, we found a preference for short and tall ruderals as revealed by previous studies (Murgui 2009, Pithon et al. 2021). Ruderals represent plant communities typical for abandoned parts of human settlements and the surrounding area, such as vacant land or brownfields. Within rural farms, they occurred on uncultivated areas in the vicinity of buildings, silage pits or manure heaps, unpaved roads, and field edges. Waste land is perceived to be without benefit for people or nature (Bonthoux et al. 2014, Villaseñor et al. 2020), but recent studies have pointed out its positive effect on bird abundances and diversity in human settlements and surrounding areas (Šálek et al. 2004, Hancock & Wilson 2004, Bonthoux et al. 2014, Villaseñor et al. 2020, Pithon et al. 2021). In contrast to other studies and our findings, Chamberlain et al. (2007) observed low utilization of brownfield habitats by the House Sparrow. Ruderal habitats e.g., on brownfields provide increased availability of invertebrate prey (Eyre et al. 2003, Jones & Laether 2012) and seeds (Šálek et al. 2004, Hancock & Wilson 2004), which make them year-round suitable habitats. Unfortunately, due to the above-mentioned reasons, they are frequently targeted for development or re-cultivation (Villaseñor et al. 2020). Additionally, farming intensification of (e.g., building new homesteads on brownfield sites, increased care of vegetation in the farm vicinity for aesthetic and hygiene reasons, expanding fields to include formerly uncultivated edges, and use of more effective herbicides and pesticides) threatens this habitat in rural areas.

Surprisingly, House Sparrows did not frequently use the farm including the cowsheds, manure heaps, silage pits or grain storages. This is in contrast with previous studies, pointing out that these sites enhance House Sparrow populations and the whole bird community (Chamberlain et al. 2007, Šálek et al. 2015a, 2018a, 2020, Rosin et al. 2016, Havlíček et al. 2021). We agree that farms are an important source of quality food for House Sparrow nestlings (see also Møller 2001), but we argue that it is probably affected indirectly due to the existence of a mosaic of habitats including short and tall ruderals (see above). For instance, antiparasitic medicaments that are toxic for many invertebrates (Lumaret et al. 2012, Ambrožová et al. 2020) and quick removal of manure off the farm (in just few days) do not allow the development of invertebrate communities. Moreover, farms play an important role in the survival of House Sparrows during the winter. This includes additional food resources (e.g., silage, compound feed for animals, storage of cereals), and heat and bird predator free shelter inside the farm buildings (Barnard 1980, Šálek et al. 2015a). Additionally, farm buildings, such as barns, hen houses, or stables provide a high diversity of various nesting places for cavity breeding species (Šálek et al. 2016, 2018a). Recent modernization of farms and intensification of farming practices (i.e., bird-proof grain storages, storage of silage and manure in water-proof containers, often made of plastic and covered with plastic tarps, use of lossless machinery and changes in sowing patterns) may reduce the suitability and accessibility of farm infrastructure for sparrows (Morris et al. 2005, Shaw et al. 2008, Rosin et al. 2016, Šálek et al. 2018a,b). On the other hand, reduction in the number of cattle kept (see e.g., Šálek et al. 2015a) and number of farms may also have a negative effect (Hiron et al. 2013, Šálek et al. 2015a, 2018a, Rosin et al. 2016).

Arable habitats and grasslands (both short grass and taller meadows) were avoided in accordance with previous studies (Šálek et al. 2015a, Havlíček et al. 2021). Arable habitats formed by relatively tall and dense vegetation on crop fields provide low availability of invertebrates, which is substantially reduced due to frequent application of agricultural chemicals or mechanical operations (Wilson et al. 1999). Moreover, the vegetation structure may limit access to prey. As described by Havlíček et al. (2021), grasslands within the study areas are mostly represented by species-poor and homogenous lawns or hayfields, that are intensively managed (usually cut within a few weeks), or by meadows with-tall and dense vegetation of Poaceae (cut once or twice a year). Both these plant formations are unsuitable due to low food availability and/or reduced accessibility to invertebrate prey (Whittingam & Evans 2004; Britschgi et al. 2006, Summers-Smith 2009; Jones & Leather 2013; Weir 2015). On the other hand, tall ruderals (see above) allow birds to sit and climb on the vegetation formed by more robust species (e.g., Chenopodoideae, *Artemisia* sp., *Urtica* sp.). This statement is supported by the observation (unpublished data), that House Sparrows used meadow habitat only in the vicinity of constructions, which allowed them to use a “sit and wait hunting strategy”. Similarly, the utilization of tall lawns by the bird community across the urban gradient was reduced, compared to shorter extensively managed sports grounds in parks (Pithon et al. 2021), which is in accordance with our results. Except for better access to food resources, the shorter herbaceous habitats (short grass and short ruderals in this study) are more safe from predators compared to taller ones (Whittingam & Evans 2004).

Similarly, artificial surfaces do not provide any amount of food resources, especially invertebrates and thus were one of the least preferred habitats in agreement with previous studies (Šálek et al. 2015a, Havlíček et al. 2021). Moreover, the proportion of artificial surface was described as a factor that negatively influences the population size of House Sparrow (Šálek et al. 2015b) and breeding success of other bird species (Corsini et al. 2020). The utilization of this habitat was observed mostly when birds collected remains of human food i.e., bread, or catching flying insects and invertebrates fallen on roads or paths.

Conclusions and applications

In this study, we determined the importance of a combination of human origin “fast-food” and natural food sources for breeding House Sparrows. Parents feeding nestling were willing to fly longer distances to preferred habitats that were mostly scattered and limited, especially in the urban environment. As most of the key habitats (e.g., farms, derelict areas) are under potential threat (replacement by less suitable habitat), we suggest the following recommendations to minimize the effect of these threats and potentially improve crucial resources for House Sparrows and other birds inhabiting human settlements (see also De Coster et al. 2015, Weir 2015, Bernat-Ponce et al. 2020, Havlíček et al. 2021). Because the House Sparrow is an extremely sedentary species (Hole et al. 2002, Anderson

2006, Liu et al. 2012) potential improvements should be aggregated and connected to suitable habitat to make it sufficiently available (De Coster et al. 2015, Bernat-Ponce et al. 2020). On the other hand, even a small loss of suitable habitats (e.g., woody plants or other natural habitats) can result in the reduction or extinction of the local House Sparrow population (Chamberlain et al. 2007, Vangestel et al. 2010, Bernat-Ponce et al. 2020).

1) The most important food resources for House Sparrow nestlings comes from human activity (e.g., debris of food from trash bins and containers or food given to poultry). However, they can disappear due to modernization, urbanization, and socioeconomical and cultural changes (Bokotey & Goban 2005, Erskine 2006, Shaw et al. 2008, Rosin et al. 2016, 2020, Žmihorski et al. 2020). As it is neither possible nor desirable to stop some of these changes, and a diet from these resources is probably of less quality than from natural sources, we recommend focusing primarily on the protection of natural food sources. However, in rural settlements, the House Sparrow can profit from the support of traditional small-scale farming, especially the keeping of poultry.

2) Despite the results of previous studies (Ringsby et al. 2006, Chamberlain et al. 2007, Šálek et al. 2015, Havlíček et al. 2021), we did not confirm the importance of farming-related infrastructure for breeding House Sparrows. We argue that farms support House Sparrows throughout the year with increased food availability, breeding opportunities, and shelter. Therefore, we suggest sustaining small and medium-sized farms focused on mixed farming. As was described in previous studies (e.g., Rosin et al. 2016, Šálek et al. 2018a), this is necessary for the protection of rural populations of House Sparrow and overall farmland biodiversity.

3) We identified that ruderal vegetation, which was typical in the vicinity of farms and derelict places, is a positively selected foraging habitat (see also Villaseñor et al. 2014, Bonthoux et al. 2020). The recent trend of farming intensification (e.g., replacement of old farming infrastructure

with new), and higher aesthetic and hygiene demands in settlements reduces and replaces these habitats with less suitable buildings, intensively managed lawns, or paved surfaces (Bonthoux et al. 2014, Villaseñor et al. 2020). We recommend establishing less managed patches with the presence of native “ruderal” plant species within human settlements. This should be combined with diversified management of grasslands (e.g., patchy mowing, wildflower strips in urban parks, gardens and inter-blocks), which together increase invertebrate and seed availability as was demonstrated within our urban settlement where some of these recommendations were applied (Lipárová 2020, Řehounek 2020, Štěrbová & Koutecká 2020).

4) Finally, shrubs and trees play a key role as a resource of invertebrate prey (e.g., Vincent 2005, Helden et al. 2012, Mackenzie et al. 2014) and shelter for birds (e.g., Whittingham & Evans 2004). Within the urban environment, shrubs and trees seem to be more scattered which leads to increased costs for the parent birds when using this habitat. We assume that shrubs in the urban habitat are less suitable due to their species composition, shape, and management (see above). Thus, we recommend an increase in the proportion and number of native woody vegetation sites, with optimized age, vertical stratification, diverse size, and a balanced proportion of trees and shrubs (Fontana et al. 2011, Pithon et al. 2021). These changes are necessary in urban environments (Seress et al. 2020), but also in smaller settlements and less urbanized areas (see de Satgé et al. 2019).

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Supplementary material

Figure S1. MCP, KDE 50 %, and KDE 95 % home-range size of all studied breeding pairs with more than 5 records in urban (black, n = 18) and rural (grey, n = 30) environments.

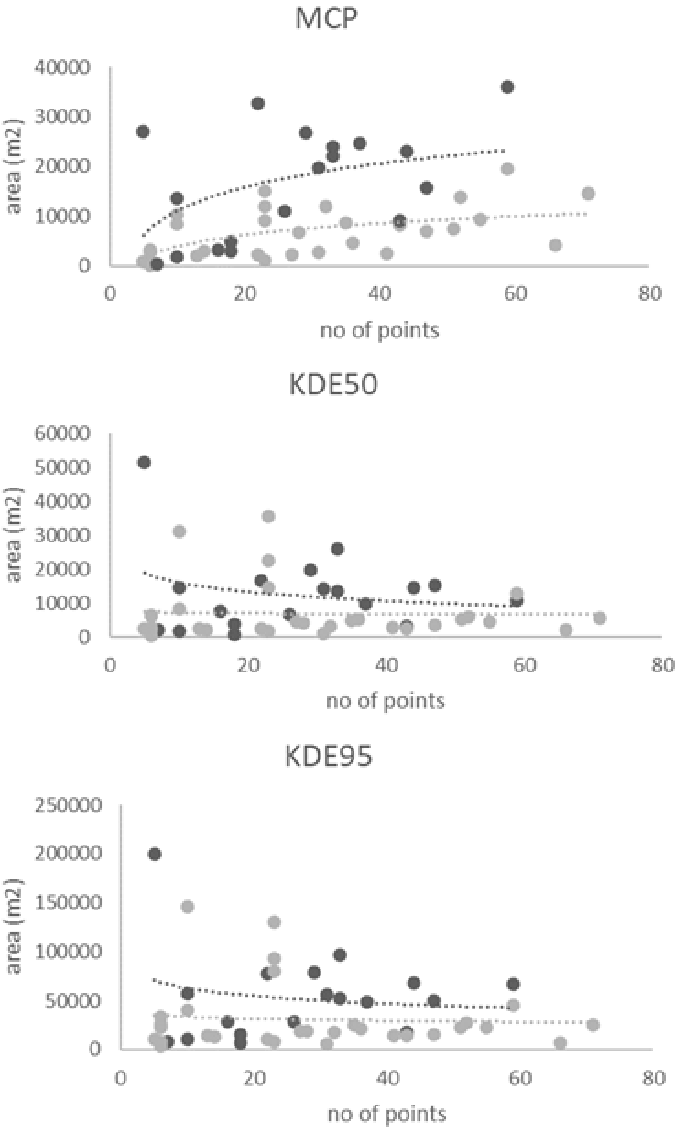

Table S1. Results of Post-hoc Tukey tests (P-values) for distances travelled by House Sparrows among all habitats (art = artificial surfaces, bin = bin stages, bui = buildings, farm = farm, gshort = short grasses, pou = poultry, rtall = tall ruderals, rsho = short ruderals, shru = shrub and trees) within city (c) and village (v) localities. Statistically significant (P < 0.050) or marginally significant (P < 0.010) values are in bold.

	c-art	**v-art**	**c-bin**	**c-bui**	**v-bui**	**v-farm**	**c-gshort**	**v-gshort**	**v-pou**	**v-rtall**	**c-rsho**	**v-rsho**	**c-shru**
v-art	**0.087**												
c-bin	0.581	**< 0.001**											
c-bui	1.000	0.697	**0.023**										
v-bui	1.000	0.247	0.999	1.000									
v-farm	**< 0.001**	0.253	**< 0.001**	0.007	**0.002**								
c-gshort	0.338	1.000	**< 0.001**	0.989	0.914	0.177							
v-gshort	**0.064**	1.000	**< 0.001**	0.622	0.175	0.344	0.999						
v-pou	1.000	**< 0.001**	0.245	1.000	1.000	**< 0.001**	0.561	**< 0.001**					
v-rtall	1.000	**< 0.001**	0.944	0.966	1.000	**< 0.001**	**0.065**	**< 0.001**	0.678				
c-rsho	1.000	0.962	0.949	1.000	1.000	0.241	1.000	0.947	1.000	1.000			
v-rsho	0.657	0.992	**< 0.001**	0.998	0.801	**0.003**	1.000	0.986	**0.019**	**< 0.001**	1.000		
c-shru	0.997	**< 0.001**	0.811	0.256	1.000	**< 0.001**	**< 0.001**	**< 0.001**	0.915	1.000	1.000	**0.006**	
v-shru	0.160	1.000	**< 0.001**	0.877	0.349	**0.007**	1.000	1.000	**< 0.001**	**< 0.001**	0.992	1.000	**< 0.001**

Table S2. Results of Post-hoc Tukey tests (P-values) for time spent by House Sparrows among all habitats within the city (c) and village (v) localities. Statistically significant (P < 0.050) or marginally significant (P < 0.010) values are in bold.

	Artificial surfaces	**Bin stages**	**Buildings**	**Farms**	**Short grasses**	**Meadows**	**Poultries**	**Tall ruderals**	**Short ruderals**
Bin stages	1.000								
Buildings	0.999	0.949							
Farms	1.000	0.999	0.999						
Short grasses	0.992	0.772	1.000	0.996					
Meadows	1.000	1.000	0.990	1.000	0.977				
Poultries	1.000	1.000	0.992	1.000	0.920	1.000			
Tall ruderals	0.176	**0.028**	0.989	0.127	0.940	0.480	**0.010**		
Short ruderals	0.243	**0.050**	0.989	0.273	0.950	0.483	**0.038**	1.000	
Shrubs and trees	0.644	**0.070**	1.000	0.711	1.000	0.784	**0.064**	0.970	0.981

Table S3. Results of compositional analysis for habitats within Kernel home-ranges based on 50% of points and habitat availability within a buffer 150 m around the House Sparrow nests. Data from the city and village were merged. Signs (+/-) refer to that habitat in a row is more/less preferred than habitat in a column.

	Buildings	**Shrubs and trees**	**Poultries**	**Arable land**	**Bin stages**	**Short ruderals**	**Tall ruderals**	**Meadows**	**Farms**	**Water bodies**
Shrubs and trees	-									
Poultries	+++	+++								
Arable land	-	-	---							
Bin stages	+++	+++	-	+++						
Short ruderals	+++	+++	-	+++	-					
Tall ruderals	-	-	---	+	---	---				
Meadows	---	---	---	---	---	---	---			
Farms	+	+	-	+++	-	-	+++	+++		
Water bodies	+	+	---	+	---	---	+	+++	-	
Artificial surfaces	+	+	---	+	---	---	+	+++	-	-

Table S4. Results of compositional analysis for habitats within Kernel home-ranges based on 95% of points and habitat availability within a buffer 150 m around the House Sparrow nests. Data from the city and village were merged. Signs (+/-) refer to that habitat in a row is more/less preferred than habitat in a column.

	Buildings	**Shrubs and trees**	**Poultries**	**Arable land**	**Bin stages**	**Short ruderals**	**Tall ruderals**	**Meadows**	**Farms**	**Water bodies**
Shrubs and trees	-									
Poultries	+++	+++								
Arable land	-	-	-							
Bin stages	+++	+++	+	+++						
Short ruderals	+++	+++	-	+	---					
Tall ruderals	---	-	---	+	---	---				
Meadows	---	---	---	-	---	---	---			
Farms	+	+++	+	+++	+	+	+++	+++		
Water bodies	+	+++	-	+	-	-	+++	+++	-	
Artificial surfaces	-	+	---	+	---	---	+++	+++	-	-

Table S5. Results of compositional analysis for used habitats and habitat availability within a buffer 150 m around the House Sparrow nests. Data from the city and village were merged. Signs (+/-) refer to that habitat in a row is more/less preferred than habitat in a column.

	Buildings	**Shrubs and trees**	**Poultries**	**Arable land**	**Bin stages**	**Short ruderals**	**Tall ruderals**	**Meadows**	**Farms**	**Water bodies**
Shrubs and trees	+++									
Poultries	+++	+								
Arable land	+++	---	---							
Bin stages	+++	+++	-	+++						
Short ruderals	+++	-	---	+++	---					
Tall ruderals	+++	-	---	+++	---	-				
Meadows	+	---	---	---	---	---	---			
Farms	+++	---	---	+++	---	-	-	+++		
Water bodies	+++	---	---	+++	---	-	---	+++	+	
Artificial surfaces	+++	---	---	-	---	---	---	+	---	---

General conclusion

This doctoral thesis focuses on describing the habitat composition and environmental factors influencing population size, distribution, breeding ecology, and foraging behaviour of House Sparrow in different Central European human settlements. These findings are relevant to understanding this species' population changes and dealing with potential threats in the future.

The first study (Šálek et al. 2015) deals with the effect of habitat composition, farming, and altitude on the distribution and population size of House Sparrow during the winter period. The occurrence of House Sparrow was positively affected by the number of instances of poultry keeping, and its density was higher in villages with dairy farms. Both of these habitats offer an abundance of food, and additionally, they can also provide shelter during the critical winter period. Similarly, woody vegetation had a positive effect, whereas the birds avoid arable land, buildings, and grasslands. Additionally, two other species, the Tree Sparrow and Eurasian Collared Dove were studied. Tree Sparrow showed the same response to the number of instances of poultry keeping, but there was no effect of farm presence on its density. The study did not find any such significant relationship for Collared Dove. Habitat preferences of Tree Sparrow and Collared Dove were similar to those found for the House Sparrow.

The second study (Havlíček et al. 2021) focused on describing the factors affecting the occurrence and population density of House Sparrow during the breeding season. Similar to the winter season (first study), the Tree Sparrow and Collared Dove were studied together with House Sparrow. Population densities of House Sparrows and Eurasian Collared doves were positively correlated with the proportion of farmsteads. The population density of Tree sparrows was positively correlated with the proportion of grasslands. Based on the more detailed dataset, House Sparrows and Eurasian Collared Doves occurred at points with an increased proportion of buildings and small-scale farms (i.e., poultry yards in most cases). The

Tree Sparrow occurred at points with an increased proportion of small-scale farms and woody plants. The habitat preference analysis showed that House Sparrow and Eurasian Collared Dove primarily preferred buildings, and Tree Sparrow preferred small-scale farms, whereas all studied species generally avoided arable habitats. Despite the previous statements, the effect of building age, as a factor influencing breeding site availability for the House Sparrow, was not revealed in this study. Additionally, in both (first and second) studies, the negative effect of altitude on the local occurrence and density of House Sparrow was demonstrated. The study discusses that the lower proportion of preferred habitats in the settlements situated at higher altitude is the probable reason.

The third study (chapter III) aims to describe the foraging ecology of House Sparrows feeding their offspring in rural and urban environments. Increased home range size and flight distance were found in urban breeding pairs. Together with differences in utilization and availability of habitats between both types of settlements, these findings imply the absence, or lower availability of critical food sources in the territories of urban-dwelling individuals, compared to rural ones. However, in both environments, the most preferred foraging sites were represented by artificial food sources (i.e., food given to poultry and food scraps from bins). Additionally, some natural sources, such as shrub and tree vegetation, and ruderal habitats typical for farms in rural settlements, play an important role. On the other hand, the importance of farms as a source of food was not confirmed, as they were not frequently used as a foraging habitat. Still, the study implies that the presence of a farm increases food availability indirectly (e.g., due to the presence of ruderal habitats surrounding farm buildings or unmanaged field margins).

Solutions to protect and support the House Sparrow population in urban habitats and farmland settlements are described in the second and third study. In particular, regarding current and potential future changes in the urban environment and agricultural landscape, which is likely to reduce some critical foraging and breeding habitats (discussed in all three studies). These suggestions are also relevant for protecting the whole bird community inhabiting similar habitats, for example, the Tree Sparrow and Eurasian Collared Dove, the species studied together with House Sparrow in the first two studies. We generally recommend (see the second and third study for more details) the support of extensive mixed small- and medium-scale farming and traditional "hobby farming" such as the keeping of poultry. Changes in farming practices and farm infrastructure (e.g., replacing of old buildings and abandoned parts with modern facilities, using new technologies and operations, etc.) has an impact on food sources and breeding opportunities for birds. In both rural and urban environments, "green space" is an important source of invertebrate food for the offspring. Therefore, we recommend (see the third study) increasing the proportion and number of woody plant patches (shrubs and trees) with more diversified structures and a higher proportion of native species instead of exotic ones. The replacement of highly managed lawns with extensive and species rich (including ruderal species) grass plots and the preservation of patches of wasteland and ruderals would also significantly increase food availability.

The results of this thesis also give rise to new questions and challenges for future research. Previous studies pointed out that farms and rural settlements are strongholds for many bird species. This thesis, for example, shows that farms support the House Sparrow in different ways during the breeding and non-breeding seasons and that the importance of farms could, in part, be due to the presence of some habitats in the vicinity. This finding implies that fine-scale habitat preference studies (e.g., as was done in this thesis – see the third study and cited studies) are required for more species inhabiting farms, villages, urban habitats, and in different seasons. According to the results and my experience from conducting the third study, I recommend using the direct observation method (at least to verify, or in combination with other methods, e.g., GPS tracking) for habitat preference fine-scale studies. Additionally, experimental studies should be combined with the methods mentioned above to evaluate the utilization of different habitats when compared to supplementary feeding with food of different quantity, quality, and controlled access. Along with increasing demands of inhabitants on green space management and higher hygiene, growing pressure on green space is expected in the future. A year-round detailed study on the effect of green space composition, structure, etc., on its utilization by birds would help to preserve and improve the suitability of this crucial habitat for the bird community in human settlements. Similarly, little is known about the importance of “hobby” small-scale farming (e.g., poultry keeping) on the whole bird community.

There are many studies dealing with the impact of different types and ages of buildings and parts of settlements on the density of House Sparrow, or the whole bird community, however, the results are ambiguous. Thus, more research based on a detailed study of breeding site selection in different types of architecture, use, and age of buildings and the parts of settlements, including the effect of surrounding habitat composition, would improve our understanding. To better understand the impact of particular factors, studies on foraging and breeding ecology should be carried out simultaneously.

The adoption of all potential improvements and conservation actions in human settlements and farms depends on the understanding and identification of the local community with the importance of protecting the birds. In this case, the House Sparrow can play a role as a generally well known and widespread species, which is also suitable for citizen-science projects, as we confirmed in the first and second studies.

Curiculum vitae

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Education

2014–present: Ph.D. in Zoology: University of South Bohemia in České Budějovice, Faculty of Science.
Thesis: The breeding and foraging ecology of the House Sparrow in rural and urban environments. Supervisors: Roman Fuchs, Martin Šálek

2014–2015: Pedagogical certificate for the High school teaching, National pedagogical institute of the Czech Republic.

2011–2014: M.Sc. in Zoology: University of South Bohemia in České Budějovice, Faculty of Science.
Thesis: House sparrow feeding ecology in contemporary rural settlement. Supervisor: Roman Fuchs

2008–2011: B.Sc. in Biology: University of South Bohemia in České Budějovice, Faculty of Science.
Thesis: The causes of decline of the House Sparrow in different types of human settlement - habitat? breeding site? diet? Supervisor: Roman Fuchs

Work experience

2019–present: Research assistant, Department of biological disciplines, Faculty of Agriculture, University of South Bohemia in České Budějovice

2020–present: Project guarantor, Technology Agency of the Czech Republic

2012–present: Zoological assessments of development projects, biological monitoring, coordination of bird monitoring, bird guide; self-employed

2017–2019: Coordinator of the bird monitoring, Department of the monitoring of biodiversity, Headquarters of the Nature Conservation Agency of the Czech Republic, Prague

2016–2018: Research assistant, Department of zoology, Faculty of Science, University of South Bohemia in České Budějovice

Study stays

2017 Terrestrial Ecology Unit, Department of Biology, Ghent University, Belgium (1 month)

2015 Konrad Lorenz Forschungsstelle (KLF), Grünau im Almtal, Austria (1 month)

2015 Terrestrial Ecology Unit, Department of Biology, Ghent University, Belgium (short stay)

2012 Centre for polar ecology, field station Petunia, Svalbard (2 weeks)

2007 Administration of the Třeboňsko landscape protected area, Třeboň (1 month)

Teaching

Faculty of Science, University of South Bohemia in České Budějovice:

Diversity of life (field presentation)
Ecology (field presentation)
Field course of alpine zoology (field presentation)
Field ornithological methods (lecture, field presentation)
Field Work I (field presentation)
Field Work II (field presentation)
Field course of alpine zoology (field presentation)
Interdisciplinary Excursion "Ecology of Biomes" (field presentation)
Vertebrate Zoology (lecture on practical lessons)
Vertebratological Excursions (field presentation)

Faculty of Agriculture, University of South Bohemia in České Budějovice:

Biological Monitoring (lecture, field presentation)
Breeding of Exotic Birds (lecture)
Ecology and Ecophysiology of Animals (lecture)
Ornithology aimed at CITES (lecture)
Taxonomy of CITES Animals (lecture)
Zoology (lecture)
Zoology A (lecture)

Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague:

Monitoring of the free-living animals (lecture)

Students

Hnídková Lucie (M.Sc., defended, Faculty of Agriculture – South Bohemia University): Distribution and abundance of wintering and breeding population of Mute Swan (*Cygnus olor*) in the South Bohemia region. (supervisor)

Konvalinová Alena (B.Sc., defended, Faculty of Agriculture – South Bohemia University): Subsequent care for permanently handicapped animals of selected species. (supervisor)

Machová Markéta (M.Sc., defended, Faculty of Science – South Bohemia University): Habitat requirements of synanthropic bird species *Passer domesticus*, *Passer montanus*, and *Streptopelia decaocto*. (consultant)

Millerová Adéla (M.Sc., defended, Faculty of Agriculture – South Bohemia University): Autumn Eurasian Crane (*Grus grus*) migration passage across the Czech Republic with special focus on the south-west Bohemia region. (supervisor)

Novotná Nikola (M.Sc., defended, Faculty of Agriculture – South Bohemia University): Domestic cats (*Felis catus*) as a phenomenon in the conservation biology - their impacts on biodiversity. (supervisor)

Černá Zuzana (B.Sc., finished – no defence yet, Faculty of Agriculture – South Bohemia University): Assessing of the risk of transparent surfaces for birds in selected urban agglomerations. (supervisor)

Balabán Michal (B.Sc, in progress, Faculty of Agriculture – South Bohemia University): The impact of hand-rearing of the Psittaciformes chicks on their future breeding behaviour and reproduction abilities. (supervisor)

Janů Kateřina (B.Sc, in progress, Faculty of Agriculture – South Bohemia University): Phenology of selected species of waders (Charadriiformes: Scolopacidae: Calidrinae) passage across the Czech Republic, analysis based on faunistical records. (supervisor)

Kalendová Pavlína (M.Sc., in progress, Faculty of Agriculture – South Bohemia University): The factors influencing population density of the non-native mammal predator (*Felis catus*) in the Central-European cultural landscape and human settlements and its impact on biodiversity. (consultant)

Loudová Hana (M.Sc., in progress, Faculty of Science – South Bohemia University): Inter-annual and inter-seasonal fidelity and dispersal of South-Bohemian population of Mute Swan (*Cygnus olor*): bird ringing data analysis. (consultant)

Papač Martin (M.Sc., in progress, Faculty of Agriculture – South Bohemia University): Biology and methodics in breeding of the exhibition Zebra Finch (*Taeniopygia guttata*), taking into account nutrition and deviations of body dimensions. (supervisor)

Patrovská Alexandra-Valerie (B.Sc, in progress, Faculty of Agriculture – South Bohemia University): Biotope preferences of the Eurasian woodcock (*Scolopax rusticola*) in the changing forest ecosystems: the possibilities of use of acoustic monitoring. (supervisor)

Rášková Dominika (M.Sc., in progress, Faculty of Agriculture – South Bohemia University): Inter-annual survival of the house sparrow (*Passer domesticus*): analysis based on the colour ringing. (consultant)

Větrovcová Kristýna (B.Sc, in progress, Faculty of Agriculture – South Bohemia University): Mapping of the feral cat inside and outside the human settlements with different farming practices. (supervisor)

Publications

Peer review publications

Havlíček, J., Riegert, J. & Fuchs, R. (submitted). Home-range size, flight distance and preferences for foraging habitats in House sparrow (*Passer domesticus*): A comparison of city and rural population.

Veselý, P., Syrová, M., Voháňková, M., Nácarová, J. & Havlíček, J. (submitted). Cowards or clever guys: an alternative strategy of shrikes defending nests against magpies.

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Havlíček, J. (ed., 2020). Závěrečná zpráva, Monitoring druhů ptáků přílohy I v PO – jižní Čechy. 21 p., Dep.: AOPK ČR.

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Conferences (selected)

Havlíček, J. (2018): The mapping and monitoring of the waders in the large scale protected areas in the Czech Republic: preliminary results. International Wader Study Group Annual Conference, Workum 2018, Netherlands. (poster)

Havlíček, J., Bandhauerová, J., Šálek, M. & Fuchs R. (2016): The current status of Sparrows in the Czech Republic: results from national monitoring. WGUS 5th International House Sparrow Meeting 3.–4. 11. České Budějovice. (oral presenatation)

Havlíček, J., Piálek, L. & Fuchs R. (2016): From populations to food, from food to genes. WGUS 5th International House Sparrow Meeting 3.–4. 11. České Budějovice. (oral presenation)

Havlíček, J. & Fuchs R. (2015): Are cities better for raising kinds than the country? Foraging habitats of the House Sparrow in different urban environments. Graduate meeting 2015. Sep. 17–19. Grünau im Almtal, Austria. (poster)

Havlíček, J. & Fuchs, R. (2014): Where is better to live? Feeding habitats of House Sparrow in rural and urban environment. 4th International House Sparrow Meeting Nov. 20–21st, Gent, Belgium. (oral presentation)

Awards

The best student poster – Zoologické dny Brno 2015

Jan Heyrovský award – 2008

Other skills and achievements

Guarantor of data in the Database of biological records – Nature Conservation Agency of the Czech Republic

Member and secretary of the committee of South Bohemian ornithological club (since 2010)

Coordinator (1 x international) and member (3x national) of conference committee

Member of Working Group on Urban Sparrows

Coordinator of Working group of the Czech society of ornithology for the House Sparrow and synanthropic species

Member (co-coordinator in 2007–2013) of Working group of the Czech society of ornithology for Research and protection of waders

Full bird ringing licence

Coordinator of Bird breeding atlas of České Budějovice city 2010–2018

Coordinator of the Report under Article 12 – The State of Nature in the EU - reporting on status and trends of bird species, Czech Republic

National contributor of the EU International single species action plan for the conservation of the European Turtle Dove *Streptopelia turtur*

Certificate of professional competence for designing experiments and experimental projects under Act on the protection of animals against cruelty.

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