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Abstract. Although rapid growth in the extent of urbanized habitats across the globe represents a major threat to biodiversity, there is growing evidence that urban ecosystems can represent suitable habitats for many taxa, including birds. Exploring aspects of bird ecology across the urban-rural gradient, including determinants of habitat associations, are crucial to understanding responses to urbanisation. Here, we examined factors affecting nest-site selection of Eurasian magpies across an urban-rural gradient, contrasting urban and non-urban habitats. The presence and density of Eurasian magpie nests was positively associated with the proportion of green urban areas, and negatively with forests, arable land and buildings, despite habitat associations differing across the urban-rural gradient. We also found a negative relationship between nest height and distance from city edge. The highest nests were found in city centre residential areas, whereas the lowest nests were in the new residential areas. We conclude that Eurasian magpies can successfully exploit urban environments, partially due to adaptation of their nesting behaviour. In particular, they construct their nests higher in urban areas to avoid the negative impacts of human disturbance and predation.

Key words: urbanisation, nest selection, urban birds, nest height, behavioural plasticity, urban habitats

Introduction

Urbanisation is a global phenomenon driven by rapid human population growth that represents a crucial threat to terrestrial ecosystems. This process has been accelerating around the world in recent decades (Vitousek et al. 1997, Sala et al. 2000, Seto et al. 2012). Conversion of natural habitats into anthropogenic habitats in particular is a major cause of land-use change worldwide (Pickett et al. 2001), with a myriad of negative consequences for ecosystem function and stability. Urbanisation is generally considered to have a negative effect on biodiversity at various spatial scales,

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most importantly due to the loss, modification or fragmentation of natural and semi-natural habitats (e.g. Aronson et al. 2014, Elmqvist et al. 2016). On the other hand, there is an increasing body of scientific evidence that some wildlife species, especially species with high ecological and behavioural plasticity, or flexible life-histories, that have adapted to live in proximity to humans, and urban and suburban areas may represent suitable habitats for a variety of species (Šálek et al. 2015a). For example, an urban environment may have increased habitat heterogeneity compared to surrounding intensively-used agricultural or afforested landscapes (Blair 1996, Cadenasso et al. 2007). Furthermore, some species may benefit from the increased availability of human-related food resources or warmer microclimates, especially in temperate regions, which may result in a high population density of some species in urban compared to rural landscapes (Møller 2009, Šálek et al. 2015a, Isaksson 2018). With urbanisation predicted to expand dramatically over the next century (Seto et al. 2012) it is crucial to understand species-specific responses to urbanisation, which may help in effective formulation of conservation measures and sustainable landscape planning of urban environments for wildlife.

Urbanisation has greatly influenced bird communities at large geographic scales, leading to decreasing species richness and community homogenisation as populations of specialist species become increasingly threatened by the rising rate of urbanisation, resulting in local extinctions (McKinney 2006, Devictor 2007). Successful exploiters of urban ecosystems are represented mainly by species characterized by large distributional ranges, broad environmental tolerance, high propensity for dispersal, marked habitat and dietary flexibility and tolerance of human activity (e.g. Møller 2009, Palacio 2020). These bird species are able to inhabit the whole urban-rural gradient, sometimes even benefiting from urbanisation, which may lead to elevated population densities in urban habitats (Møller 2009). Corvids (Aves: Corvidae) are considered successful bird groups that have colonized urban environments, and are characterized by substantial habitat and dietary plasticity (Kulemeyer 2009). These characteristics have been linked to increased brain size, which may be another prerequisite for urban colonization. In particular, species with a large-brain (e.g. corvids) may better cope with novel conditions and be able to express innovative

behaviour, e.g. during feeding (Sol et al. 2005, Kulemeyer 2009). For example, urban populations of the rook *Corvus frugilegus*, common raven *Corvus corax*, jackdaw *Corvus monedula*, Eurasian jay *Garrulus glandarius*, Eurasian magpie (*Pica pica*) and hooded crow *Corvus cornix* are known to inhabit European cities and are assumed to be the successful urban exploiters, despite geographical differences in species-specific establishment and urbanisation success (Kulemeyer 2009).

The Eurasian magpie is a medium-sized sedentary and omnivorous corvid inhabiting a variety of open or semi-open habitats with hedges, bushes, or patches of trees and shrubs. In Central and Western Europe, its breeding distribution is mainly associated with human-modified landscapes (Hagemeijer & Blair 1997). Especially since the 1960s and 1970s, the population of Eurasian magpies has rapidly increased across many European countries, with magpies increasingly colonising suburban and urban habitats (Birkhead 1991, Gregory & Marchant 1996, Hagemeijer & Blair 1997, Luniak et al. 1997, Jokimäki et al. 2017). Urban and suburban populations of Eurasian magpies have increased faster than rural populations. For example, Jerzak (2001) found that Eurasian magpie populations in western Poland increased three times faster in urban compared to rural landscapes. It was also shown that urban Eurasian magpies have higher breeding success (Eden 1985). Within the urban environment, the Eurasian magpie may utilize a wide variety of urban habitats (Luniak et al. 1997); though it primarily uses habitats with an area of green cover and avoids densely built-up areas (Jokimäki et al. 2017). Moreover, as a specific adaptation to living in close proximity to humans, the Eurasian magpie may increase its nest height with increasing level of urbanisation. Higher nests may be more secure from humans and mammalian predators (e.g. Antonov & Atanasova 2002, Wang et al. 2008, Zbyryt & Banach 2014).

The aim of this study was to investigate factors affecting nest-site selection of Eurasian magpies across an urban-rural gradient. More specifically, we explored i) the effect of habitat composition on the presence and numbers of Eurasian magpie nests, and ii) the effect of urbanisation and tree species on nest height selection. We predicted that population densities would change across the rural-urban gradient, with the highest densities at the city edge. We further predicted that green urban habitats would be preferred, and that built-

up, arable or forest habitats would be avoided, though the pattern of habitat associations might vary across an urban-rural gradient. Finally, we predicted that iii) nest height would decrease along an urban-rural gradient.

Material and Methods

Study area

The research was conducted in and around the medium-sized city of České Budějovice (94,000 inhabitants, 48°57′ N, 14°28′ E), South Bohemia, Czech Republic, Central Europe (Fig. 1). The study area, with a total area of 85.3 km², is located at altitudes ranging from 380-540 m a.s.l. and characterised by a moderate continental climate (annual temperature: 7.8 °C, precipitation: 600-620 mm; Červinka et al. 2014, Šálek et al. 2015b). The urban environment mainly consists of anthropogenic habitats, including built-up areas (low to high-density residential developments, commercial and industrial buildings; 7.1%) or artificial surfaces (e.g. roads, streets, pavement networks or parking spaces; 13.3%). The semi-natural habitats within the urban environment mainly consist of green urban habitats (formed by private gardens, public parks, lawns, green areas along watercourses), and shrub and forest fragments; 11.0%). The city is surrounded by intensively-used farmland that is primarily used for arable production (especially cereals, maize, and rapeseed; 41.1%), and grasslands (e.g. intensive hayfields or pasture, with fragments of ruderal vegetation; 16.8%). Forests (6.7%) are represented by small uniform copses and established secondary coniferous or mixed stand forestry plantations that are dominated by Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, with occasional broad-leaved trees and aquatic habitats, including rivers, streams and man-made fishponds (4.0%).

Study design

To investigate the effect of urbanisation intensity on Eurasian magpie habitat selection, we monitored nest distribution across an urban-rural gradient, including the city centre, city edge and surrounding farmland, and in contrasting urban and non-urban habitats that differed in human activity and habitat composition (see also Šálek et al. 2015b). The city edge was defined as a 200-m buffer zone around the city border (represented by a continuously built-up area), including both (sub) urban and farmland habitats. The urban centre was represented by the area within the 200-m buffer in the direction of the city centre. The farmland zone comprised habitats outside the 200-m buffer. We divided the study area into eight urban or non-urban habitats: i) urban centre representing the area with the highest human population density and characterised by a high proportion of artificial structures and built-up areas, consisting of old multi-storey buildings, especially built in the 18th and 19th centuries. Green spaces were mainly located in inner courtyards and small-scale private gardens; ii) garden colonies (allotment gardens) consist of a large proportion of private gardens with extensive hobby farming. Built-up areas are represented by small cottages and garden sheds; iii) industrial and commercial sites represent areas with low human population density and a high proportion of artificial surfaces. This category mainly includes commercial zones, parking
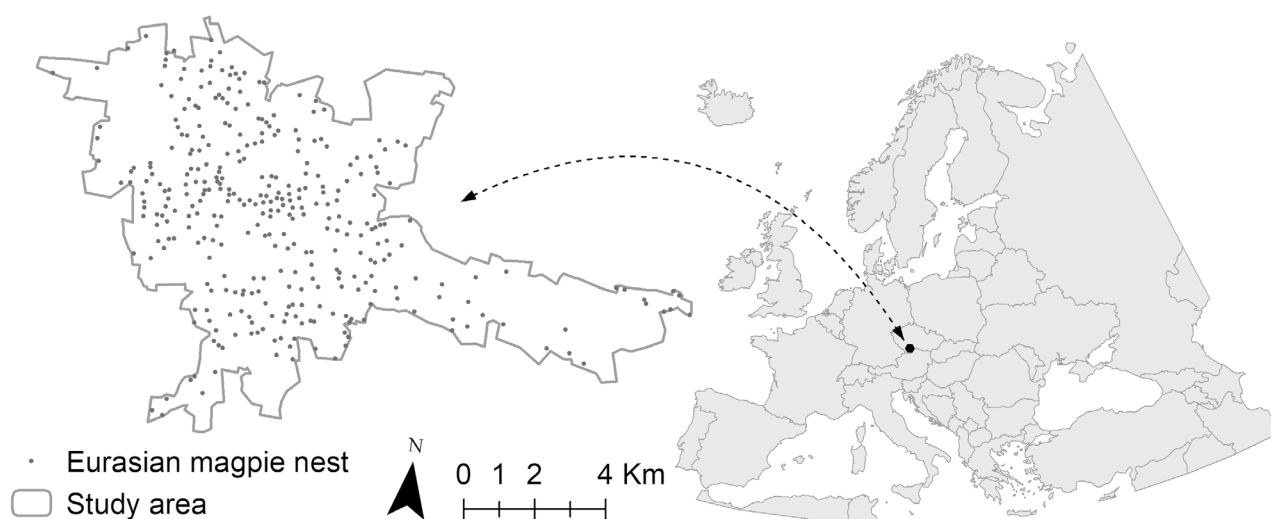
Fig. 1. Maps showing location of the study area in the medium-sized city of České Budějovice (Czech Republic) and location of Eurasian magpie nests.

zones, industrial parks, warehouses, factories, or brownfield sites with a small proportion of semi-natural vegetation (e.g. various types of grasslands, shrub and tree patches); iv) parks and cemeteries represent urban areas dominated by semi-natural vegetation with a small proportion of artificial surfaces and built-up areas with low human population density; v) panel housing comprises built-up areas with multi-story blocks of flats built during the 1990s and 1980s or earlier. Green areas are represented by open-public spaces, such as lawns, native and non-native shrubs, small copses and scattered trees; vi) residential areas represent built-up areas mainly consisting of single-family houses mostly built from the beginning of 19th century onwards, but not less than 25 years old. These houses are typically surrounded by a substantial proportion of private gardens; vii) new residential areas consisting of built-up areas with newly built one to two-story single-family or terraced houses not older than 25 years. Green areas comprise private gardens with a considerable proportion of non-native vegetation. Finally, viii) farmland represents the area with the lowest human population density and consisting of a mosaic of farmed (arable fields and pasture) and non-farmed habitats (including forest fragments and non-cropped vegetation, such as hedges, isolated trees and shrub patches), with a negligible proportion of artificial and built-up areas (see Table S1).

To study the effects of habitat composition on the presence and nest density of Eurasian magpies, the study area was divided into 400 × 400 m mapping squares (n = 650; Fig. 1). Within each mapping square, we determined the proportion of the seven main habitats that may represent important predictors of Eurasian magpie distribution within the human-dominated landscape (e.g. Jokimäki et al. 2017). We evaluated the proportion of buildings, artificial surfaces, green urban areas, grasslands, arable, forest habitats and aquatic habitats. Aquatic habitats were excluded from subsequent analyses, as this habitat does not represent suitable habitat for the study species. The built-up areas are composed of a variety of buildings (multi-story buildings, multi-story blocks of flats, single-family houses and garden sheds) and industrial or commercial units. Artificial surfaces are mostly composed of pavements, roads, streets, railway networks or parking spaces. The green urban areas are mainly composed of grassland habitats (lawns, meadows, and brownfield sites), parks, orchards,

and private gardens. Arable habitats are primarily used for intensive cultivation of cereals, maize, oilseed rape and lucerne, and grasslands mostly consist of hayfields and pasture, with a smaller proportion of ruderal vegetation. In each square, we also estimated the proportion of non-mapped area and the distance (m) of the square centroid from the city edge. The area of each habitat within a square was obtained from 1:10,000 ZABAGED (Primary Geographic Data Base) land cover maps, using GIS tools (QGIS 2012). For the purpose of the habitat selection analysis, we generated a similar numbers of random points (according to the number of Eurasian magpie nests) using GIS Tool Random Point Generator (Jenness 2005) that were randomly spread over the entire study area.

The survey of Eurasian magpie nest distribution was based on searching for nests in the non-breeding season (November-February 2018/2019) when deciduous trees were without leaves and nests could be readily seen. During the survey, all available places/habitats within urban (e.g. built-up areas, roads, streets, pavements and pathways as well as orchards, parks, and inner yards) and non-urban habitats (e.g. non-cropped vegetation, hedges, isolated tree and shrub patches, forest fragments, forest edges, farmland) were checked. The exact position of individual Eurasian magpie nests and nest height were plotted on detailed aerial maps (1:5,000; Seznam Maps 2015) and recorded on GPS devices. Nest height was estimated visually by the same person (M. Šálek) to avoid inter-observer variation. In cases when two nests were situated less than 100 m apart, we treated this as one breeding territory; these records represented only a minor part of the total dataset and most consisted of unfinished or older nests in proximity to the main nest (e.g. in the same tree). The location and height of 335 Eurasian magpie nests across the urban-rural gradient, along with information on urban and non-urban habitats, were included in the dataset.

Statistical analysis

We used the data from 400 × 400 m mapping squares covering the whole study area to test the effect of habitat representation (i.e. proportion of grasslands, green urban areas, artificial surfaces, buildings, forests and arable land) on the presence of Eurasian magpie nests (binomial variable) and distance of the centroid of each square from the city edge (n = 650 squares). We also performed an additional analysis in which we used only quadrats including Eurasian magpie nests (n =

402 squares) to test the effect of quadrat centroid distance from the city edge and number of Eurasian magpie nests, a variable with a Poisson distribution. The effect of each habitat type (i.e. primary predictors) was calculated using variance partitioning by principal coordinate analysis of neighbour matrices (PCNM) in Canoco 5 (ter Braak & Šmilauer 2012), an approach recommended by Marrot et al. (2015). This multivariate analysis enabled us to separate the effects of geographical position (i.e. space predictors) from the effects of the primary predictors (Legendre & Legendre 2012). This 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. identifying 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 (see Šmilauer & Lepš 2014).

Habitat preferences were computed as the $\log_2$ index between the number of Eurasian magpie nests and the same number of random points within each habitat category (i.e. grasslands, green urban areas, artificial surfaces, buildings, forests and arable land) according to Sunde et al. (2001). Firstly, we computed preferences for the complete dataset and used categories within the urban-rural gradient (i.e. urban core, urban edge and rural). We compared the numbers of magpie nests with random points for each category using a Chi-squared test. This test was performed for the whole study area, as well as for the main categories along the urban-rural gradient (core, edge and farmland).

The effect of factors on nest height was computed with a GLMM with an identity link function using R 3.5.1 software (R Core Team 2018), with tree species included in the model as a random factor. We used habitat (urban centre, residential areas, new residential areas, panel housing, parks and cemeteries, industrial and commercial places, garden colonies and farmland) and distance of nest from city edge (m) as fixed factors in the model.

Results

The relationship between the distance from the city edge, Eurasian magpie nest presence or nest density, and habitat composition within 400 × 400 m mapping squares was tested by two multivariate PCNM analyses (Table 1). In the first PCNM analysis, we tested the presence of Eurasian magpie nests as a binomial variable. Distance of square centroid from the city edge and Eurasian magpie nest presence/absence together explained 48.4% of variability and spatial predictors explained 2.3% of variability. The shared fraction was 10.9% of variability. We found a clear gradient along the first ordination axis, with proportions of some habitat variables showing a negative correlation with this axis (correlation coefficients: buildings –0.88, artificial surfaces –0.94 and green urban areas –0.91) while others showed a positive correlation (forest 0.89 and arable land 0.86). Proportion of grassland was negatively correlated with the second ordination axis (–0.85; Fig. 2a). Distance of square centroid from the city edge was positively correlated (0.68) with the first ordination axis. Presence of Eurasian magpie nests was positively correlated with an increased proportion of buildings, artificial surfaces and green urban areas, whereas absence of Eurasian magpie nests was characterised by an increased proportion of forests, arable land and grasslands (Fig. 2a).

The results of the second PCNM analysis, including only squares occupied by Eurasian magpie nests, showed a higher contribution of the number of magpie nests and distance of quadrat centroid from the city edge (11.0% of variability) than spatial predictors (2.8% of variability). The shared fraction was 12.4% of variability. Similar to previous analysis, we found a gradient on the first ordination axis in habitat composition within a square. A negative correlation with this axis was found for proportions of artificial surfaces (–0.96), buildings (–0.91) and city green areas (–0.89). A positive correlation with the first ordination axis was found for proportions of arable land (0.87) and forest (0.97). Proportions of grassland showed
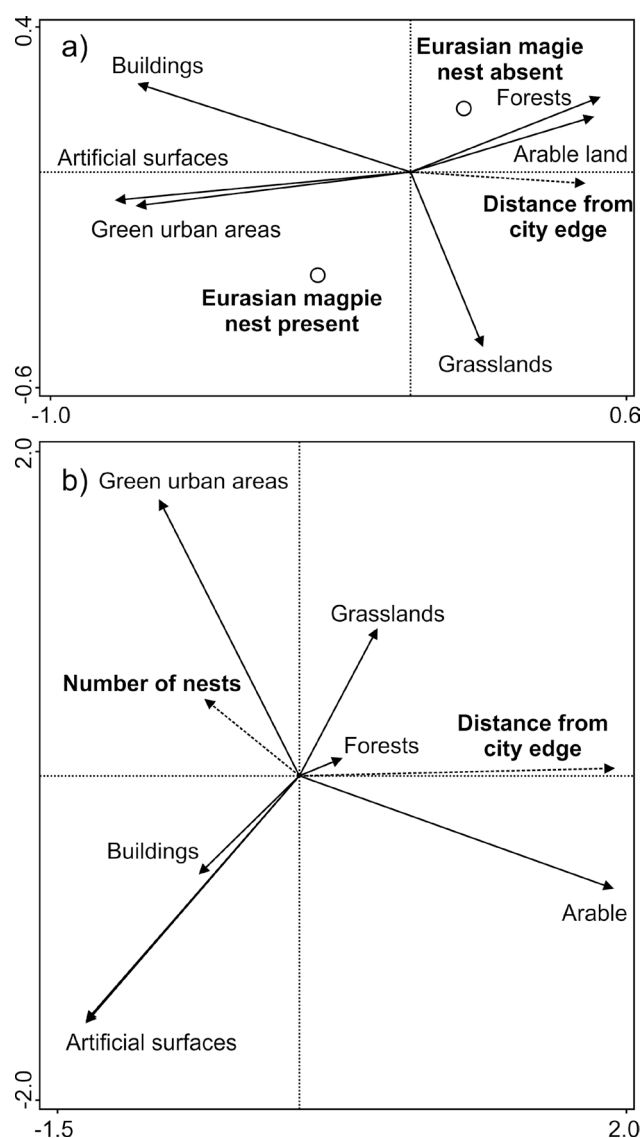
Fig. 2. Projection scores for the main habitat types within 400 x 400 m squares with respect to distance from city edge and a) presence of nests in a square (n = 650 squares) and b) number of nests within a square with at least one nest (n = 402 squares). PCNM analysis, I. and II. ordination axes together explain 14.6% and 13.3% of variability, respectively.

a positive correlation with the second ordination axis (0.85; Fig. 2b). Distance of square centroid from the city edge was positively correlated with the first ordination axis (0.66). The number of Eurasian magpie nests showed a weak positive correlation with the second ordination axis (0.22; Fig. 2b). The number of nests was positively correlated with the proportion of green urban areas and negatively with the proportion of arable habitats. The proportion of grasslands, buildings and artificial surfaces were not related to the number of nests.

The relationship between the distance from the city edge and number of Eurasian magpie nests in the square was not linear. In particular, we found that

for nest presence/density the highest probability of nest occurrence was between –1,200 and –400 m. In another words, the highest breeding density was recorded within the city area near its edge (Fig. 3).

Magpie nest habitat preferences among the main habitats significantly differed for the whole study area (Chi-squared = 185.7, df = 5, $P < 0.001$), as well as for the main categories along the urban-rural gradient (core: Chi-squared = 75.6, df = 5, $P < 0.001$; edge: Chi-squared = 136.8, df = 5, $P < 0.001$; farmland: Chi-squared = 86.8, df = 5, $P < 0.001$).

Based on $\log_2$ (use/available) indices, we found that Eurasian magpies in general preferred green urban areas and, to a lesser extent, forest and grassland. Arable land and buildings were avoided (Fig. S1a). However, when we used categorisation on the urban-farmland gradient, we found that some habitats were differently preferred by Eurasian magpie in urban areas and farmland. For example, magpies showed a preference for breeding in city edge habitat (and urban core) compared to forest and grassland. However, the opposite habitat-specific preference was found for Eurasian magpies breeding on farmland (Fig. S1b).

In total, we found 335 Eurasian magpie nests, of which 293 nests (87.5%) were found in broadleaved trees, 34 (10.1%) in conifers, 3 (0.9%) on electric pylons and 5 (1.5%)) in unknown trees. Nests were found in 28 tree species/genera. Common oak *Quercus robur* and silver birch *Betula pendula* were the most frequently utilised tree species, accounting for 24.5% and 16.1% of Eurasian magpie nests, respectively (Table S2). The effect of nest height was significantly affected by habitat utilisation and distance from the city edge (Table 2). Eurasian magpie nests were situated higher in the urban centre, residential areas and industrial and commercial sites. The lowest nest heights was found in new residential areas (Fig. S2). Nest height was negatively correlated with the distance from the city edge (Fig. 4). We additionally found that Eurasian magpie nests were built higher on specific tree genera, e.g. on *Populus* sp. or *Quercus* sp. (Fig. S3). Consequently, we looked at the distribution of nest-tree species within our study area. We found that the same tree species were used by Eurasian magpies as a nesting tree with similar frequency in urban areas and farmland (Fig. S3). Thus, we do not believe that the negative relationship between nest height and distance from the city edge is influenced by tree species distribution.

Table 1. The effect of primary (environmental) predictors and spatial (PCO) predictors on habitat structure within 400 x 400 m squares with the presence (n = 650 squares) of Eurasian magpie nests and their number within a square (n = 402 squares). PCNM analyses, I. and II. ordination axes together explain 14.6% and 13.3% of variability, respectively.

Eurasian magpie nests	Predictor	% of explained variability	Pseudo-F	P
Binomial variable (0/1)	Occurrence of nest	17.6	29.9	0.002
	Distance to city edge (m)	76.4	162	0.002
	PCO.30	11.1	63.6	0.002
	PCO.10	2.9	17.1	0.002
	PCO.8	2.9	17.4	0.002
Poisson variable (1-5)	Distance to city edge (m)	91.2	192	0.002
	Number of nests	3.3	6.9	0.002
	PCO.30	11.1	63.6	0.002
	PCO.10	2.9	17.1	0.002
	PCO.8	2.9	17.4	0.002
	PCO.25	2.6	15.7	0.002

Discussion

A detailed understanding of the spatial distribution, habitat selection and species-specific adaptation of birds to urban environments may provide crucial information about the impact of urbanisation on their populations and, therefore, may represent an important tool for bird conservation and sustainable landscape planning of urban spaces. Previous studies have demonstrated that corvids are a successful bird group that have colonised various urban habitats across Europe, especially through their high habitat and dietary flexibility and tolerance for human activity. Here, we showed that Eurasian magpie habitat selection and nest placement differs significantly across the urbanisation gradient, and in contrasting urban and non-urban habitats, which brings an important perspective to its adaptation to the urban environment.
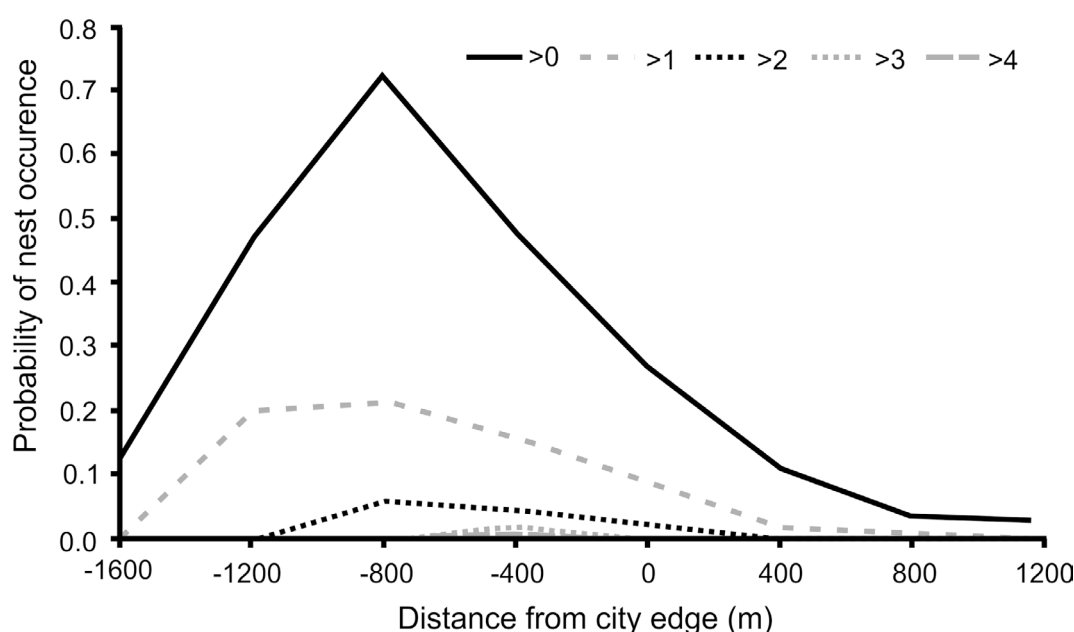
Fig. 3. The probability of Eurasian magpie nest presence with square centroid distance from city edge for summed data for at least one (> 0), two (> 1), three (> 2), four (> 3) and five (> 4) nests within a 400 x 400 m square (number of squares with Eurasian magpie nests/total number of squares within a distance band). Numbers on the x-axis represent the lower range of each 400 m distance category from the city edge. For distance values, the city edge represents the zero value, negative values represent a gradient to the city centre, and positive values represent a gradient to rural areas.

Table 2. The effect of selected factors on Eurasian magpie nest height using GLMM analysis (n = 317 nests).

Independent variable	df	Chi	% of explained variability	beta	P
Habitat utilization category	11	24.4	1.2	-	0.002
Distance from city edge	12	4.7	0.2	−0.39	0.031

Both multivariate analyses showed that both the presence and number of nests within mapping squares were positively correlated with the proportion of green urban areas (see also Jokimäki et al. 2017). More specifically, separate habitat analyses across the urban-rural gradient confirmed a preference for green urban areas in all three habitat areas. Eurasian magpie nest presence was also positively correlated with an increasing proportion of grassland and artificial surfaces. The proportion of artificial surfaces was, however, positively correlated with the proportion of green urban areas and we propose that the positive relationship between the proportion of artificial surfaces and magpie nest presence was an artefact. The absence of Eurasian magpie nests within mapping squares was connected with an increased proportion of forest, arable land, and buildings.

These results correspond well with nest habitat selection of Eurasian magpies across European urban ecosystems. In particular, preference for green urban areas and grasslands is related to availability of tree species suitable for nesting (Jokimäki et al. 2017) and the availability of food resources during the nesting period (i.e. especially surface-dwelling invertebrates; Tatner 1983). Arable land, forest and buildings are generally unsuitable habitats for the Eurasian magpie due to the lack of nesting (arable habitats and buildings) or foraging (forest) opportunities. Interestingly, the habitat selection analysis suggests that habitat selection of breeding Eurasian magpies may differ across the urban-rural gradient. For example, grasslands were preferred only in urban habitats (city centre and city edge), whereas forests were preferred only at the city edge and were avoided
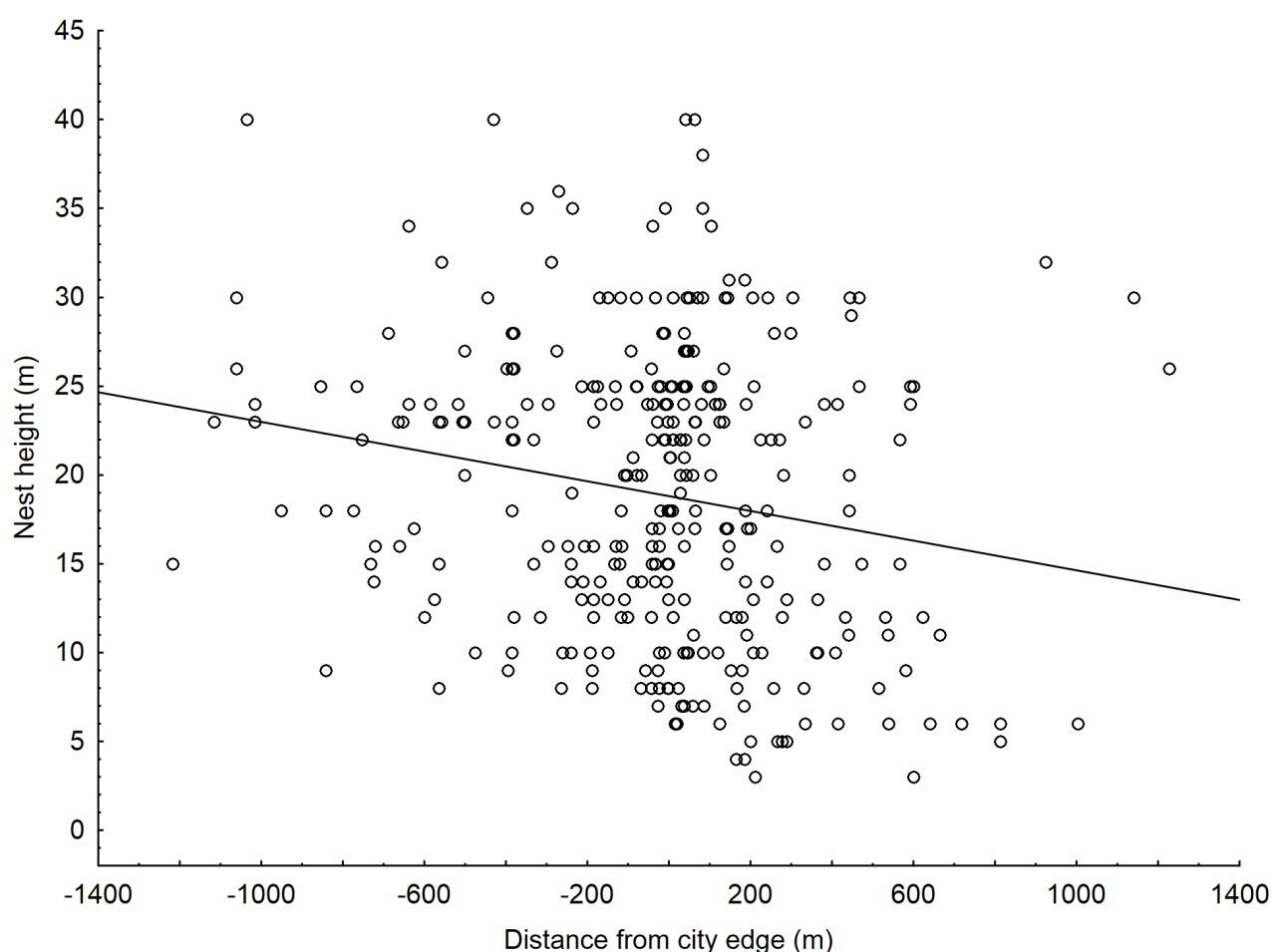
Fig. 4. Eurasian magpie nest height in relation to distance from city edge.

in the rural landscape. The negative response of rural magpies to grasslands and forests may be associated with the structure of these habitats. For example, grasslands in rural landscapes are mainly represented by intensively managed (treeless) hayfields, that are unsuitable for breeding and foraging, whereas grasslands in the urban environment are mainly formed by semi-open grassland enriched by isolated or scattered trees (e.g. urban parks). Similarly, the preference for forest at the city edge may be linked to the higher suitability of small fragments of (sub)urban forests with diffuse edges representing suitable breeding habitats for Eurasian magpies and songbirds, contrasting with large homogeneous forests in open landscapes (Andrén 1992, Šálek et al. 2015c).

Our results confirm that Eurasian magpies are flexible in nest site selection (see also Vogrin 1998, Mérő et al. 2010, Jokimäki et al. 2017), which is suggested not only by the high number of trees species utilised (28 species), but also the use of artificial structures (electric pylons). In accordance with previous studies, we documented higher utilisation of deciduous tree species over conifers (Vogrin 1998, Mérő et al. 2010, but see Jokimäki et al. 2017). Furthermore, we found significant differences in nest height across the urbanisation gradient. Nest height was negatively correlated with distance from the city edge, and the highest nests were found in the urban centre, residential areas, industrial and commercial sites, whereas nest height was the lowest in new residential areas. This result corresponds with previous research documenting that the nest height of Eurasian magpies increased with increasing level of urbanisation (Jerzak 2001, Wang et al. 2008, Wojciechowska & Dulicz 2014). A similar pattern (i.e. higher nest height of urban birds in contrast to rural counterparts) was also found for another corvid species, the Florida scrub jay *Aphelocoma coerulescens* (Bowman & Woolfenden 2002). Urban centres and industrial and commercial sites represent busy and noisy areas with high human activity or traffic. The higher location of nests within these habitats may be related to avoidance by Eurasian magpies of human activity (Eden 1985, Wang et al. 2008), or predation risk by native or domesticated mesocarnivores (e.g. domestic cat *Felis catus* and stone martens *Martes foina*) that reach their highest densities in urban environments (Červinka et al. 2014, Šálek et al. 2015a). Previous studies have shown that Eurasian magpie nests situated higher above the ground

were more successful than nests situated at lower heights (Jerzak 2001, Antonov & Atanasova 2002). Moreover, increased nest height in these areas may be a result of the adaptive behaviour of Eurasian magpies that may mitigate the negative impacts of increased urbanisation. For example, increased urban noise can significantly impair communication between chicks and parents or decrease the ability to detect predators. Finally, since nest height depends on tree species (e.g. Prinzinger & Hund 1981), we also compared nest tree occurrence within habitats. The highest nests were found on poplars *Populus* sp., common alders, firs *Abies* sp. and oaks *Quercus* sp. that were distributed randomly among habitats across the urban-rural gradient. Therefore, we do not believe that the distribution of tree species biased our results.

Conclusion

Our study confirms a pattern previously reported in other European cities that the Eurasian magpie successfully exploits the urban environment, especially green urban habitats, including gardens, orchards or avenues of mature trees that represent crucial nesting habitats in an urban environment (Jokimäki et al. 2017, Szala et al. 2020). An important adaptation of Eurasian magpies to living in an urban environment may be one of adjusted nesting behaviour (Wang et al. 2008), as magpies select higher trees to nest on within urban habitats than in rural habitats. Greater nest height may help mitigate the effects of disturbance and predation risk from humans and urban carnivores. Further comparative research across the urban-rural gradient and contrasting urban habitats are needed to evaluate the effect of human activity or intensity of urbanisation on breeding biology (e.g. breeding performance), which may bring valuable insights into breeding and behavioural adaptations of birds in a highly anthropogenic landscape.

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Supplementary online material

Fig. S1. Overall Eurasian magpie habitat preferences (a) and preferences divided by three main categories along the urban-rural gradient (b). Preferences were computed as $\log_2$ (use/available) based on numbers of Eurasian magpie nests (n = 335) and random points (n = 335). Standard errors of means are shown.

Fig. S2. Eurasian magpie nest height in relation to different urban and non-urban habitats. Squares – medians, boxes – 25-75% of data, whiskers – non-outlier ranges.

Fig. S3. Eurasian magpie nest height in relation to tree genus. Note that three nests were located on electricity pylons. Squares – medians, boxes – 25-75% of data, whiskers – non-outlier ranges.

Table S1. Land-use composition (%) within individual habitat categories and urbanisation gradient of the study area.

Table S2. Location of Eurasian magpie nests within the study area.

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