Research Paper

Recent colonization and nest site selection of the Hooded Crow (*Corvus corone cornix* L.) in an urban environment

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Abstract

The adjustment of Hooded Crows (~~*Corvus corone cornix*~~*Corvus corone cornix* L.) to urban habitats has been ongoing in many European cities in the past decades, yet its causes and mechanisms remain largely unknown. The aims of this study were to study the colonization process and the nest site selection of this species in the city of Debrecen, Hungary. During seven years of our study (2006~~-~~–2012), we localized 231 crow nests on 18 different tree species. The city area used for nesting and both the number and density of nests increased continuously. Crows avoided closed forests and built-up areas and had highest nesting densities in open forested areas, parks and tree rows. Hooded Crows preferred to nest high up on oaks (especially under mistletoes), pines and poplars. Crows built their nests higher in trees in the city than in rural areas and relatively higher in habitats with shorter trees and in conifers than in deciduous trees. Although the increasing use of less-preferred tree species and lower nesting heights indicated that pairs have recently started to use suboptimal nest sites, we detected no sign of saturation of the city nesting population. Our results identified preferences but also confirmed flexibility in nest site selection, which may explain why the Hooded Crow is a successful colonizer of urban habitats. We expect that the population will increase further, which may cause increased predation on songbirds and more complaints from people~~thus~~; thus, our study is important for urban planning, nature conservation and game/wildlife management.

Keywords: Breeding biology; Niche; Nesting biology; Urban environment and ecology; Urbanization

1 I~~NTRODUCTION~~ntroduction

The adjustment or adaptation of birds to urbanization appears to be concurrent with the development of industrial civilization (Evans, Hatchwell, Parnell, & Gaston, 2010; Kalotás, 1995; Marzluff, McGowan, Donnelly, & Knight, 2001), and is still an active and expanding phenomenon globally. A city can be considered a special ecosystem due to its characteristic abiotic and biotic environment and its species (Bezzel, 1985; Davis & Glick, 1978; Marzluff et al., 2008; Parlange, 1998). Urbanization is often associated with decreases in the diversity of bird species (Suhonen & Jokimäki, 1988), which results in the homogenization of the bird fauna (Crooks, Suarez, & Bolger, 2003; Jokimäki & Suhonen, 1993; Rotterborn, 1998), often creating conservation problems such as the loss of natural habitats or threatened species (Clergeau, Croci, Jokimäki, Kaisanlahti-Jokimäki, & Dinetti, 2006).

The Hooded Crow (*Corvus corone cornix* L. 1758) initially lived only in rural habitats and avoided cities (Cramp & Perrins, 1994; Faragó, 2002). The quick adjustment of this species to urbanized areas has been observed in many

European cities since 1960. Several studies documented the crow's settlement and subsequent continuous population increase in urban environments in Hungary (Juhász, 1983; Kövér & Juhász, 2008; Tapfer, 1978, 1985), Finland (Hugg, 1994; Jokimäki & Kaisanlahti-Jokimäki, 2012; Vuorisalo et al., 2003), Norway (Munkejord, Hauge, Folkedal, & Kvinnesland, 1985; Parker, 1985), Poland (Mazgajski, Zmihorski, Halba, & Wozniak, 2008), and Russia (Konstantinov, 1982; Korbut, 1996). Despite the high number of observations in Europe and the knowledge gained in related crow species in North America (Marzluff et al., 2001; McGowan, 2001), the effects of urbanization on Hooded Crow have rarely been investigated in detail and the reasons behind the increasing use of urban habitats are still largely unknown.

Several factors can drive the adjustment of birds to urban areas (Vuorisalo et al., 2003). First, cities can provide milder more stable microclimates, ample opportunities for nesting, and diverse, continuous and predictable sources of food (Bedő & Heltai, 2003; Kalotás, 1995; Vuorisalo et al., 2003). Second, cities can provide decreased risks of predation for adults (Kalotás, 1995; Vuorisalo et al., 2003), because the main predators of Hooded Crows (e.g., Northern Goshawks *Accipiter gentilis* and Pine Martens *Martes martes*) tend to avoid cities or appear there in low densities. Locally, disturbance by human activities, such as intense game management activity outside the cities or a decrease in the persecution of corvid nests in urban areas partly due to EU legislation, can also be influential factors (Sorace, 2001; Withey & Marzluff, 2005). Third, urban environments can offer habitats for crows when competition for nest sites or food resources in rural areas, e.g. with Magpies (*Pica pica* L.) is intense. Finally, Hooded Crows are highly intelligent and ecologically flexible, enabling them to exploit the advantages cities provide and to adapt to ecosystems fundamentally altered by humans (Ilyichev, Konstantinov, & Zvonov, 1990; Konstantinov, 1982; Von Busche, 2001). These observations raise an interesting but so far unresolved question: why have Hooded Crows adapted so late (1960s onwards), but adjusted better than most other species? The ecological flexibility of this species makes it an ideal species to study several of such key issues on the effects of urbanization on birds.

For any urbanized species, the knowledge of carrying capacity, i.e., the population size at which the population growth rate would equal zero (Braun, 2005), is highly important for planning and management. However, the exact determination of carrying capacity is particularly problematic in urban environments. This is because carrying capacity is often population-specific and depends on many types of resources, e.g. availability of food, water and nesting sites, interaction with other species, predators and diseases (Anderies, Katti, & Shochat, 2007; Marzluff et al., 2001). Furthermore, when the variability in resource availability is low, as is often the case in urban environments, even individuals of low competitive ability can survive and reproduce, which would not happen if competition for resources existed. This mechanism, termed as the credit card hypothesis (Shochat, 2004), makes the determination of carrying capacity extremely difficult in cities. The carrying capacity of Hooded Crows in cities has been estimated only in Finland and was based on the density of nests. In Turku, for instance, nest densities of 1.4~~ to ~~–25.5 nests/km^2 were detected depending on habitat type (Hugg, 1994), while in Helsinki, this figure was 18.4 nests/km^2 (Vuorisalo et al., 2003). We do not know of any other estimates on nesting density or carrying capacity of Hooded Crows in urban environments outside of Finland, although establishing thresholds for carrying capacity could provide important information for city planners to make better decisions.

The aims of this study were (i) to document the process of urbanization of Hooded Crows in the city of Debrecen (E-Hungary) between 2006 and 2012, (ii) to study the factors influencing nest site selection, and (iii) to identify whether these factors changed with time, which could provide information on which factors facilitate the urbanization process. To answer these questions, we documented the expansion of nesting sites and estimated the nesting density of Hooded Crows and characterized three aspects important in nest site selection: habitat type, tree species used for nesting, and height of the nest.

Based on observations in previous reports (particularly by McGowan, 2001; Vuorisalo et al., 2003), we tested five hypotheses. First, we expected that Hooded Crows will prefer open, loosely forested areas for nesting and will avoid closed forests or completely open areas. Second, we hypothesized that Hooded Crows will prefer pine *Pinus* spp., and oak *Quercus* spp. trees for nesting. Pines and oaks are usually the tallest trees and provide the best nesting sites, i.e., highest level of protection from tree-climbing mammal nest predators and best location to detect aerial predators. Third, we predicted that within any tree, Hooded Crows will nest as high as possible to maximize nest protection. Fourth, if nesting higher is associated with the urbanization process, nesting heights will be different between countryside and city nests (possibly the “adjustment” stage of coloni~~s~~zation, Evans et al., 2010). Thus, we tested whether such a difference exists by comparing our measurements to nesting heights reported from countryside nests in previous studies. Finally, we examined whether the three main factors changed with time to test the hypothesis that with the occupation of the best nesting sites, the increasing population started using less-then-optimal sites for nesting. Such a tendency could be interpreted as a sign of approaching maximum nest density, i.e., a proxy for carrying capacity for the species in the studied city (possibly the “spread” phase of coloni~~s~~zation, Evans et al., 2010). Even though the above information on the breeding biology of Hooded Crows is essential, both for urban conservation and wildlife management, our knowledge is still rather incomplete in urban environments in Hungary and elsewhere, and here we aim to fill this gap.

2 M~~ATERIALS AND METHODS~~aterials and methods

2.1 Hooded Crow

The Hooded Crow typically nests solitarily, with a stable territorial system maintained from year to year (Hewson & Leitch, 1982; Smedshaug, Lund, Brekke, Sonerud, & Rafoss, 2002). In Hungary, pairs appear at their nest~~-~~ sites as early as February, and they start nest-building soon after. The crows use many species of trees for nesting. In rural areas, Faragó (2002) found nests in seven tree species (*Acer campestre*, *Carpinus betulus*, *Pyrus pyraster*, *Morus alba*, *Salix*~~ spp., Alnus spp. and Fraxinus spp.~~ spp., *Alnus* spp. and *Fraxinus* spp.). In urban environments, crows used a higher number of species. Juhász, Kövér, & Gyüre (2009) found nests on 12 tree species in the city of Debrecen (*Quercus robur*~~obinia pseudo-~~, *Pinus silvestris*, *Pinus nigra*, *Sophora japonica*, *Celtic occidentalis*, *Robinia pseudo**acacia*, *Platanus acerifolia*, *Ulmus pumila celer*, ~~*Pinus silvestris*, *P. nigra*, *Sophora japonica*, *Celtic occidentalis*, *Robinia pseudoacacia*, *Platanus acerifolia*, *Ulmus pumila celer*,~~ *Acer saccharinum*, *Gleditsia triacanthos*, *Maclura pomifera*, and *Populus alba*). In rural areas of Hungary, Faragó (2002) estimated the average nesting height at 6.4 m based on measurements taken by tape or the triangle method (range 3~~–13 m, n~~–13 m, *n* = 45). In areas of low disturbance, Hooded Crows can build nests as low as 3–4 m (Havasi, 1993) and may even nest on the ground (Ternovác, 1983). More recently, observations of nesting on high-voltage pylons have become more common (Ujhelyi, 2005). In rural areas in other countries, average nesting height was reported as 9 m (Loman, 1975) and 11 m (Hessel & Elmberg, 2010) in Sweden, at 14.5 m (Kulczycki, 1973) and 9.9 m (Zduniak & Kuczynski, 2003) in Poland, at 12.6 m in Germany (Abshagen, 1963) and at 9.9 meters in Finland (Tenovuo, 1963).

2.2 Study area

We studied the nesting of Hooded Crows in Debrecen in eastern Hungary. Debrecen is the second largest city in Hungary (c. 210 000 inhabitants) and is the center of the county of Hajdú-Bihar. The traditional town structure consists mainly of multistorey built-up areas along the major roads and of peripheral suburban areas of one-storey buildings with many trees and garden vegetation. Since the 1960s, the city has undergone substantial urbanization due to the emergence of industrial areas and residential concrete block buildings, which caused the almost complete loss of the traditional agricultural town character of the city. Today the inner city consists of completely built-up metropolitan areas, surrounded mostly by calm, narrow, treeline-bordered streets of the old agricultural town, which are then surrounded by urban parks and concrete block buildings. On the periphery, suburban residential areas, weekend gardens and industrial areas are found, whereas the Great Forest, the first nationally protected area in Hungary (declared in 1939) embraces the city from the north. The city thus offers a heterogeneous structure of different types of urban habitat from fully built-up areas to suburban parks and closed forests. The Hooded Crow was first reported as a nesting species here in 1959 (Juhász, 1983). The species then virtually disappeared for 20 years and nested in the city again only in 1972 and then again in 1979 (Juhász, 1983). The continuous presence of the species began in the 1980s, mostly in the cemetery, the zoo and the neighboring park forest in the northern part of the city (Juhász, 1999). Since then, the Hooded Crow has become a permanent, common breeding species in Debrecen, observable in virtually all parts of the city (Juhász et al., 2009).

2.3 Field methods

As a reference for the surveys, we laid a grid of nine 4-km^2 squares over the city so that the central grid cell was in the center of the city (total ~~n~~*n* = 36 squares or “study area”). We monitored crow activity before the breeding season (late March, early April), when the trees were still leafless, and when Hooded Crows began to occupy territories and build nests. We then searched for active/occupied nests systematically by walking all streets, squares and parks in the study area during the nesting season, i.e., April and May. We also recorded confirmed absences, when no crows were seen on a street/square. We considered a nest as active/occupied, when the female bird was seen incubating. Numerous volunteers (university students) helped with nest-searching surveys.

For each nest found, we noted the tree species, tree height, the height of the nest in the tree, the placement (under/near mistletoe or not) and the GPS coordinates. We also described the habitat type either as a single tree, tree row, park, or forest patch. We classified a ‘single tree’ when it stood as a solitary tree, i.e., there were no other trees within 25–30 m, or when there were only much smaller trees or bushes surrounding it. We defined a ‘tree row’ as a tree line beside any street or road. A ‘park’ means an area where we find mainly trees in open forest (canopy cover < 70%) settings as well as other infrastructure (e.g. a building, lake, trail, etc.). A ‘forest patch’ means an area fully covered by trees. We used a laser rangefinder (TruPulse 200) to measure the height of the nest and the tree. We recorded the GPS coordinates of every nest using a hand-held receiver (Garmin GPSMap 60 CSx). We followed Zuckerberg, Huettmann, ~~&~~and Frair (2011) for data management: the collected data were described with ISO metadata and are available online at the US Geological Survey website (Kövér, Juhász, & Huettmann, 2012).

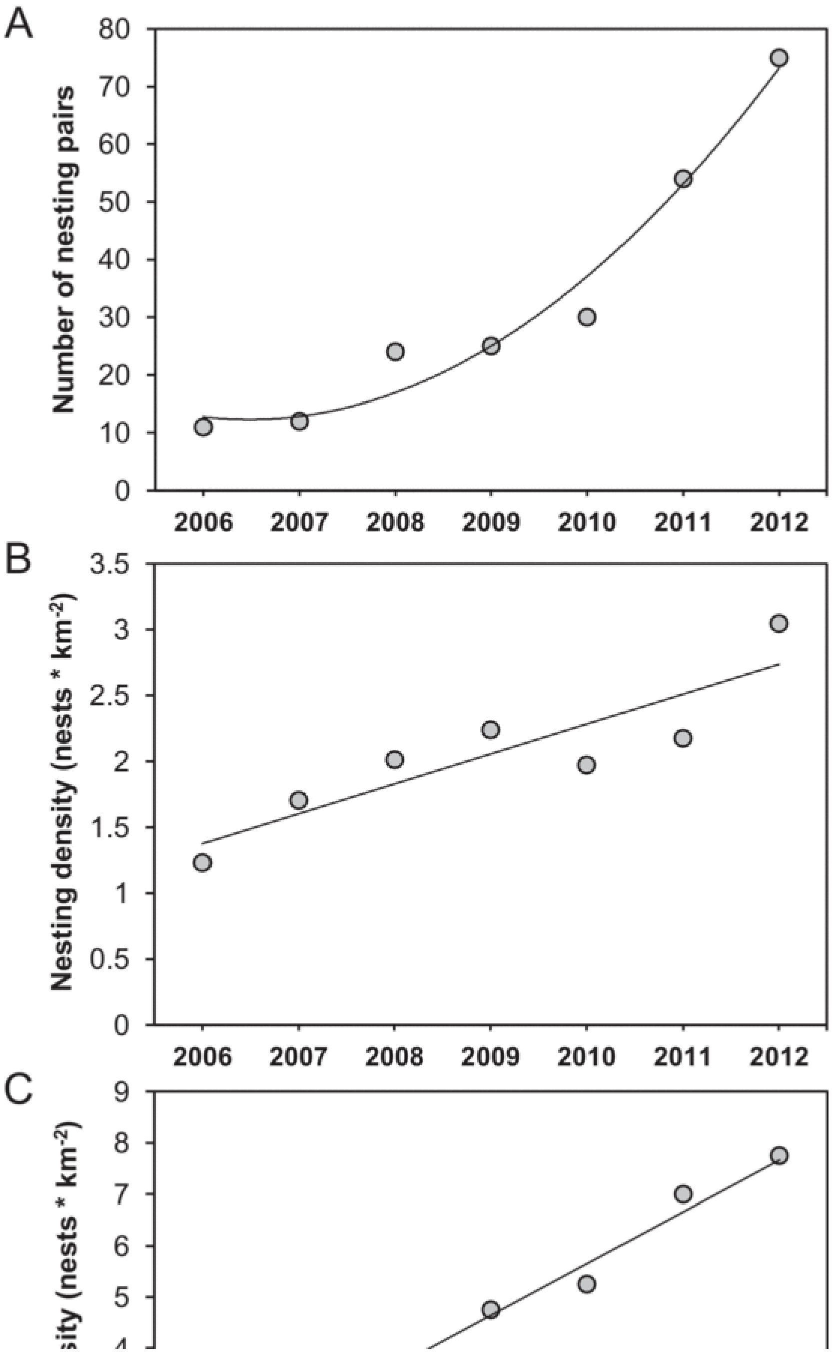
2.4 Data analysis

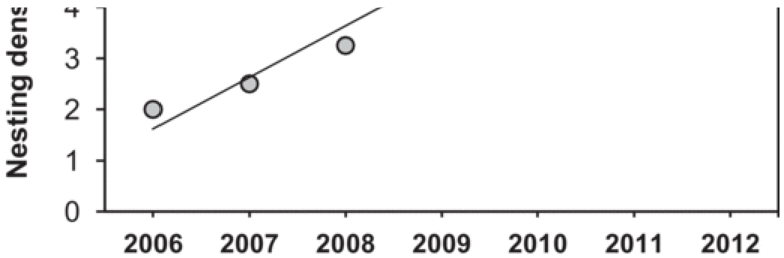
Our response variables were the number and density of nests and the height of the nest and the tree. Nesting density was estimated both for the total area in which nests were known in the city and for the northern part (4 km^2) of the city, where nesting first occurred and is still concentrated. Total nesting area was calculated as the area of a rectangular density kernel fitted among the most peripheral nests for every year using ArcGIS 10.0. The northern center of nesting was defined as the traditional Great Forest area of the city and which includes parks, the university hospital, the city zoo, a sport complex, closed forest patches and the city cemetery. For nesting height, we used both the absolute field measurement (in m) and a relative height, the latter was defined as the height of the nest expressed as the proportion of the total tree height (e.g. 0.8 for a nest at 8 m on a tree of 10 m height).

We tested differences in response variables by habitat type (see definitions above), tree species and year as independent variables. We analyzed the temporal change in the number and density of nesting pairs by simple linear and non-linear (polynomial) regression to allow the detection of possible non-linearity. Because of the heterogeneity of variances in tree height data, we used the nonparametric Kruskal–Wallis test to identify differences in tree and nesting height between urban habitat types and among tree species. We compared the mean height of countryside nests (data taken from literature reports) and of city nests (measured in this study) by one-sample ~~t~~*t*-tests. We tested whether Hooded Crows show preferences to tree species by a chi-square test when its assumptions were met by the data. When the number of cases was too low (~~n~~*n* ≤ 5 in 20% or more of the expected values), we pooled data from the rarest categories. We compared the proportion of tree species used by Hooded Crows to proportions expected under the null hypothesis of no preference to tree species. To estimate the availability of different tree species in the city (expected proportions), we used data on tree species in northern and central Debrecen (25,142 trees in 393 streets or parks in an area of 12.5 km^2), obtained from the Mayor's Office of the city of Debrecen. We used data only from those nests (~~n~~*n* = 124) that were in the 12.5-km^2 area from where tree species data were available and used only trees that were old enough to host crow nests (age 20 years or more). We conducted statistical analyses using the SPSS 17.0 program package (SPSS Inc., 2008) or PAST version 2.17 (Hammer, Harper, & Ryan, 2001).

3 R~~ESULTS~~esults

During seven years of study, we found 231 active/inhabited nests. The number of nests found per year increased throughout the study period (Fig. 1A~~)~~). The relationship was non-linear and indicated that the increase has accelerated recently. Total nesting density in the surveyed area increased from 1.2 to 3 nests/km^2 in a linear fashion (Fig. 1B), whereas nest density in the northern, most preferred area increased linearly from around 2 to almost 8 nests/km^2 in the seven years (Fig. 1C), showing no sign of saturation.





Fig~~ure~~. 1 The number of nests found (A), total nesting density (B) and nesting density in the northern, most frequently used area of the city (C) per year between 2006 and 2012. The regression line in A was fitted by second-order polynomial non-linear regression (~~R~~R^2 = 0.967, slope of ~~Y~~year^2 = 2.0 ± S.E. 0.56, ~~t = 3.530, p = 0.024), and in B and C~~ t = 3.530, p = 0.024), and in (B) and (C) by simple linear regression (B: ~~R~~R^2 = 0.783, slope of ~~Y~~year = 0.2 ± S.E. 0.05, ~~t = 4.227, p = 0.008; C: R~~ t = 4.227, p = 0.008; C: R^2 = 0.979, slope of ~~Y~~year = 1.0 ± S.E. 0.06, ~~t = 15.350, p < 0.0001).Figure~~ t = 15.350, p < 0.0001).

The area used for nesting increased during the seven study years (Fig. 2). Nests in 2006 and 2007 were concentrated in the northern, open forested areas of the city (sport complex, park forest, cemetery; Fig. 2). In 2008, many nests were built south-west from the major northern center of nesting, whereas in 2009 and 2010, nesting again concentrated in the northern parts (Fig. 2). There was a large increase in both the number of nests (Fig. 1) and the area used for nesting (Fig. 2) between 2010 and 2011. In the two most recent years (2011, 2012), nesting pairs were found in several distant, southern and western parts of the city (Fig. 2).

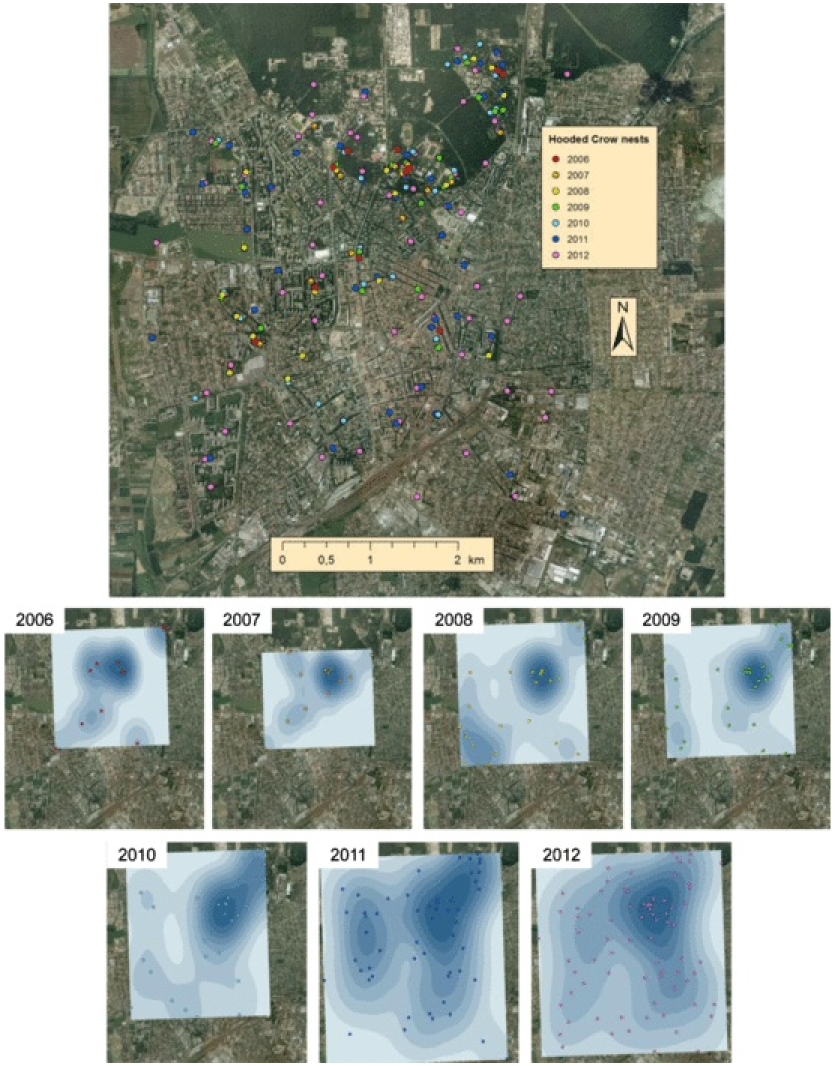


Fig. 2 The location of active/inhabited nests found between 2006 and 2012 (~~n~~ n = 231) in our study area (36 km^2, A) and kernel densities (nine classes) drawn to highlight centers of nesting in different years (B).

There were very few nests in closed forests (dark green areas in Fig. 2), which may indicate a tendency for Hooded Crows to avoid nesting in closed forests. Furthermore, apart from the northern nesting center, more pairs used the more forested western parts than the less forested eastern parts of the city (Fig. 2), which showed that Hooded Crows avoid city sections with a high proportion of built-up areas. Nests were found in similar proportions in the four major habitat types (tree rows: 28%, park: 25.5%, single tree: 24%, forest patch: 22.5%, ~~n~~ n = 231), although there were interesting patterns in the use of habitat types over time (Fig. 3A~~)~~). Single trees were used rarely and the frequency of use decreased until 2010, when a sharp increase occurred in the use of this habitat type (Fig. 3A). The proportion of nests on single trees increased significantly from 17% before 2011 to 29% in 2011 and 2012 (~~χ2 = 5.137, p~~ χ^2 = 5.137, p = 0.023). There was a large increase in the number of nests in tree rows between 2007 and 2008, followed by a near-linear increase between 2009 and 2012. The proportion of nests in tree rows increased marginally non-significantly from 13% before 2008 to 30% in 2008 and after (~~χ2 = 2.878, p~~ χ^2 = 2.878, p = 0.090). Finally, the number of nests in parks increased slightly until 2011, followed by a sharp increase in 2012.

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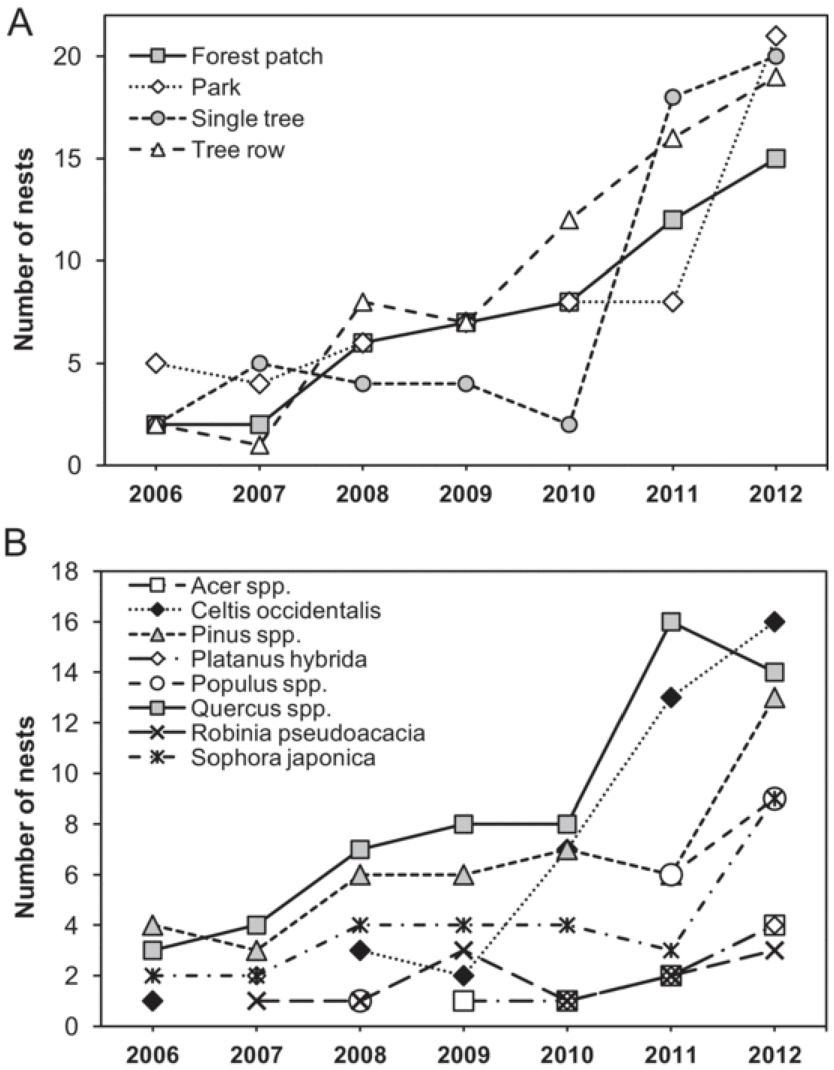

Fig~~ure~~. 3 Changes between 2006 and 2012 in the number of nests in different habitat types (A), in the tree species used for nesting (B), and in the mean height of nests per tree species (C). Each data point represents one year, and lines are for visual guidance only. Error bars are om~~m~~itted for clarity and data points are jittered along the ~~*x*~~ *X* axis for visibility in ~~C.Figure~~(C).

We found Hooded Crow nests on 18 species of trees. As predicted, most nests were detected on oaks (*Q~~uercus robur n = 59, and Q. rubra n~~. robur n = 59, and Q. rubra n* = 1, 26% total) and pines (*P~~inus silvestris n = 27, P. nigra n~~. silvestris n = 27, P. nigra n* = 15 and *Picea abies ~~n~~ n* = 3, 19% total). Other frequently used species included *C~~eltis~~. occidentalis* (18%), followed by *S~~ophora~~. japonica* (12%), usually present in tree rows, and *Populus* species (7%), usually present as single trees (13 or 81% of 16 *Populus* trees used for nesting were single trees). Finally, ten other species were used less frequently (<5%, in order of decreasing frequency: *R~~Acer~~. pseudoacacia, P. acerifolia, A. saccharinum, A. platanoides~~Gleditsia~~, U. pumila celer, G. triacanthos*, *Juglans nigra*, *J. regia*, *M~~aclura~~. pomifera*, *Tilia tomentosa*).

The comparison of trees used for nesting and tree species availability showed significant differences between observed and expected proportions (Table 1; ~~x~~ $\chi^2 = 51.006$, df = 8, ~~p~~ $p < 0.0001$). Crows appeared to prefer nesting on pine (*Pinus* spp.), poplar (*Populus* spp.) and oak (*Q~~uercus~~. robur*) trees (Table 1). In contrast, maple (*Acer* spp.) and black locust (*R~~obinia~~. pseudoacacia*) were underrepresented (i.e., avoided by crows), whereas common hackberry (*C~~eltis~~. occidentalis*), London planetree (*P~~latanus~~. acerifolia*) and pagoda tree (*S~~ophora~~. japonica*) were used proportionally to their availability (Table 1). Crows nesting on oaks appeared to prefer nest sites under mistletoe (*Loranthus europaeus*) because 70% of the nests on oak trees (~~n~~n = 60) were under mistletoe, whereas we did not observe such a tendency on other tree species.

Table 1 Number of Hooded Crow nests on different tree species (~~n~~n = 124) and the number of nests expected under the null hypothesis of no preference for tree species in northern and central Debrecen, corresponding to random selection of tree species by crows.

Tree species	Number of nests	
	~~Tree speciesobservede~~Observed	Expected
Acer spp.	6	38
Celtis occidentalis	36	34
Pinus spp.	11	0.2
Platanus acerifolia	8	10
Populus spp.	12	2
Quercus robur	20	6
Robinia pseudoacacia	3	8
Sophora japonica	19	18
Other	9	8

The use of tree species varied characteristically with time (Fig. 3B). Nesting on oaks (*Quercus* spp.) increased sharply between 2010 and 2011, and nesting on pines (*Pinus* and *Picea* spp.) and on *S~~ophora~~. japonica* increased sharply from 2011 to 2012 (Fig. 3B). However, the largest increase was in using *C~~eltis~~. occidentalis* for nesting, which began in 2010 and continued until 2012, resulting in *C. occidentalis* being the most frequently used tree species in 2012 (Fig. 3B). The proportion of nests on *C. occidentalis* significantly increased from 9% before 2010 to 24% in 2010 and after (~~χ2 = 6.822, df = 1, p~~χ^2 = 6.822, df = 1, p = 0.009).

The mean absolute height at which nests were built was 16.4 ± S.D. 2.45 m (range 12~~–23 m, n~~–23 m, n = 231), which corresponded to a relative height of 88% ± S.D. 7.6%, indicating that Hooded Crows preferred to build nests high up in the trees. Nesting heights, both absolute and relative, differed significantly among tree species (Table 2). The relative height of the nests was largest on *Pinus* species (95%), followed by *Quercus* and *Platanus* species (88% each) and was lowest on *Populus* and *Gleditsia* trees (80% each, Table 2). Relative nest height was significantly higher in coniferous trees (94.6 ± 5.30%, ~~n~~n = 45) than in deciduous trees (86.4 ± 7.25%, ~~n = 186; Mann-Whitney U = 1475, p~~n = 186; Mann–Whitney U = 1475, p < 0.0001).

Table 2 Mean ± S.D. nesting height and proportion of height in different tree species used by Hooded Crows for nesting. Relative height (%) is compared to the total height of the tree on which the nest was built.

Tree species or genus	Nesting height	Relative height	~~N~~N
Acer spp.	16.8 ± 3.15	83 ± 7.4	8
Celtis occidentalis	15.6 ± 1.91	87 ± 5.3	42
Gleditsia triachanthos	12.0 ± 0.00	80 ± 1.8	2
Juglans spp.	17.0 ± 1.41	90 ± 5.9	2
Maclura pomifera	12.0 ± 0.00	80 ± 0.0	1
Picea abies	16.7 ± 1.53	86 ± 3.4	3
Pinus nigra	14.5 ± 2.39	94 ± 6.5	15
Pinus silvestris	17.1 ± 1.98	96 ± 3.8	27
Platanus acerifolia	18.2 ± 2.39	88 ± 7.2	9

Populus sp.	18.1 ± 3.05	80 ± 10.5	16
Quercus spp.	16.9 ± 2.42	88 ± 7.5	60
Robinia pseudoacacia	17.1 ± 1.81	87 ± 4.6	11
Sophora japonica	16.0 ± 2.12	86 ± 5.9	28
Tilia tomentosa	12.0 ± 0.00	86 ± 0.0	1
Ulmus pumila celer	15.2 ± 1.33	86 ± 4.9	6
~~Kruskal-Wallis H31.7161.01p0.001< 0.0001~~Kruskal–Wallis *H*	31.71	61.01	
p	0.001	<0.0001	

The height of trees differed among habitat types (Kruskal~~-Wallis H = 21.75, df = 3, p~~–Wallis $H = 21.75$, df $= 3$, $p < 0.0001$) because single trees and trees in forest patches were slightly taller than trees in parks and tree lines (Fig. 4A~~)~~). Correspondingly, the absolute height of nests also differed by habitat type (Kruskal~~-Wallis H = 10.77, df = 3, p~~–Wallis $H = 10.77$, df $= 3$, $p = 0.012$). However, Hooded Crows appeared to compensate for tree height because the relative height of nests was highest in the parks (Fig. 3B, Kruskal~~-Wallis H = 21.82, df = 3, p~~–Wallis $H = 21.82$, df $= 3$, $p < 0.0001$), where trees were generally shorter. Moreover, the absolute height at which nests were built was substantially and significantly higher than in rural areas of Hungary (6.4 m, Faragó, 2002) or other countries (Sweden: 9 m (Loman, 1975), 11 m (Hessel & Elmberg, 2010); Poland: 14.5 m (Kulczycki, 1973), 9.9 m (Zduniak & Kuczynski, 2003); Germany: 12.6 m (Abshagen, 1963); Finland: 9.9 m (Tenovuo, 1963); one-sample ~~*t-tests, t > 12.00, p*~~*t*-tests, $t \geq 12.00$, $p < 0.0001$ for each of the seven comparisons).

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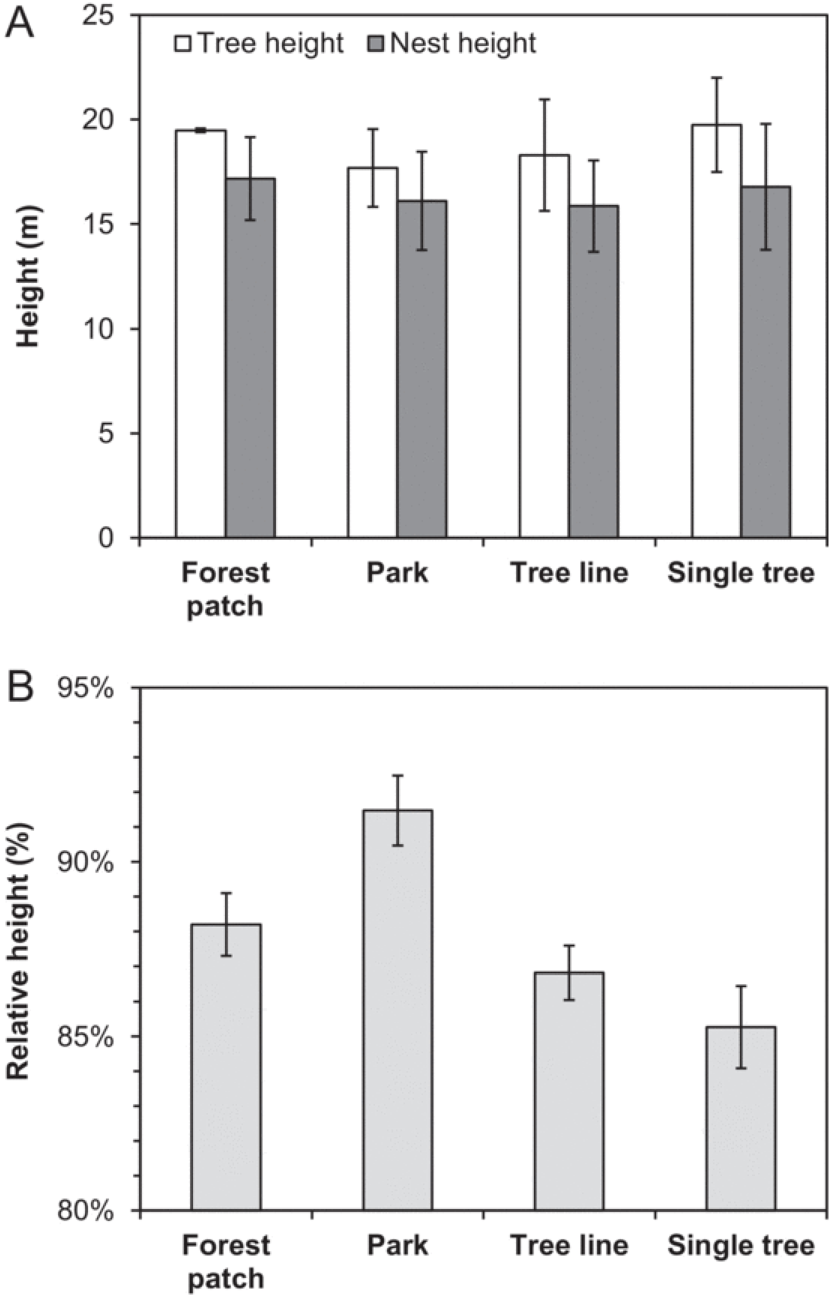

Fig. **4** Mean ± S.D. height of nesting trees and nests (A) mean ± S.E. relative height of nests (B) in the four nesting habitat types.

4 DISCUSSIONiscussion

Our study provided three key results. First, we documented a continuous increase of an urban population of Hooded Crows between 2006 and 2012. There was no sign of saturation of the nesting population because both the area and the density of nesting increased continuously. Second, we found that the population increase was associated with changes in habitat use, tree species and nesting heights. Crows avoided closed forests and built-up areas and showed an increasing use of single trees and tree rows. Crows preferred nesting on oaks (especially those with mistletoe), pines and poplars, and increasingly used other species such as *C~~eltis occidentalis and Sophora~~. occidentalis* and *S. japonica* as the population increased. Finally, crows built their nests as high as possible, compensated by nesting higher within the tree in habitats with shorter trees, and nested significantly higher in the city than in rural areas found in earlier reports. Taken together, these patterns indicate that the population increase of Hooded Crows is associated with their use of new resources, including less-than-optimal sites for nesting.

4.1 Increasing nesting population

Evans et al. (2010) separated the colonization process into three phases: arrival, adjustment and spread. Our results suggest that the Hooded Crow in Debrecen is probably in the last, spreading, phase, i.e., after an adjustment period that likely took place in the 1990s. In the past decades, Hooded Crows have shown spectacular adjustment to urban habitats in Debrecen (Fintha, 1994; Juhász, 1983), in which one key factor~~s~~ is the good nesting opportunities in the urban areas (Juhász et al., 2009; Kövér & Juhász, 2008). Alternatively, Hooded Crows may have increased because population control by hunting decreased in rural areas and ceased in the city. However, to our knowledge, there was no organized control of this species in Debrecen. Although there is sporadic control of this species in Hortobágy National Park 40 km west of the city and in game management units near the city, the level of control is probably too low to explain the large increase of the urban population (similarly to the findings of Clucas & Marzluff, 2012). Another explanation for the increase is if competing species, e.g. Magpie *P~~ica~~. pica*, declined. However, we currently know no competitor bird species either in urban or rural environments for the species. The increase of the urban population can be more related to a recent adjustment or adaptation of Hooded Crows to the urban environment. Our results suggest that changes in nest site selection, e.g. in habitat types and tree species rarely used previously, and high up in the trees can be such adjustments. Along with other factors such as increased food availability near commercial, anthropogenic food sources (Baltensperger et al., 2013) such as the zoo and parks in the northern part of the city, this plasticity in nest site selection can explain the increasing trend observed. The increase of the urban population in a related species, the American Crow (*Corvus brachyrhynchos*) could also be explained by the higher availability of food due to human refuse, and could be linked to the considerably smaller territories in urban than in rural environments (Marzluff et al., 2001; McGowan, 2001).

4.2 Habitat preference of Hooded Crows

Crows clearly avoided closed forests and built-up areas, and colonized open wooded areas (open forests, parks, tree rows and even single trees). Hooded Crows have increasingly used tree rows and single trees for nesting rather than forest patches. Tree rows are particularly interesting because this is the habitat type which is probably most similar to the nesting habitats preferred in non-urban areas near roads or along agricultural fields (Cramp & Perrins, 1994; Faragó, 2002). The increasing number of nests in these habitat types and especially on *C~~eltis occidentalis and Sophora~~. occidentalis* and *S. japonica* in tree rows and on single *Populus* spp. trees, with a parallel decrease in the height of nests provide evidence that Hooded Crows have started to exploit new resources, i.e. initially suboptimal sites, for nesting.

4.3 Tree species and nesting height preference: antipredator benefits?

As expected, Crows most frequently used oaks and pines for nesting, suggesting that these trees provide the best sites for nesting. Nesting on oaks and pines started early in the colonization process and increased in frequency more or less similarly with the exception of year 2011, when the number of nests on pines slightly decreased. Oaks and pines were the most frequently used tree species in six of the seven years, with the exception of the most recent year (2012), when *C~~eltis~~. occidentalis*, usually planted in tree rows in Debrecen, became the most frequently used tree species (Fig. 3). Previous studies (Cramp & Perrins, 1994; Jollet, 1985) also reported a strong preference for oak as a nesting tree in Hooded Crows. This preference may be related to the tendency that Hooded Crows can also build their nests high up on these trees. Our observations on absolute and relative nesting heights showed that crows preferred to build nests high up in the trees, and that they even compensated (nested higher up) in habitat types where trees were shorter. Finally, comparisons of nest heights in Debrecen and those in rural environments in Hungary and elsewhere suggested that Hooded Crows in the city built their nests higher than crows that live outside of the cities. This finding is in line with previous observations in American Crows that pairs in suburban areas build their nests higher up in the trees than do pairs in rural areas (McGowan, 2001). Tree height thus appeared to be one of the most important elements of nest site selection for Hooded Crows.

The tree and height preference of nesting may be related to the success of colonization of the urban habitats. Building nests as high as possible may be beneficial to crows by enabling them to avoid human disturbance and to obtain safety from predators. Nesting high up in the trees and near/under mistletoes may provide protection against predators such as mammals moving on the ground or the understorey (pine martens, domestic cats) and also enable crows to detect aerial predators (e.g. jays, goshawks) or upperstorey mammal predators (e.g. squirrels). However, recent studies suggest that anthropogenic disturbance may better explain nest site selection in crows than predation per se (Clucas & Marzluff, 2012). Although anthropogenic disturbance may also play a role in the city studied here because nesting has been concentrated to the less disturbed northern parts, tree rows, that are increasingly used for nesting, are often located along roads with heavy traffic, which suggests an increasing tolerance of crows to disturbance.

Even though the differences in nesting heights among habitats were significant, these differences were rather small (Fig. 4), suggesting that nesting height is probably more important than the actual nesting habitat of the urban Hooded Crow. The species prefers about the same nesting height (around 16.4 meters) in all types of urban habitat, and appeared to compensate for shorter trees (i.e., nesting higher) in parks, suggesting that crows can find their secure nesting heights at 16~~-~~–17 m. When we compared nesting height among the different tree species, we found significant differences between trees (Table 2), which can be explained by the different characteristics (branch and leaf structure) of the given tree species. Notably, we found evidence that relative nest heights were greater on conifers than on deciduous trees, which was also reported in American Crows (McGowan, 2001).

4.4 Nesting area and density: future perspectives

Both the number and density of nests has increased continuously in the study area since 2006, and particularly since 2010, especially in the northern part of the city, where the increase was close to linear. The rate of increase varied among the years, and it accelerated particularly in 2006~~–2008 and 2010–~~–2008 and 2010–2012. Both 2006 and 2010 were wetter-than-average years (e.g. http://weatherspark.com/history/32213/2014/Debrecen-Hajdu-Bihar-Hungary), when food resources such as amphibians, passerine eggs and young etc. were plentiful. This may have led to high nesting success, which may at least partly explain the acceleration of population increase in subsequent years. The near-linear increase of population size in the northern part of the city suggested that nesting sites and territories are still available and that there is no leveling off (saturation) of the nesting population, even in the best nesting areas. Because we currently cannot yet estimate the maximum nest density or the carrying capacity of Hooded Crows in Debrecen, we have to rely on the Finnish results that show much larger numbers than was found in our study (c.f. Fig. 1): 1.4~~-~~–25.5 nests/km^2 (Hugg, 1994) and 18.4 nests/km^2 (Vuorisalo et al., 2003). These observations suggest that further increase in the total nesting population is likely and that nest density is still away from its maximum or the carrying capacity for the studied population, with all its implications.

Many questions remain about the urban status of Hooded Crows and their direct interaction with people. Hooded Crows are top predators (Juhász et al., 2009) because they are effective predators of songbirds and their eggs and juveniles (Cramp & Perrins, 1994; Jokimäki & Huhta, 2000; Jokimäki et al., 2005). During this study, we have directly observed two cases of crow predation of nests of European Greenfinch (*Carduelis chloris*) and suspected predation of other passerine nests. It is well known that crows use a wide variety of artificial food resources (zoos, dumps, garbage bins, park restaurants etc.; Baltensperger et al., 2013). The first centers of nesting in Debrecen occurred in on near the zoo in the northern part of the city, where crows started to use food given to the captive animals. However, we currently know little on the importance of such resources in different areas or habitat types. Therefore, a thorough assessment of the feeding ecology of crows in urban environments is necessary. We also know little on the potential role of crows as vectors of parasites and diseases and whether they could be dangerous for humans or/and their pets. Thus, an assessment of the parasitic fauna of this species is also highly due. Finally, crows have shown a tendency to adjust to human disturbance to the extent that there are many complaints from citizens about bird predation by crows (Kőszegfalvi, 2008) or about the crows' turbulent, disturbing and aggressive habits to people and/or their pets (Szemadám, 2006). If such complaints from urbanites increase with the increase of the crow population, a reduction of crow numbers may become necessary. However, crow control is a complex question because hunting is not feasible in urban areas; instead, some trapping method (e.g. Larsen box-trap or Ladder trap, Bub, 1995) followed by the translocation of individuals captured can be a solution if the problems persist. Lastly, Hooded Crows may not only threaten the local avifauna but can also provide benefits to some species. For example, Long-eared Owls (*Asio otus*) use abandoned crow nests for nesting, and we have observed annually more and more owls in the city. Moreover, crows can have an important role in removing food and other organic waste thrown away by people.

5 Conclusion

We documented a population explosion of Hooded Crows in an urban environment in Eastern Europe and associated changes in nesting habits. Although crows preferred open wooded areas and nested high mainly on oak and pine trees, they also nested lower on more concealed trees and higher in less concealed trees, and relatively higher in areas with shorter trees. We also identified flexibility in nest site selection, such as using less~~-~~-preferred habitat types and tree species, which at least partly explain why the Hooded Crow is a successful colonizer of urban habitats. We currently cannot predict the maximum nest density or the carrying capacity of Hooded Crows in Debrecen, and the recent increase in the number of nesting pairs, nesting area and nesting density is expected to continue in the future. Our results thus represent a unique snapshot in space and time and will be very useful in urban planning, nature conservation and game/wildlife management as they represent the best available science (Braun, 2005) in Hungary and Eastern Europe for this urban species.

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Highlights

- We documented a 7-year population explosion of Hooded Crows in an urban environment.
- Crows preferred to nest high on pine, poplar and oak trees in open areas and parks.
- Population increase was linked with more flexible use of resources for nesting.
- Crows started to nest in tree rows and single trees of previously unused species.
- Crow population will likely grow further and represent challenges for urban planning.

Queries and Answers

Query: '*Corvus cornix* L.' has been changed as '*Corvus corone cornix* L.' in the article title. Please check and correct if necessary.

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