Ornis Fennica 87:61–68. 2010

Long-term spatio-temporal dynamics of corvids wintering in urban parks of Warsaw, Poland

Michał Żmihorski*, Ryszard Halba & Tomasz D. Mazgajski

*M. Żmihorski, Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warsaw, Poland. * Corresponding author's e-mail: zmihorski@miiz.waw.pl*
R. Halba, Department of Ecology, University of Warsaw, Banacha 2, 02-097 Warsaw, Poland. E-mail hary@biol.uw.edu.pl
T.D. Mazgajski, Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warsaw, Poland. E-mail mazgaj@miiz.waw.pl

Received 19 March 2009, accepted 10 February 2010

Wintering in urban habitats seems to be a profitable and an increasingly important strategy for many bird species. In central Europe, the corvids Rook, Jackdaw, Magpie and Hooded Crow constitute one of the most abundant groups of wild vertebrates in cities. Counts of corvids wintering in Warsaw, central Poland were conducted in three parks from October to December during 18 seasons (1977–2003; 258 separate daily counts, 26,166 records). We tested the effects of date, year, park identity and snow cover on the observed densities, and that of snow depth on the vertical distribution, of corvids. From October to December, the densities of Rook and Jackdaw increased while those of Magpie and Hooded Crow decreased. The density of Rook decreased, and that of the other species increased, in the long-term. Apart from the Rook, the densities of these species also varied among parks. Snow occurrence negatively affected the densities of Rook and Jackdaw, but it had no significant effect on the densities of Magpie and Hooded Crow. The vertical distribution of Rooks and Jackdaws depended on the depth of snow cover: almost all individuals were observed in trees when the cover was deep, suggesting a change in foraging strategy during snowy periods. After excluding the factors snow, year and park from the models, corvid densities correlated with each other, suggesting that factors other than competition, such as food availability, may be responsible for synchronizing the dynamics of these species in urban parks.

1. Introduction

The choice of particular wintering strategy is crucial for birds living at high latitudes of the Palaearctic region. The decision on over-wintering strategy involves a trade-off between costs related to migration over long distances and costs of being resident, i.e., coping with local weather conditions and available resources, especially in the north. In Central and Northern Europe, where winters are more severe than in more southern latitudes in terms of temperature, snow and ice, wintering in urban habitats seems to be a profitable strategy for many bird species. As the survival of over-wintering birds primarily depends on weather conditions, especially winter temperature, and food availability (e.g., Lahti *et al.* 1998, Robinson *et al.* 2007), urban habitats appear particularly attractive. This pattern is connected to milder temperatures in built-up than in rural landscapes (e.g., Kuttler 2008) and to the ability of using anthropogenic food sources and shelter, potentially bringing additional advantages to species wintering in cities (e.g., Luniak 2004). As a result, one could expect birds to migrate to cities during winter (Górski 1976, Winiecki 2000), resulting in high densities of especially omnivorous birds in urban areas (Jokimäki & Suhonen 1998). The favorable climatic conditions of urbanized habitats, together with the increased availability of food resources that may exceed the energy requirements of omnivorous birds (Lancaster & Rees 1979), raises a question about the effect of these factors on the spatio-temporal dynamics of wintering species.

Over-wintering birds with access to artificial feeding are spatially and temporally more predictable than individuals without this access (Roth & Vetter 2008), which allows one to assume that such populations in cities might also be more stable. On the other hand, the severity of winter weather conditions may affect the degree of autumn dispersal of birds from city outskirts to the centre (e.g., Górski 1976, Winiecki 2000), which in turn may affect the dynamics and inter- and intra-specific interactions in bird communities. Snow occurrence can be expected to reduce food availability and force wintering birds for additional movements within the heterogeneous, urban landscape.

Studies on city birds have mostly concentrated on breeding season, whereas studies carried out in non-breeding seasons mainly describe over-wintering communities (Jokimäki & Suhonen 1998, Jokimäki *et al.* 2002). In the present study, we focused on the spatio-temporal dynamics of wintering birds in relation to weather conditions using long-term data on four sympatric corvids. The corvid community wintering in Central Europe is mainly composed of four, closely related species: Rook *Corvus frugilegus*, Jackdaw *C. monedula*, Hooded Crow *C. cornix* and Magpie *Pica pica*. During winter months, these birds constitute one of the most abundant groups of wild vertebrates in cities and reach peak densities in urban parks (Luniak 1981). We investigated particularly the effect of snow occurrence on the density and foraging strategy of the focal species.

2. Material and methods

The study was carried out in Warsaw, Central Poland (52° N, 21° E). This region is affected by the relatively mild and wet oceanic climate of Western Europe, as well as by the colder, drier continental climate of Eastern Europe. In this region, the mean ambient temperature during winter is ca. –2°C, and snow cover lasts on average 60–70 days during the year (Mączak 1990). Local weather conditions are significantly influenced by the city being milder in the center as compared to its outskirts (Mączak 1990). The administrative borders of the city encompass 494 km^2, with 1.6 million inhabitants. We counted birds in three urban parks: Saski (SAS; 16 ha), Krasiński (KRA; 10 ha) and Żeromski (ZER; 6 ha). Saski is closest and Żeromski is farthest away from the city centre. These parks are similar in shape and vegetational structure, with old *Tilia*, *Populus* and *Acer* trees predominating. The ground is covered by regularly-mowed grass intersected by paths and pavements. All three plots are regularly visited by people.

Bird counts used in the analysis were conducted by students of the Warsaw University's Faculty of Biology and by the authors during 18 seasons between 1977 and 2003. We assumed that data on corvids are reliably collected, as the focal species are large, easily distinguishable, and easy to count. All counts were conducted during October–December using a standard protocol. During the counts, an observer slowly walked through the park and counted all observed individuals of a given species. Each route was established so as to observe the corvids over the whole park; birds passing over were not counted. The study months were chosen to cover periods of both mass and low occurrence of wintering Rooks and Jackdaws, to describe the temporal variation in their appearance. In total, 258 daily counts and 26,166 records were used in the analysis. Because the parks were of different sizes, all observations for a particular park and particular date were converted to individuals per hectare prior to the analysis.

We evaluated the effect of snow cover on the density and foraging strategy of corvids. We as-

Table 1. General linear models for densities of four corvid species wintering in urban parks of Warsaw during 1977–2003. Year and day from 1 October were model covariates, and park (SAS, KRA, ZER; see text) and snow occurrence (presence/absence) were fixed factors. Values of F statistic and respective significance levels are presented. Symbols (+/–) denote the direction for significant covariate effects, and "NS" indicates a non-significant effect (not included in the final model). Significance (P) levels: * <0.05; ** <0.01; *** <0.001.

Source	Rook	Jackdaw	Magpie	Hooded Crow
Model	54.37 ***	31.65 ***	19.71 ***	28.52 ***
Intercept	28.00 ***	56.64 ***	6.33 *	64.80 ***
Day	(+) 132.66 ***	(+) 16.32 ***	(–) 15.56 ***	(–) 30.33 ***
Year	(–) 28.19 ***	(+) 57.37 ***	(+) 6.91 **	(+) 66.97 ***
Park	NS	43.78 ***	29.17 ***	16.41 ***
Snow occurrence	18.28 ***	11.56 ***	NS	NS
Park x Snow	NS	NS	NS	NS
Variance explained (R_{adj}^2)	38.4	37.4	23.5	30.6
Levene's test (P value)	0.986	0.452	0.261	0.418

sumed the mechanism to be that the occurrence of snow cover would decrease the availability of food resources. Due to sample-size limitations, the foraging strategy could only be assessed for the two most common species, viz. Rook and Jackdaw. For the foraging strategy analysis purposes, we conducted all-winter counts in the three parks during 2002–2004 so that we classified birds according to their foraging strategy: (1) active search for food on the ground, and (2) a "sit-and-wait" strategy, i.e., perched on a tree and waiting for a foraging opportunity. The latter relies on sudden appearances of human-provided food. For this part of the study, we collected data on 2647 individuals of the two species during 31 counts.

To compare the dynamics of corvid species, we investigated whether species densities were affected by the season, study park (SAS, KRA, ZER), study year and snow occurrence. The time of the season was expressed as being the day since October 1, i.e., ranging from 1 to 90. Information about snow depth was obtained from Daily Agrometeorological Bulletin published by the Institute of Meteorology and Water Management (Warsaw, Poland) for each day of counts.

The statistical analysis was based on a General Linear Model (GLM) with the densities of particular corvid species being the dependent variable. The densities were square-root transformed to approach a normal error distribution. Day and year were used as covariates, whereas park (SAS, KRA or ZER) and snow occurrence (present or absent) were fixed factors. Additionally, interactions among the factors were tested. Statistically non-significant (P >0.05) factors, covariates and interactions were not included in the final model. The GLM was conducted for each species separately to elaborate possible species-specific responses. Variance homogeneity for each GLM run was confirmed using Levene's test (see Table 1). Pearson correlation was used to explore density correlations between different species. Here, we used standardized residuals of the densities derived from the effects of significant predictors included in the GLM instead of raw densities, because this way we were able to correlate densities of different species independently of the effects of day, park, year and snow (which could potentially synchronize densities). Finally, linear regression was used to analyze the relationship between the number of Rooks and Jackdaws observed off the ground (expressed as percentages from all observed birds of a particular species) and snow depth. SPSS 13.0 software was used for the statistics (SPSS 2004).

3. Results

Rooks dominated the corvid community in the study parks with a total of 18,625 records (71.2% of all records). The Rook density varied between 0 and 19.81 individuals/ha per park, and the maximum total abundance was 317 individuals. Jackdaws produced a total of 4231 records (16.2%),

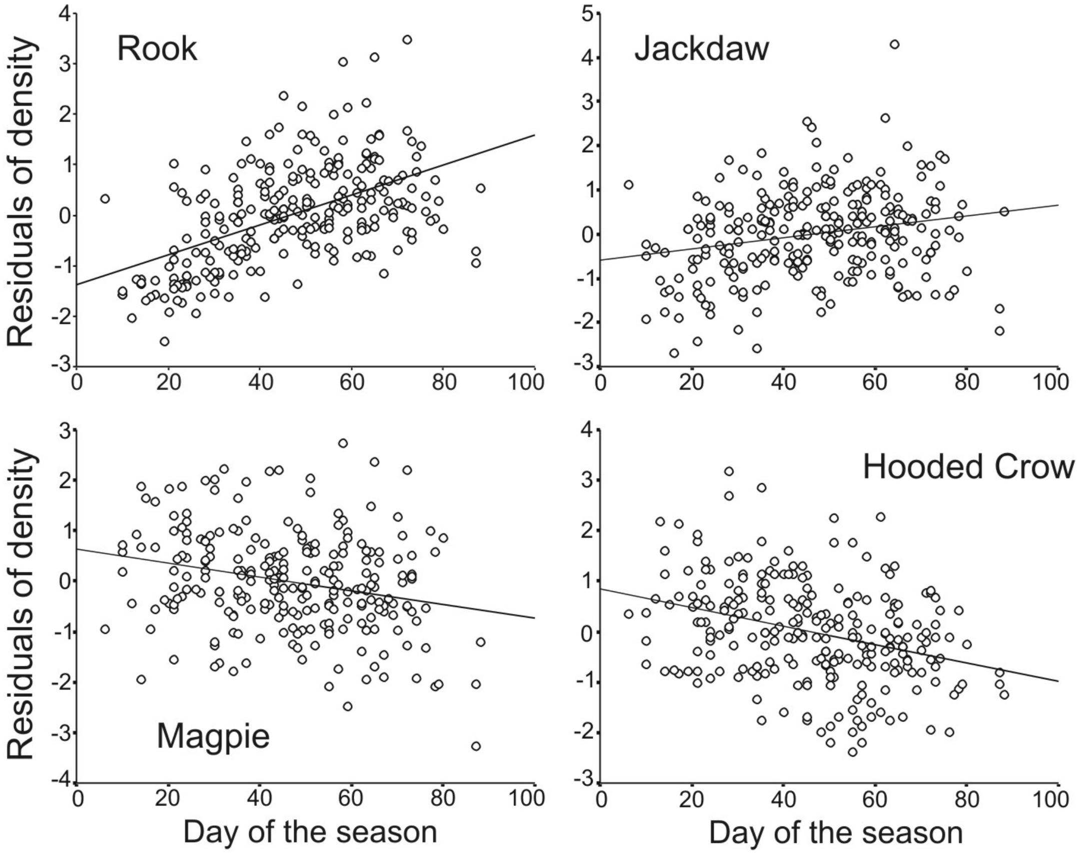

Fig. 1. Densities of four corvid species wintering in urban parks in Warsaw during October–December (value 1 on horizontal axis = 1 October) during 1977–2003. The density values are standardized residuals of the GLM after excluding the effects of year, park and snow (see Table 1).

their density varying between 0 and 10.2 ind./ha per park, followed by Magpie (1796, 6.8%, 0–3.0 ind./ha) and Hooded Crow (1514, 5.8%, 0–2.6 ind./ha). The densities of these corvid species significantly depended on the analyzed variables with the exception of the interaction between park and sampling period, which was not included in any of the four models. The final models explained 23–38% of species-specific variability in density (Table 1).

Densities of the focal species changed significantly over the autumn-winter season (i.e., the 90 days from October 1 to the end of December; Table 1, Fig. 1). The densities of Rook and Jackdaw increased, while those of Magpie and Hooded Crow decreased during the season (Fig. 1). The densities were unstable during 1977–2003, however. Rook density significantly decreased, and the three remaining species significantly increased, during the study years.

In general, densities of the four species remarkably varied among parks and were lowest in ZER. The densities of Jackdaw, Magpie and Hooded Crow significantly differed among the parks, but no clear pattern was recorded (Fig. 2). Jackdaw density was highest in SAS and lowest in ZER, a tendency similar to the Rook. However, the differences for the Rook were not significant, and the variable park was therefore excluded from the final model (Table 1). The density of Magpie was the highest, and that of Hooded Crow was the lowest, in KRA.

The presence/absence of snow significantly affected only Rook and Jackdaw densities. Both species significantly declined in the studied parks if snow was present. In contrast, snow had no sig-

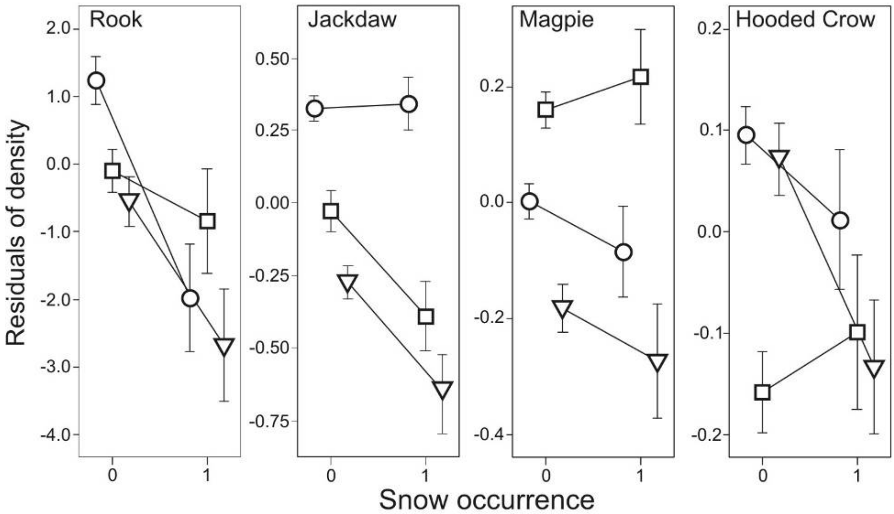

Fig. 2. Densities (mean + 95%CI) of four corvid species wintering in three urban parks in Warsaw (circles = SAS, squares = KRA, triangles = ZER; see text) separately for periods with (1) and without (0) snow cover. Jittering along the x axis was used to distinguish overlapping symbols. The density values are standardized residuals of the GLM after excluding the effects of year and day of the season (see Table 1).

nificant effect on the densities of Magpie and Hooded Crow (Fig. 2). Moreover, snow depth significantly affected the foraging strategy (indicated by individuals being observed foraging on the ground or perching on trees) of Rooks and Jackdaws in the parks. During periods without snow cover, the majority were observed on the ground, whereas deep snow cover was associated with almost all Rooks and Jackdaws perching in trees (Fig. 3). This relationship was highly significant for Rook (linear regression; $R = 0.77$; $F = 40.24$; $P < 0.0001$) and for Jackdaw ($R = 0.64$; $F = 17.75$; $P = 0.0003$).

Dynamics of particular species correlated with each other. After excluding the effects of explanatory variables in the GLM, species-specific densities (residuals of the GLM summarized in Table 1) were significantly and positively correlated with all pairs of species (Pearson correlation; $R > 0.14$, $P < 0.025$ for all pair-wise comparisons).

4. Discussion

Season, snow occurrence, year and park in question significantly affected the densities of the studied corvid species. Clearly, the distribution and density of a given corvid species in an urban park is not random. The analyzed predictors explained one-third of the density variation; we discuss possible mechanisms behind these observations below.

Corvid densities changed significantly from the beginning of October until the end of December. Interestingly, two opposite patterns were recorded: Rook and Jackdaw increased, while Magpie and Hooded Crow decreased during the autumn-early winter season. For Rook and Jackdaw, these changes could be explained by individuals arriving from breeding grounds located in north-eastern Europe (Böhmer 1973, Hubalek 1983, Luniak *et al.* 2001). Moreover, the increase in number of these two species may be driven by deteriorating winter conditions, which in turn force birds to migrate from agricultural areas and city outskirts to city centers (Górski 1976). However, Rook and Jackdaw decreased after snow fall; thus, the hypothesis on movements from farmland to cities seems to be unjustified. On the other hand, Magpies and Hooded Crows declined during the three autumn-winter months. Since the Magpie population is sedentary (Cramp & Perrins 1994), plausible explanations for its decline are a shift in habitat preference and a regular movement within

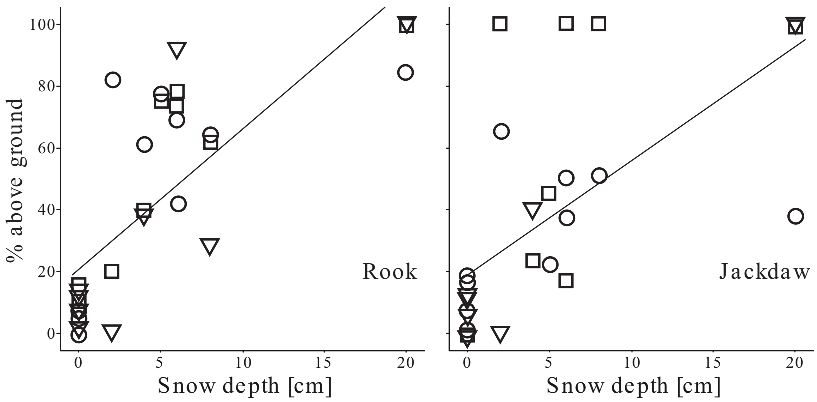

Fig. 3. Vertical distribution of Rooks and Jackdaws (percentages of individuals observed perching on trees) in three urban parks in Warsaw (circles = SAS, squares = KRA and triangles = ZER; see text) in relation to the depth of snow cover.

the city. It is also possible that these local movements are forced by an increase in Rook numbers – the most numerous and also larger species – and by competition within the corvid community, forcing Magpies and Hooded Crows to switch their foraging habitats within the city. Also, mortality should be taken into account as an explanation of the observed seasonal declines of Magpie and Hooded Crow. However, after excluding the effects of snow, park and year on species-specific densities, the densities of all corvid species appeared to be positively correlated, which should not take place in the case of strong inter-specific competition. Thus, other factors, such as food, may be responsible for the synchronization of the dynamics of these species.

The density of Rooks showed a long-term decline, while the densities of the remaining species increased during the 27 study years. These results confirm earlier observed long-term changes in the abundance of wintering corvids (Mazgajski & Szczepanowski 2005, Mazgajski *et al.* 2005, 2008, Vökler 2007). Since the exact origin of corvids wintering in Warsaw is not well known, it is difficult to identify the factors directly driving these long-term changes. However, climate-related forces, such as the long-term decline of winter severity, may be plausible (Hubalek & Capek 2008).

The densities of Jackdaw, Magpie and Hooded Crow varied significantly among parks. These differences were not expected, as the three study plots are relatively similar in terms of vegetation structure and management. The parks were distributed across an urbanization gradient, so the observed differences in corvid densities may result from different species-specific sensitivity to anthropogenic pressure. Jackdaw density was highest in SAS, which is located closest to the city center, and lowest in ZER, located farthest away from the center. This agrees with the reported preferences of the Jackdaw for highly populated areas during winter (Mazgajski *et al.* 1997; Jokimäki & Suhonen 1998). Magpie and Hooded Crow, on the other hand, did not show such a clear pattern. The former peaked in KRA, while the Hooded Crow was scarce in that park. Such lack of overlap may indicate competitive interaction between these species or dispersion according to resources. In general, densities of the four studied species were lowest in ZER, the park located furthest away from the center, which follows Jokimäki and Suhonen's (1998) findings that the highest densities of omnivorous birds may be observed in areas of high urbanization.

Snow cover significantly affected densities of only Rook and Jackdaw and had no significant effect on Magpie and Hooded Crow. It is possible that differences in foraging and diet composition among the species (Waite 1984) are responsible for this discrepancy and make Rooks and Jackdaws more affected by snow cover. The remarkable effect of snow cover on foraging birds has been previously reported for several species (Summers & Underhill 1996, Halonen *et al.* 2007, Wikar *et al.* 2008; but see Żmihorski & Rejt 2007). A decline of Rooks and Jackdaws as a response to snow cover can be driven by the migration behavior both at a local (within the city) and at a larger spatial scale (e.g., movements to southern areas). Moreover, changes in the behavior of Rooks and Jackdaws in relation to the depth of snow cover may suggest that these species change their foraging strategy in relation to food availability. Deep snow cover may reduce the availability of 'natural' food and force birds to look for supplementary sources of food.

The spatiotemporal dynamics varied remarkably among the four corvid species wintering in urban habitats. These species did not exhibit similar changes among plots or periods with and without snow, or during the progression of the autumn-winter season. The discrepancies observed may be driven both by differences in the mobility, body size, food preferences, roosting strategy or interspecific interactions of the focal species, or by competition within the avian community. Nevertheless, we showed that the densities of corvids exhibit long-term changes and are also prone to local and short-term factors. The importance of snow cover for the two most numerous species indicates that weather factors remain important even in an urbanized landscape. The strong responses of Rook and Jackdaw to snow cover may indicate that at least some of the resources utilized by these birds in the city were 'natural', i.e., other than supplementary feeding, waste, and so on, since anthropogenic food is less likely to depend on weather conditions.

Acknowledgements. We are grateful to the students of Warsaw University responsible for collecting the observational data used in this study. Anonymous referees provided helpful comments to previous versions of the manuscript. Barbara Przybylska kindly improved the English.

Pitkäaikainen tila- ja aikamittakaavan talvikauden dynamiikka puistoalueiden varislinnuilla Varsovassa, Puolassa

Talvehtiminen kaupunkiympäristössä vaikuttaa edulliselta ja yhä tärkeämmältä lintujen strategialta. Keski-Euroopassa mustavaris, naakka, harakka ja varis muodostavat yhden kaupunkien runsaimmista villeistä selkärangatonryhmistä. Varislintuja laskettiin Varsovassa, Keski-Puolassa, kolmessa puistossa loka–joulukuussa 18 kautena (1977–2003; 258 päiväkohtaista laskentaa, 26 166 havaintoa).

Tutkimme päivämäärän, vuoden, puiston ja lumipeiton vaikutuksia havaittuihin tiheyksiin, sekä lumen paksuuden vaikutuksia pystysuunnassa varislintujen olinpaikkaan. Lokakuusta joulukuuhun mustavaris- ja naakkatiheydet kasvoivat, mutta harakka- ja varistiheydet alenivat. Pitkällä aikavälillä mustavaris väheni, mutta muut lajit runsastuivat. Mustavarista lukuun ottamatta varislintutiheydet vaihtelivat merkitsevästi myös puistojen välillä. Lumipeitto vaikutti negatiivisesti mustavaris- ja naakkatiheyksiin, mutta harakan ja variksen tiheyksiin sillä ei ollut merkitsevää vaikutusta. Lumipeitteen paksuus vaikutti mustavariksen ja naakan pystysuuntaiseen esiintymiseen: lähes kaikki yksilöt havaittiin puissa (eikä maassa) lumipeitteen ollessa paksu, mikä voi indikoida ravinnonhankintastrategian vaihtumista lumijaksoilla. Kun selitysmalleista poistettiin ajankohdan, lumen ja puiston vaikutus, eri lajien runsaudet korreloivat keskenään. Tämä viittaa siihen, että muut kuin kilpailutekijät (kuten ravinnon saatavuus) voivat samanaikaistaa näiden lajien dynamiikkaa kaupunkipuistoissa.

References

Böhmer, A. 1973: On the wintering of Rook *Corvus frugilegus* near Basel. — Der Ornitologishe Beobachter 70: 103–112. (In German with English summary)

Cramp, S. & Perrins, C.M. 1994: The Birds of the Western Palaearctic. Vol. VIII. — Oxford University Press, Oxford.

Górski, W. 1976: Investigations on birds wintering in fields near Poznań. — Acta Ornithologica 16: 79–116. (In Polish with English summary)

Halonen, M., Mappes, T., Meri, T. & Suhonen, J. 2007: Influence of snow cover on food hoarding in Pygmy Owls *Glaucidium passerinum*. — Ornis Fennica 84: 105–111.

Hubalek, Z. 1983: Roosts and habitats of *Corvus frugilegus* wintering in Czechoslovakia. — Acta Scientarum Naturalium Brno 17: 1–52.

Hubalek, Z. & Capek, M. 2008: Migration distance and the effect of North Atlantic Oscillation on the spring arrival of birds in Central Europe. — Folia Zoologica 57: 212–220.

Jokimäki, J. & Suhonen, J. 1998: Distribution and habitat selection of wintering birds in urban environments. — Landscape and Urban Planning 39: 253–263.

Jokimäki, J., Clergeau, P. & Kaisanlahti-Jokimäki, M.-L. 2002: Winter bird communities in urban habitats: a comparative study between central and northern Europe. — Journal of Biogeography 29: 69–79.

Kuttler, W. 2008: The urban climate – basic and applied aspects. — In Urban ecology (eds. Marzluff, J.M., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., ZumBrunnen, C. & Simon, U): 233–248. Springer.

Lahti, K., Orell, M., Rytkonen, S. & Koivula, K. 1998: Time and food dependence in Willow Tit winter survival. — Ecology 79: 2904–2916.

Luniak, M., Kozłowski, P., Nowicki, W. & Plit, J. 2001: Birds of Warsaw 1962–2000. — Atlas Warszawy 8. IGPiP PAN, Warszawa. (In Polish with English summary)

Luniak, M. 1981: The birds of the park habitats in Warsaw. — Acta Ornithologica 18: 335–370.

Luniak, M. 2004: Synurbization – adaptation of animal wildlife to urban development. — In Proceedings of the 4th International Symposium on Urban Wildlife Conservation (eds. Shaw, W.W., Harris, L.K. & VanDruff, L.): 50–55. University of Arizona, Tucson.

Mazgajski, T.D., Kędra, A.H. & Tykarski, P. 1997: Comparison of methods for establishing interspecific number relations in winter concentrations of corvids. — Notatki Ornitologiczne 38: 61–67. (In Polish with English summary)

Mazgajski, T.D. & Szczepanowski, R. 2005: Size of corvid community wintering in Warsaw. — In Corvids of Poland (eds. Jerzak, L., Kavanagh, B.P. & Tryjanowski, P.): 427–434. Bogucki Wyd. Nauk., Poznań. (In Polish with English summary)

Mazgajski, T.D., Woźniak, A. & Żmihorski, M. 2005: Changes in the number of corvids wintering in Warsaw over thirty years 1975–2004. — In Corvids of Poland (eds. Jerzak, L., Kavanagh, B.P. & Tryjanowski, P.): 419–426. Bogucki Wyd. Nauk., Poznań.

Mazgajski, T.D., Żmihorski, M., Halba, R. & Woźniak, A. 2008: Long-term population trends of corvids wintering in urban parks in Central Poland. — Polish Journal of Ecology 56: 521–526.

Mączak, S. 1990: Uwarunkowania klimatyczne. — In Środowisko przyrodnicze Warszawy (eds. Biernacki, Z., Kazimierski, J. & Wróblewski, A.): 289–296. PWN, Warszawa. (In Polish)

Robinson, R., Baillie, S., Crick, H.Q.P. 2007: Weather-dependent survival: implications of climate change for passerine population processes. — Ibis 149: 357–364.

SPSS 2004: SPSS 13.0 for Windows. — SPSS Inc., Chicago, USA.

Summers, R.W. & Underhill, L.G. 1996: The dispersion of Arctic breeding birds according to snow-free patch dimensions during the spring thaw in the north eastern Taimyr Peninsula, Russia. — Polar Biology 16: 331–333.

Vökler, F. 2007: Wintering populations of crow species in Mecklenburg-Western Pomerania – results of a night roost survey in winter 2004–05. — Vogelwelt 128: 131–140. (In German with English summary)

Waite, R.K. 1984: Winter habitat selection and foraging behaviour in sympatric corvids. — Ornis Scandinavica 15: 55–62.

Wikar, D., Ciach, M., Bylicka, M. & Bylicka, M. 2008: Changes in habitat use by the Common Buzzard (*Buteo buteo* L.) during non-breeding season in relation to winter conditions. — Polish Journal of Ecology 56: 119–125.

Winiecki, A. 2000: The wintering strategy of Rooks *Corvus frugilegus* Linnaeus, 1758, in Poznań, west Poland. — Acta Zoologica Cracoviensia 43: 135–164.

Żmihorski, M. & Rejt, Ł. 2007: Weather-dependent variation in the cold-season diet of urban Kestrel *Falco tinnunculus*. — Acta Ornithologica 42: 107–113.