Correlation between height and site distribution of nest holes occupied by Jackdaws
*Corvus monedula* LINNÆUS, 1758, in Poland

(with 4 text figs.)

Współzależność między wysokością i położeniem wnęk gniazdowych zajmowanych przez kawki *Corvus monedula* LINNÆUS, 1758, w Polsce

Abstract: The distribution of nests occupied by Jackdaws was analyzed in three colonies: a castle in Cracow, the old ruins of Kamieniec and the iron frame-work of a railway bridge in Wroclaw, each of which provided man-made nest-holes of the same type at different altitudes. The nesting pairs preferred the holes above the minimum height of ca. 3.5 meters, selecting the upper holes (modal value 10—12 m) most frequently in two colonies. In Kamieniec, where the walls have large vertical extent up to 38 meters, the nest-sites inhabited revealed more even distribution. The aggregations of nests in the two colonies are discussed on the basis of e.g. the total “compactness of colony” (measured by a special index $C_j$), of colonial interactions between birds and of connections to adjacent grassland areas.

I. INTRODUCTION

The aggregations of nest-holes occupied by Jackdaws are regarded as a manifestation of highly social behaviour resulting from other social nesting habits (LORENZ 1938; GRANT & NETTLESHIP 1971; HÖGSTED 1980). Yet there is a question whether nests are evenly distributed in colonies with an abundant number of holes of the same size available or whether the Jackdaw specifically prefers nests at certain heights. These habits might be related to a selective advantage to the breeding success as presented by SMETANA (1980; cf. NICE 1957; SIMOCHKO 1975). However, there are few data on the influence of the height on the distribution of nest-holes.

Three Jackdaw colonies in SW Poland provided material for testing the site distribution of nests. In the three colonies, a 19th century fortification in Cracow, the ruins of an old castle in Kamieniec and a bridge in Wroclaw (all in SW Poland), the nest-holes were man-made and were of the same size but at different heights. It was characteristic of the colonies that (1) the maximum heights of the constructions from 15 to 38 meters above the ground provided adequate altitudinal diversity for nest distribution (cf. FOLK 1968; KULCZYCKI
1973; Smetana 1980), (2) man did not obstruct or disturb nesting in any colony, (3) the colonies were surrounded by grassland areas which provided feeding areas (see e.g. Lockie 1956; Antikainen 1978; Podkoverkin 1980) and (4) the colonies were situated in separated areas with the minimum distance of 0.7 kilometers from the nearest Jackdaw community or solitary nest thus providing a possibility of more homogeneous habitat preference and nesting habits of the community.

The text is the second part of an experimental study of Jackdaw communities commenced by Antikainen (1981).

II. THE COLONIES STUDIED

The 19th century fortification surrounding the Kościuszko Mound in Cracow (50°4′N, 19°51′E) on the top of a hill about 3.5 kilometers from the city centre was the main study colony called later also “Mound” or “castle” (in Figs 2 and 4). The polygonal fortification encircling inner yards and a center cone of earth consists of 250 meters of outer walls, which can be divided into 9 different sections on the basis of the height of the walls and varying parts of the buildings. The wall constructions mainly comprise three rows of holes at the approximate altitudinal distance of 5 and 7.5 meters from one another. Beam holes and ornamental niches with square or rounded entrances of 15—20 centimeters in extent (the depth of ca. 0.8 meters in the walls) provide Jackdaws with nest-sites, in which height is the only variable (cf. Antikainen 1978). Large grassland areas, the slopes of the hill, the parks: Błonia, Jordana and Krakowski lie on the outskirts of the Kościuszko Mound (see Grodziński 1971 and 1980).

The second study colony was located at Kamieniec Ząbkowicki (50°32′N, 16°52′E) in the district of Wałbrzych. The ruined towers and walls of the castle up to more than 30 meters in height and 110 meters in length are surrounded by deciduous forests. This colony is later also called “ruins”. For each of the 3—4 storeys of the building I found 4—5 beam holes of approximately 30×30 centimeters, most of which were occupied by Jackdaws. The ruins of the castle on the top of the hill adjoin cultivated fields on one side.

The third Jackdaw colony occupied a railway bridge across the River Odra in Wroclaw—Popowice (51°8′N, 17°1′E). The constructions consist of three sets of framework, in each of which juncture of the bridge beams provides hollows accepted by Jackdaws for nest-sites. The mutually similar hollows are distributed at different altitudinal levels (the maximum height ca. 14 meters above the river).

III. METHODS

The study colonies were checked by the author on the following dates: the Kościuszko Mound on 10th and 12th May, Kamieniec 30th April and Popowice on 25th April and 2nd May in 1980. The observations took place from 8.30
to 12 a. m. and from 2 to 8.10 p. m. Binoculars were used when watching the colonies from different directions. In addition I carried out general observations in Cracow from the Sigismundus Tower of the Wawel cathedral on 27th March, from the tower of the Jesuit Church on 28th March and Mariacki Church on 31st March and 2nd April, from the roof of the Zoological Institute and from the top of the Kościuszko Mound on 2nd April. All the nest-sites occupied by Jackdaws, nest traffic and flight routes to feeding grounds I managed to detect were immediately marked on the map and also on special charts of the study colonies. The surroundings of the colonies were checked by using the mapping method (see e. g. TOMAŁOJC and PROFUS 1977 and GRODZIŃSKI 1971).

In all observation periods the weather was favourable for the activities of birds (over 10°C, mostly sunny).

The heights of walls and the distances between nests were estimated by counting the number of bricks or by the basic components of the constructions.

The index of “compactness of colony” \((C_j)\) is calculated by the formula:

\[
C_j = \frac{1}{n} \left( \frac{\sum_{i=1}^{n} z_{ij}}{y_j} \right)
\]

where \(n\) = the number of nests in the colony, \(z_{ij}\) = the shortest distance of the nest \(i\) to the closest nest known in the colony, \(y_j\) = area of the colony \(j\) in hectares (built area, Table I, cf. LOMAN 1975).

The extent of grassland areas round the colonies was estimated within the distance of 1.5 kilometers.

Some data and hints were obtained from Polish ornithologists.

IV. RESULTS

The total distribution of the height of the nest-holes available for Jackdaws in three study colonies varies from ca. 1.5 to 36 meters. The total range for niches occupied is 3.5—30 meters. As seen in Fig. 1 heights are divided into three groups with the modal value of 10—12 meters. Altogether 71% of all nests in the three colonies concentrate on the height of 10—20 meters. However, the mean heights of the colonies of Kamieniec (\(\bar{x} = 23.1 \pm 6.65\)) and Popowiec (\(\bar{x} = 13.1 \pm 0.85\)) differ significantly \((t = 5.94, \ df = 29, \ p < 0.001)\), as well as the means calculated for Kościuszko Mound \((\bar{x} = 10.3 \pm 3.49)\) and Kamieniec \((t = 7.22, \ df = 45, \ p < 0.001)\), but not the means of the Kościuszko Mound and Popowiec \((t = 1.72, \ df = 44, \ p < 0.10)\). The deviation of heights in Kamieniec is remarkably large. No difference \((t = 1.88, \ df = 225, \ p < 0.10)\) can be found when the mean of the Kościuszko Mound and Kamieniec data combined are compared with the mean obtained by ANTIKAINEN (1978) at Finnish ruins, castles and churches.
Table I

The area of the study colonies and the area studied in the surroundings of the colonies (see the text). The values are approximations.

<table>
<thead>
<tr>
<th>Colony</th>
<th>Area of colony (in ha)</th>
<th>Study area (in ha)</th>
<th>No of nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kościuszko Mound</td>
<td>3.15</td>
<td>35.60</td>
<td>37</td>
</tr>
<tr>
<td>(The Castle)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kamieniec</td>
<td>0.88</td>
<td>13.00</td>
<td>16</td>
</tr>
<tr>
<td>(The Ruins)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wroclaw-Popowice</td>
<td>0.65</td>
<td>12.00</td>
<td>15</td>
</tr>
<tr>
<td>(The Bridge)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>4.08</td>
<td>60.60</td>
<td>68</td>
</tr>
</tbody>
</table>

Fig. 1. The distribution of the height of the nest-holes in the study colonies categorized in the intervals of two meters (number of nests: 63).

The distance of the nest-holes occupied by Jackdaws from the topmost available holes is seen in Fig. 2 (cf. Loman 1975). Thus, the nests in the colonies of the Kościuszko Mound and Popowice are on an average closer to the maximum nesting height than those in Kamieniec. This is also shown in Table II. In Kościuszko Mound and Popowice the proportion occupied holes to those available is highest at the upper level. In the ruins of Kamieniec the holes at the lower level are more frequently occupied (29%).
The number of the holes available for Jackdaws and the number and the percentages of nests occupied on three vertical levels in the study colonies. The ranges/means of heights at different levels below in meters. For the description of levels, see the text.

<table>
<thead>
<tr>
<th>Colony</th>
<th>Upper level</th>
<th></th>
<th>Middle level</th>
<th></th>
<th>Lower level</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of holes</td>
<td>Nests</td>
<td>Occupied %</td>
<td>No. of holes</td>
<td>Nests</td>
<td>Occupied %</td>
</tr>
<tr>
<td>Kościuszko Mound (The castle)</td>
<td>183</td>
<td>27</td>
<td>14.8</td>
<td>106</td>
<td>7</td>
<td>6.6</td>
</tr>
<tr>
<td>Range/mean</td>
<td>6—16.5</td>
<td>20</td>
<td>20.0</td>
<td>3.5—11.5</td>
<td>22</td>
<td>18.2</td>
</tr>
<tr>
<td>Kamieniec (The ruins)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range/mean</td>
<td>28—30</td>
<td>12</td>
<td>66.7</td>
<td>20</td>
<td>3</td>
<td>25.0</td>
</tr>
<tr>
<td>Wroclaw—Popowice (The bridge)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range/mean</td>
<td>12.5—14</td>
<td>11</td>
<td></td>
<td>9.5(3.5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total/mean</td>
<td>221</td>
<td>43</td>
<td>19.5</td>
<td>140</td>
<td>14</td>
<td>10.0</td>
</tr>
</tbody>
</table>
Fig. 2. Relation between the mean height (in m) of nest-holes and the distance from the topmost holes in the study colonies. Horizontal lines denote standard deviations (SD).

Fig. 3. The distribution of nest-holes occupied by Jackdaws in Mound castle, divided into the nine sections of the castle and in relation to the height of holes available at upper level (thick line), at middle level (solid line) and at lower level (broken line). Horizontally shaded parts in the columns denote the percentage of the occupied holes of the total number of upper holes available; the vertically shaded parts indicate the total number of occupied holes (363 holes available, 37 occupied).
The variation of the maximum nesting height (due to the wall height) indicates that the sites at the upper level are not everywhere equally inhabited (Fig. 3). In the sections number 5—7 of the fortifications surrounding Kościuszko Mound altogether 5 holes, i.e. 9.1% are occupied while in taller sections number 1—3 and 8—9 altogether 22 holes, i.e. 12.2% are inhabited. The difference is, however, insignificant.

Fig. 4. The correlation (regression lines) between nest height above the ground and the number of nests occupied by Jackdaws in the three study colonies. The nests are grouped in two-meter categories.

The available data indicate a slight correlation between the nest height and the number of nest-sites occupied by Jackdaws (Fig. 4). Although there are differences in the heights of the uppermost holes in the constructions, which are in the Kościuszko Mound fortification ca. 16.5, in Kamieniec ruins 30 and in Popowice bridge 14 meters, positive correlations can be found in the following coefficients (r) respectively: 0.444, 0.102 and 0.500. About 63% of the nests at Kamieniec ruins (n = 16) were located in towers, which are the highest parts of the ruins.

The range of the distance to the closest nest in the study colonies varies in the Kościuszko Mound from 1.5 to 20 meters, in Kamieniec from 4 to 15 meters and in Popowice only from 4 to 6 meters. The minimum value of the
mean distance belongs to Popowice and the largest to Kamieniec (Table III). The difference between Popowice and Kamieniec is statistically significant ($t = 3.76$, df = 29, $p < 0.001$), but not between Mound and Kamieniec ($t = 2.06$, df = 45, $p < 0.025$) nor between Mound and Popowice ($t = 1.44$, df = 44, $p < 0.10$).

Table III

<table>
<thead>
<tr>
<th>Distance in meters</th>
<th>Kościuszko Mound (The castle)</th>
<th>Kamieniec (The ruins)</th>
<th>Wrocław—Popowice (The bridge)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>16</td>
<td>8</td>
<td>10</td>
<td>34</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>4</td>
<td>5</td>
<td>19</td>
</tr>
<tr>
<td>15</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>20</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Mean</td>
<td>5.9</td>
<td>8.8</td>
<td>4.7</td>
<td>6.40</td>
</tr>
<tr>
<td>SD</td>
<td>5.02</td>
<td>4.30</td>
<td>0.94</td>
<td>4.47</td>
</tr>
</tbody>
</table>

The compactness of a colony can also be measured by a special index $C_i$, which is in Mound only 0.250, in Kamieniec 1.595, but in Popowice as high as 93.320 (cf. Loman 1975: 171). Thus, the latter value indicates the highest degree of nest aggregations in the colony.

Although there are difficulties in the definition of the extension of the grassland area encircling the colonies, the positive correlation can be found between it and the size (number of pairs) of the nesting colony: $r = 0.935$, ($t = 21.46$, df = 66, $p < 0.001$). Inversely, the size of the colonies and the distance from grasslands indicate the strong negative correlation: $r = -0.822$ ($t = 11.55$, df = 66, $p < 0.001$).

V. DISCUSSION

The dispersion pattern of nests occupied varies among Jackdaw populations considerably ranging from scattered nests to the compact colonies with even more than 100 pairs. Jackdaws occasionally build open nests. This breeding habit is considered to have been brought about by e. g. human interference (limiting the number of holes), by predation by Crows *Corvus corone* and by the availability of natural holes (Antikainen 1978: 4; Röell 1978; Högestedt 1980).
Inversely, in the study colonies the artificial constructions themselves exclude predominantly the facts presented above. The Carrion Crow is absent. Nest-holes are available in abundance at varying heights. The height of nests functions both as an intracolonial and an intercolonial pattern which results in stability in Jackdaw populations (cf. Colwell 1975: 283).

The maximum height of the walls (framework) in constructions was the criterion for selecting the investigated colonies in order to test the correlation between height and the site distribution of nest-holes. The sample represents three different categories: Kamieniec — the total height nearly up to 38 meters, Mound, a community with medium height of walls. The bridge with iron niches in Popowice supplies the lowest maximum height. The mean heights of nest-holes in each colony reflect these categories.

The data of my study reveal that although similar nest-holes at acceptable distances from the closest neighbour nest are available for Jackdaws, the holes are not inhabited with the same frequency as could be expected (Table IV), if the maximum height of nest-holes (walls or constructions) is relatively small. This is clearly seen in the situation in the bridge of Popowice. Thus, the birds occupy the holes highest up more frequently.

The selection of nest-holes by the Jackdaws is also connected with the minimum height. Many authors report that Jackdaws only occasionally nest in walls or constructions below 1.5—3 meters (e. g. Holyoak 1967; Folk 1968; Kuczynski 1973; Antikainen 1978 : 7; cf. Goodwin 1976), which is thus confirmed by this study. In Czechoslovakia Folk (1968) reports the modal value of 4—6 meters (36%) for nest height in buildings. However, he does not make difference between chimneys, ruins, castles etc. In his data the percentage of the height below 3 meters is zero, but of the height of 35—40 meters is 10%. In Popowice the hollows located at the lower level, i. e. 3.5 meters above the rails, were totally discriminated, which explains the significant deviation from the even distribution expected. But when the range of heights for the available nests is large, the holes are occupied quite evenly. The colony of Ka-

<table>
<thead>
<tr>
<th>Colony</th>
<th>Chi²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kościuszko Mound</td>
<td>8.19</td>
<td>&lt;0.025</td>
</tr>
<tr>
<td>Kamieniec</td>
<td>0.37</td>
<td>0.75</td>
</tr>
<tr>
<td>Wrocław—Popowice</td>
<td>19.70</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
mieniec ruins confirms this statement (lower level 15 meters!). The holes at the middle and even at the lower levels are more equally wanted as nest-sites. The same main tendency is revealed by the positive correlation between the height and the number of nest holes occupied at Kościuszko Mound.

The data of my study also provide contradicting evidence of the correlation mentioned above. With the increase of the number of nesting pairs in the colonies the correlation to the height seems to be negative: \( r = -0.639, (t = 6.74, df = 66, p < 0.001) \). I assume that this result is brought about by a complex of factors. Contrary to other colonially nesting birds, e.g. Puffins Fratercula arctica (Grant & Nettingship 1971), the members of Corvidae seem to have an optimal size of a colony, in Rooks Corvus frugilegus below 35 pairs (Józefik 1976) and in Jackdaws in Finland about 8—15 pairs (Antikainen 1978: 8; cf. Antikainen 1981) and in Poland 20—35 pairs (Luniak 1964; Kulczycki 1973; Grodziski 1976; cf. Glutz von Blotzheim 1962 and Folk 1968). In large colonies the most suitable nest-sites are occupied by strong (old) pairs. Their highly social interaction leads to a cluster of nests in optimal places inside colonies (Röell 1978). The evidence of it comes from Kościuszko Mound fortification, where the site distribution of the nests occupied shows aggregations in the sections within the shortest distance from grassland areas (cf. Goodwin 1976). The compactness of the colonies, such as that at the upper level in Popowice, is highest in these sections.

North (1972) reports a strong preference for nesting sites higher than 10 feet in the House Sparrow Passer domesticus in Wisconsin. He placed nest-boxes at 3-foot intervals on trees with the result that only the topmost boxes were utilized. Smotana (1980) used lower heights, 1.5, 3, 5 and also 6.3, 8 and 19.1 meters on Jackdaws in Kazakhstan (USSR). According to his statements the upper boxes were most occupied and had even higher breeding success (cf. Borczyński & Sokolowski 1953 and Simchko 1975). Folk (1968) presented that 65% of nests in tree holes were at the height of 4—10 meters, 55% of nests in buildings at 4—14 meters and remaining 45% at 17—45 meters. However, in his material e.g. the proportion of chimneys is not analyzed. In Finland the mean height of Jackdaw nests in tree holes coincides with that of the Black Woodpecker Dryocopus martius, i.e. 5.9 meters. In the Cathedral of Turku the majority of nests (more than 90 pairs nested in the 1960's) were situated over 40 meters above the ground and distributed between 45—80 meters (my own unpublished observations). The Domestic Pigeon Columba livia domestica occupied holes at lower levels. Competition may also have had an influence on the results of nest-site distribution in the study colonies in some way. In Kamieniec the Kestrel Falco tinnunculus, the Starling Sturnus vulgaris and the House Sparrow were recorded nesting inside the colony itself. The House Sparrow also bred at Mound together with the Collared Turtle Dove Streptopelia decaocto and the Blackbird Turdus merula. The bridge colony of Popowice had no other accompanying species.

The discussion about the correlation between height and the distribution
of nest-holes occupied by Jackdaws can be summarized as follows: (1) An important role is played by the minimum height of holes which naturally contributes to the security of nests, (2) the higher the nest-holes are located the more of them are occupied, (3) however, in high walls and large constructions aggregations of nests are distributed evenly, (4) in low constructions only nest holes located relatively high are occupied. Besides, (5) the total “compactness of the colony”, (6) connections with grassland areas and (7) interspecific competition contribute to aggregations of nest-sites inside a colony.

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REFERENCES


STRESZCZENIE

Praca nawiązuje do założenia, że skupiska gniazdowe kawek są wyrazem ich wysoko rozwiniętego behawioru socjalnego i socjalnych obyczajów legowych. Postawiono w niej pytanie, czy o rozmieszczeniu gniazd kawek decyduje obfitość dostępnych wnęek (nisz), czy też ptaki te specyficznie wybierają gniazda na pewnych wysokościach.

Autor analizuje rozmieszczenie gniazd zajętych przez kawki w ich trzech wybranych koloniach w południowej Polsce, usytuowanych (1) na forcie Kopca...
Kościuszki w Krakowie, (2) w starych ruinach zamku w Kamieńcu Ząbkowickim i (3) żelaznych przęsłach mostu kolejowego na Odrze we Wroclawiu—Popowicach (tab. I). Na każdej z tych budowli kawki zajmują sztuczne wnęki tego samego typu na różnych wysokościach (fig. 1). Skupiska gniazd w dwóch koloniach autor opisuje w oparciu o ocenę tzw. całkowitej zwartości kolonii ("compactness of colony"), mierzonej za pomocą specjalnego wskaźnika Cj, wyjaśnia je powołując się na interakcje między ptakami w kolonii i powiązania z przyległymi terenami ląkowymi i parkowymi.

Stwierdzono, że pary lęgowe zajmują wnęki położone na wysokości powyżej 3,5 metra, nigdy niżej niż 3,0 m, mimo że dostępne dziury na gniazdo były rozmieszczone na wysokościach 1,5—36 m. Wybór nisz gniazdowych przez kawki jest zatem związany z wysokością minimalną, co wiąże się z gwarancją bezpieczeństwa lęgow. W dwóch koloniach (Kraków, Wrocław—Popowice) najliczniej były zajmowane wnęki w górnych partiach budowli (wartości modalne 10—12 m), zwłaszcza w konstrukcji najniższej z badanych, jaką był most. W Kamieńcu, gdzie ściany sięgają 38 m od ziemi, zajęte wnęki gniazdowe są bardziej równomiernie rozmieszczone (fig. 2, tab. II). Wykazano, że dostępne miejsca na gniazda w górnych poziomach budowli nie są wszędzie jednakowo wykorzystane (fig. 3); istnieje słaba korelacja pozytywna (r = 0,10—0,50) między wysokościami lokalizacyjną gniazda, a liczbą zajmowanych wnęk (fig. 4). Rozrzut gniazd w koloniach jest zróżnicowany, silniej zaznacza się on w budowlach większych (tab. III). Potwierdza to wskaźnik zwartości kolonii Cj, który jest wyraźnie większy w odniesieniu do kolonii w Popowicach (93,320) niż w Kamieńcu (11,595) i Krakowie (0,250). Wykazano ponadto zależność skupiskowości kolonii od ich powiązań z okolicznymi terenami zielonymi, jak też od międzygatunkowej konkurencji.

Redaktor pracy: prof. dr Z. Bocheński
STREŚCZENIE

Praca nawiązuje do materiału, ze skupieniu głosadów kawek są wyczynem odzwierciedlającym rozgwieżdżenie ich krążenia społecznego i socjalnych obyczajów tegoż etnika. Należy wziąć pod uwagę, że w rozmieszczeniu głosadów kawek decyduje odmiana dostępnych źródeł, o czym w pracy specjalnie wskazuje przykład na pewnych wysokościach.

Analizuje rozposażenie głosadów zajętych przez kawki w ich terenach wybranych kołonii w południowej Polsce, uwzględniających (1) na forcie Kopce