

The wintering strategy of Rooks *Corvus frugilegus* LINNAEUS, 1758, in Poznań, west Poland

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Abstract. The functioning of the wintering assemblages of the Corvids in Poznań is based on the system of daily flights to feeding grounds, which is stable in time and space. The elements of the system are: the basic roost, routes of flights to feeding grounds and sites of temporary stay (post-feeding concentration points, pre-roosting concentration points), and feeding grounds. According to the author, the main reason for establishment of the system, including the basic roosting place, is the fact that it facilitates the exchange of information about food resources. The energetic and antipredatory functions are of secondary importance. The wintering Rooks roost in a communal roosting place and during the day they disperse over an area distanced up to 25 km from this place. At the beginning and end of the winter season, they are foraging in agrocenoses, using the strategy of active search for food. In the peak of winter they come to urbanized environments and use the expectation of food strategy. The effectiveness of this strategy depends on the experience of individuals, therefore young birds remain outside the urbanized areas. The energy costs of the Jackdaws' stay in the least urbanized areas, e.g. parks and in agrocenoses, are similar. The Rooks' penetration of the city is caused by the need to save energy (less energy is used for flights). The most attractive source of food for Rooks are waste dumping grounds. Strong fluctuations in the number of Rooks foraging there are the result of increased food competition. The change in the type of foraging is accompanied by shortening of the routes of daily flights between the roosting place and feeding grounds. The changes are induced by: a decrease in the availability of food and its irreproducibility in agrocenoses, the need to save energy for flights, and a shortening of daylight equivalent to shortening of foraging time.

Key words: Rook, Corvids, wintering assemblage, zone of daily dispersion, feeding grounds, foraging strategy, energy saving, communal roost, city.

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I. INTRODUCTION

Poznań is a traditional wintering site of the Corvids at least from the beginning of this century (HAMMLING 1933, SOKOŁOWSKI 1936). As a result of the shortening of migration routes by Eastern European populations (BUSSE 1969), the size of wintering assemblages of the Corvids, with absolute domination of Rooks, has increased. In the early 70s the wintering assemblage in Poznań was

composed of 28-30 thousand birds (BERESZYŃSKI & ŻOŁADKOWSKI 1980), while in the mid 80s its size increased to 100 thousand. The species composition was characterised by the dominance of Rooks (85-90%), small contribution of Jackdaws (10-15%) and up to 200 individuals of carrion crows. The birds roosted on one of the two alternative communal roosts, at least from winter 1967/68 till 1998/99.

The Rooks showed a special relationship with the city as a feeding place, in particular in the middle of winter. This relationship was manifested as a shortening of the routes of daily flights from the roost localized in Poznań to distant feeding grounds and an increase in the number of individuals feeding in the city. Analogous relationships with urbanized areas were evidenced as a rule for other cities in Central and Eastern Europe.

The Corvids wintering in Central and Eastern Europe form large permanent wintering assemblages. The Rooks and Jackdaws rest at night on communal roosts located in the vicinity of cities. During daylight they disperse over sometimes distant feeding grounds (e.g. ALLEN & YOUNG 1982, GLUTZ & BAUER 1993). Despite intense research, the reasons why the birds form communal roosts are still ambiguous (e.g. ALLEN & YOUNG 1982, CACCAMISE 1993, CACCAMISE & MORRISON 1988).

In the winter of the years 1982/1983 – 1985/1986 a comprehensive study on the biology of the Corvids, particularly Rooks, wintering in Poznań, was carried out. In the winters of 1983/84 and 1984/85 the size of the daily disperse zone of the species and its habitat preferences were studied, while in 1983/84 the subject of concern was the biology of the species in different habitats in the city of Poznań, as well as on the functioning and the role of wintering roost of the Corvids in Poznań. The recognition of the above required determination of:

- time of wintering
- size of wintering assemblage of the Corvids and its species composition
- location and durability of roosts
- characterization of morning and evening flights, in particular the routes of flights and sites of temporary concentrations
- the spatial organization of the wintering assemblage of Rooks in Poznań with main emphasis on the estimation of the daily dispersal zone and food habitat preferences
- assessment of the significance of urban habitats as feeding grounds for wintering Rooks.

II. STUDY AREA

Poznań is the largest city of the Wielkopolska region (Fig. 1, Fig. 8). In the years of the study about 570 thousand citizens inhabited the city area of about 230 km². The city administrative limits cover a few zones with habitats differing in character. The oldest central part (city) is located on the River Warta. It is surrounded by districts with detached and semi-detached houses and new housing estates with blocks of flats of different heights. The city has 45 parks with a total area of 1097 ha and is surrounded by forests, tree stands, and a mosaic of agrocenoses. The landscape of the region is predominantly agricultural in character; land in agricultural use occupies about 66% of the area (of which 87% are arable fields and 12% are meadows and pastures), forests occupy about 21% of the area, urban area is 3.2%, and water reservoirs 2.3%. Within 50 km from Poznań there are a few smaller towns of which in this paper are discussed Września pop. 25.000, Środa Wlkp. pop. 24.000 and Szamotuły pop. 17.000 (Fig. 1).

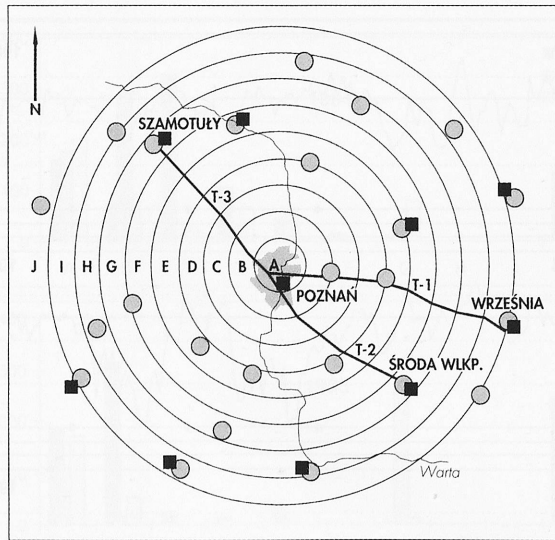


Fig. 1. The area of study; division in sections (A-J), localization of train transects (T-1, T-2, T-3), localization of cities (circles) and recognized wintering roosts of the Corvids (squares).

III. DAILY DISPERSAL ZONE OF ROOKS WINTERING IN POZNAN

A. Methods

The study was conducted in the winter of the years 1983/84 and 1984/85. These winters were average in the aspect of atmospheric conditions, but the winter 1984/85 was more severe – with lower temperatures and more snow (Fig. 2).

The so-called railway transect method was used which will be described below.

- The map of Poznań and its vicinity was supplemented by a system of concentric circles of radii increasing by 5 km (Fig. 1), obtaining a system of rings called sections A-J, with a common centre in the middle Poznań (A). This central sector included the basic roost.

- In both seasons the data were collected in the same way. The Rooks were counted from the window of a train separately on three routes (transects): Poznań-Września (T-1), Poznań-Środa Wlkp. (T-2), and Poznań-Szamotuły (T-3). The average speed of the trains was 50-60 km/h, stopping for short times at intermediate stations. In the cities of destination there were analogous assemblages of Rooks and Jackdaws of a few thousand individuals.

- Each of the three transects was checked once a month from November to March, in the middle decade of the month.

- The checks were made between 10 a.m. and 1 p.m., at the time when the Rooks did not move between the roost and the feeding grounds.

- On the way from Poznań to a given city, the Rooks seen in the area up to 150 m on one side of the railway track were counted, while on the return, after a break of 10 to 60 minutes – those on the other side. It was assumed that the possible movements of Rooks from one side of the track to another were compensated.

- No field glasses were used – identification of morphologically close species (Rook, Carrion Crow, Jackdaw, Raven) was not difficult over a distance of 150 metres.

- Results for each sector (5 km length, 300 m width, and 1.5 km² area) were sums of the counts on both sides of the track. The terminal sections of the transects were shorter than 5 km, Fig. 1, so

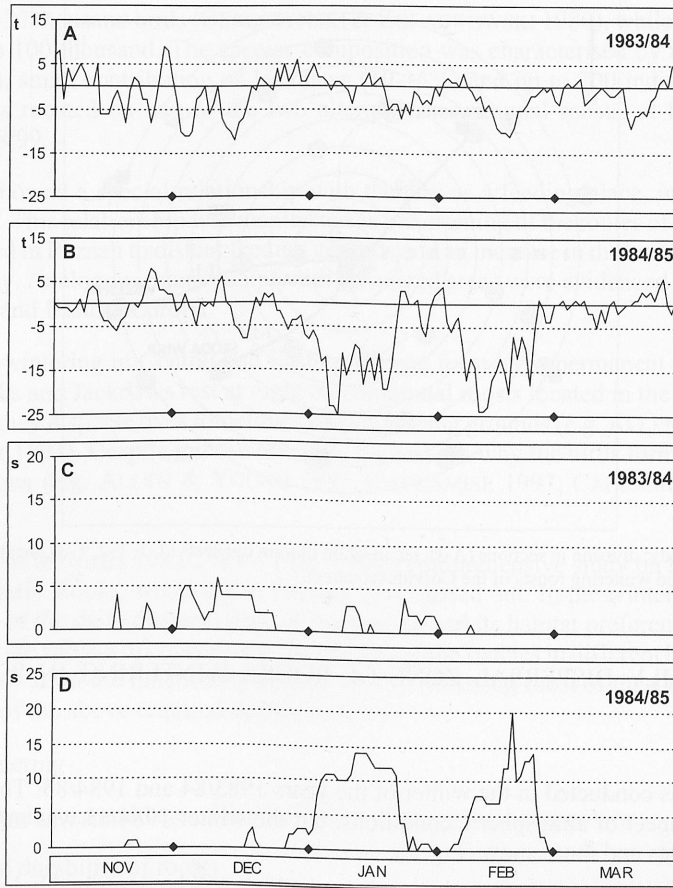


Fig. 2. Meteorological conditions in Poznań: A, B – minimum day temperature (t – $^{\circ}\text{C}$); C, D – day time snow precipitation (s – cm).

the absolute number of birds in all sectors was presented as density (number of individuals per square kilometre).

– In the urbanized area, especially in Poznań, the number of birds was underestimated by 10-20%, whereas in the open space it was close to the actual number.

– The parameters noted were: the size and species composition of the Corvid flocks, distance of the birds from the houses, habitats of occurrence according to the preliminarily assumed categories and type of behaviour, see the section Results.

– In this work only the information concerning the Rooks is provided. In the case of mixed-species flocks, the size of the flock was the absolute number of Rooks observed.

B. Results

The density of Rooks observed along different transects in the same month and at the same distance from Poznań differed, see for instance Fig. 3, but, nevertheless certain regularities in the Rooks' distribution were noted. With increasing distance from the roost in Poznań the density of Rooks decreased, practically to zero in section F, thus over a distance of 25 km from the roost. An increase in Rook density was again observed from section G (transects T-2 and T-3), in section I

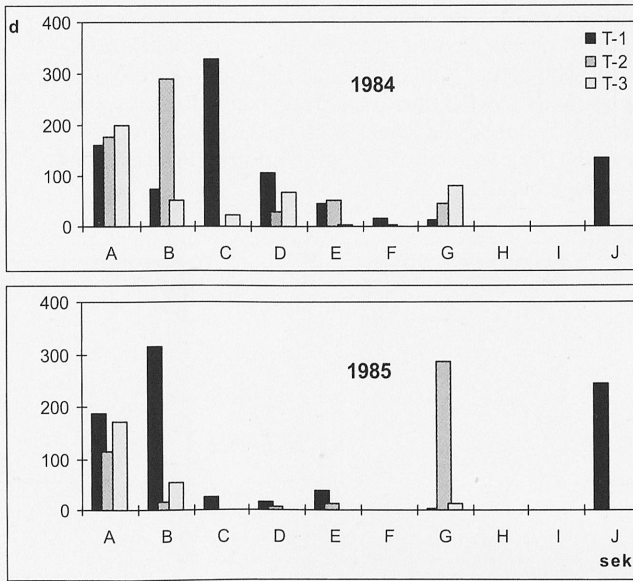


Fig. 3. The density of Rooks (d = individuals per km^2) in subsequent sectors (A-J), along the transects (T-1, T-2 and T-3) in February 1984 and February 1985.

(T-1), or near other roosts smaller than that in Poznań in Września, Środa Wlkp., Szamotuły (see Fig. 1).

The results for the main zone of dispersion – sections A-F, indicate non-uniform distribution of birds in time and space (Fig. 4). At the beginning and end of wintering (November and March) the

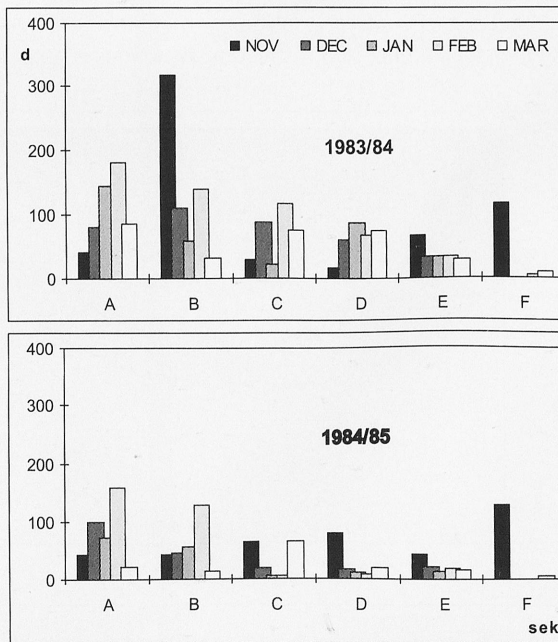


Fig. 4. Changes in the density of Rooks (d = indiv. per km^2) in the winters 1983/84 and 1984/85 (November – March) in the main daily dispersion zone (A-F sections). The density is a mean for the three transects (T-1, T-2, T-3).

Rooks were equally dispersed over the whole area of feeding grounds. From December to February an increasing tendency to prefer feeding grounds nearer the main roost was observed. This was more pronounced during the harder winter of 1984/85. The shortening of the distance between the roost and the feeding grounds was accompanied by a change in the type of feeding grounds. It was found that starting from November, the Rooks preferred feeding grounds nearer houses (Fig. 5). In February practically all the birds were already within the urbanized areas or, outside the city, no further than 50 m from village buildings.

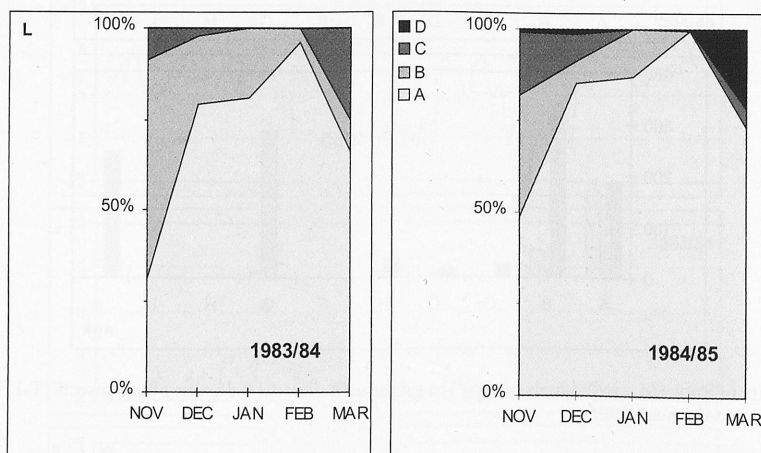


Fig. 5. Changes in the distance from buildings of rook groups present in the main day dispersion zone (A-F sections) in the winter 1983/84 and 1984/85. Distance classes: A: 0-50 m, B: 50-100 m, C: 100-200 m, D: > 200 m.

As follows from Fig. 6, the open agroecosystems – fields and meadows – are the main feeding grounds at the beginning and end of wintering. During particularly cold periods some of the Rooks withdrew from them and then the number of birds feeding near houses, in gardens and orchards, sig-

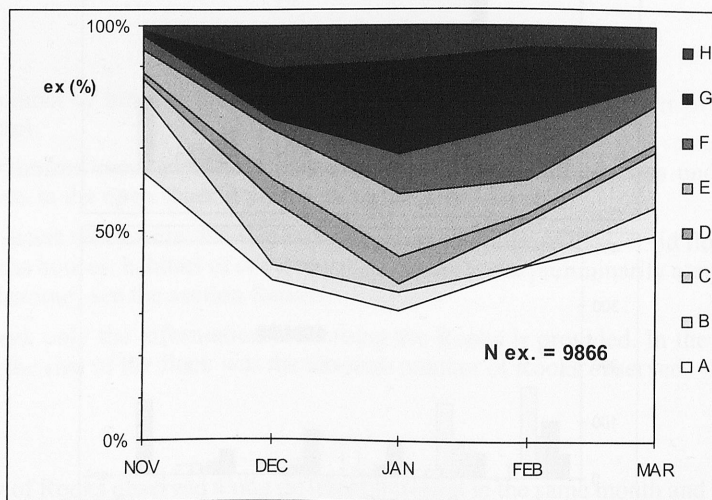


Fig. 6. Changes in the contribution of Rooks (%) observed in different habitats; data combined for the two seasons 1983/84 and 1984/85 collected along the three transects (T-1, T-2, T-3) in the main day dispersion zone (A-F sections). The types of habitats: A – fields, B – meadows, C – idle land, D – orchards, E – vicinity of buildings, F – other, G – inactive birds sitting on trees, H – birds flying at the time of observation.

nificantly increased. Particularly interesting is the large number of birds which did not feed during these periods but sat motionless on trees and roof tops (Fig. 6, category G). This was accompanied by changes in the size of the observed flocks (Fig. 7). It was established that, from the beginning of winter, the size of the flocks in the fields successively decreased, while that of those in idle land and near human dwellings increased. The birds feeding among buildings, those motorically inactive or observed while flying occurred in small groups throughout the winter.

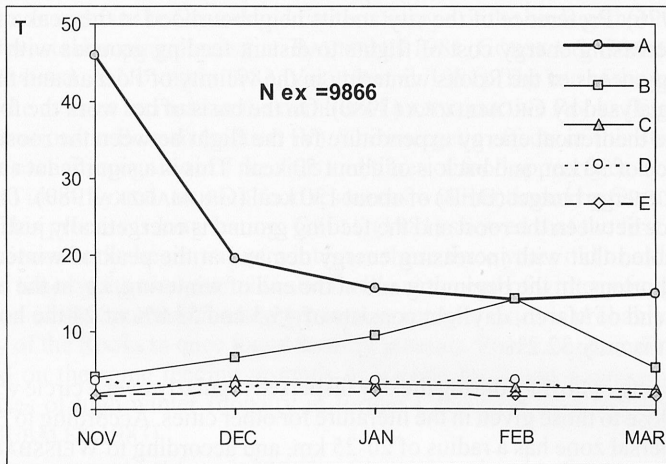


Fig. 7. Changes in the mean size of flocks (T – number of individuals) in selected types of habitat; data from the two winters 1983/84 and 1984/85 collected along the three transects (T-1, T-2, T-3) in the main day dispersion zone (A-F). Types of habitat: A – fields, B – idle land, C – vicinity of buildings, D – inactive birds sitting on trees, E – birds flying at the time of observation.

To sum up, the collected results indicate that the feeding grounds of the Rooks belonging to the wintering assemblage roosting in Poznań, are within the circle of a radius of 25 km. In winter the Rooks successively shorten the flying routes to the feeding grounds and prefer the habitats of the city and its vicinity, or in the direct neighbourhood of village buildings. They partly withdraw from agrocenoses, which are the main feeding grounds at the beginning and the end of winter. In the coldest periods the birds tend to feed closer to human dwellings. At these times the contribution of motorically inactive birds is the greatest.

C. Discussion

The existence of wintering roosts of the Rooks in cities is a common phenomenon in Central and Eastern Europe (e.g. BAUMANIS 1981, GLUTZ & BAUER 1993, GREVE 1983, GRODZIŃSKI 1976, GRÜLL 1981, HUBALEK 1979, 1983, JADCZYK 1994, JADCZYK & JAKUBIEC 1995, SCHRAMM 1974, STORK & JÄNICKE 1977, TIKHANSKIY & NOVIKOV 1982, TWELKMEYER 1983). Some authors claim that large urban agglomerations are the centres of the greatest wintering assemblages of the Corvids. Only in Western Europe, e.g. in the British Isles, Switzerland and Spain, are the Rooks wintering places near their rookeries (e.g. BUSSE 1969, COOMBS 1978, ENA 1984, FOODWIN 1994, GLUTZ & BAUER 1993, GOODWIN 1976).

The results of the study prove that during the winter Rooks change their food habitats. At the beginning and the end of winter the preferred feeding grounds were agrocenoses. At the peak of winter an increase in the number of Rooks was observed in Poznań and, outside Poznań, in the immediate neighbourhood of village buildings. This was more pronounced during the harder winter of 1984/85 and was accompanied by a decrease in the number of Rooks observed in the fields. In Western Europe Rooks feed in agrocenoses all year round (COOMBS 1978, GOODWIN 1976), while in the

Central and Eastern part of the continent mainly not in winter, therefore in the breeding period and during migrations (e.g. GLUTZ & BAUER 1993, JABŁOŃSKI 1979). It has been proved that the Rooks wintering in the cities of Central Europe temporarily move to areas outside the city in the milder periods (GÓRSKI 1976, GRODZIŃSKI 1971, GRÜLL 1981). This evidence means that fields and meadows are the preferred food habitats (primary feeding grounds) and the penetration of the Rooks into the cities is forced by external factors. These factors are a decreased availability of food on fields and meadows covered with snow and the irreproducibility of food resources in these habitats in winter (GÓRSKI 1976). Preference of the city and its neighbourhood at the peak of winter is also a consequence of increasing energy cost of flights to distant feeding grounds with decreasing temperature. The energy needs of the Rooks wintering in the vicinity of Poznań and the energy cost of their flights were analysed by GROMADZKA (1980). On the basis of her work the following calculation was made. The theoretical energy expenditure for the flight between the roost and the feeding ground, at a distance of 30 km, and back is of about 50 kcal. This is a significant amount in relation to an average daily energy budget (DEB) of about 130 kcal (GROMADZKA 1980). Therefore, a shortening of the distance between the roost and the feeding ground is energetically justified. In this context it should be noted that with increasing energy demand at the peak of winter the time of the effective feeding shortens. In the beginning and at the end of wintering, i.e. at the beginning of November and at the end of March, daylight consists of 45.3 and 53.8% of 24 the hours, while at the end of December it is only 32.2%.

The Rooks roosting in Poznań during the day dispersed regularly over a circle with a radius of 25 km. This value is close to those given in the literature for other cities. According to HUBALEK (1980) the main daily dispersal zone has a radius of 20-25 km, and according to WEISSBACH (1978) 20-30 km. The maximum distance covered every day by wintering Rooks, reported by different authors, range from 18 to 47 km (HUBALEK 1980, 1983, GRÜLL 1981, MCKILLIGAN 1980, SCHRAMM 1974, 1985, STORK & JÄNICKE 1974, STORK et al. 1976, WATSON 1967). In this context it is interesting that the Rooks belonging to small assemblages (a few thousand individuals) wintering in Września, Środa Wlkp., or Szamotuły (Fig. 1) feed only within a small zone around these cities (Fig. 3). Unfortunately, there are no corresponding data from other cities in Central Europe. It may be supposed that the size of the daily dispersal zone is related to the size of the assemblage and is determined by the tendency to avoid competition on feeding grounds. It has been shown that about 100 000 birds roosting in Poznań disperse during the day over an area up to 25 km from the roost, which gives an average density of about 50 individuals per km². The same value was reported by HUBALEK (1980) as the average for the former Czechoslovakia.

The above evidence contradicts the thesis that the food resources at the out of city feeding grounds are the factor limiting the size of the winter assemblages of the Corvids. There are sufficient premises to claim that such a factor is the area of the urbanised habitats. It has been shown that at the peak of winter the Rooks gather in the immediate neighbourhood of human dwellings, this being manifested by penetration of the Rooks into the city of Poznań. A similar was earlier noted in Poznań by GÓRSKI (1976) and GÓRSKA & GÓRSKI (1980) and in other European cities by GÓRSKI (1981), GRODZIŃSKI (1976), GRÜLL (1981), LUNIAK (1972), and SCHRAMM (1985).

It is commonly assumed that the optimization of animal foraging occurs by specialisation in one of the two strategies: that of searching for food and that of feeding by expectation. The main difference between them is the energy expenditure required to obtain food. Natural selection prefers the strategy which increases the difference between cost and the profit – the optimum foraging strategy (PIANKA 1981). In the field and meadows Rooks follow the strategy of active search for food. This involves the penetration (in groups) of the area over which the irreproducible food is relatively uniformly distributed. This is the way of feeding of Rooks in the Central and Eastern Europe in seasons other than winter. It has been shown that the success of such feeding increases in larger flocks (HÖGLUND 1985) where a certain cooperation has developed (CHANTREY 1982, PINOWSKI 1959). The Rooks belonging to the assemblage studied use this strategy at the beginning and at the end of winter, when they form larger flocks and search for food in fields and meadows. Their stay in urban-

ized areas requires a change in feeding behaviour. In the city and in the close neighbourhood of human dwellings in villages, the potential food is distributed discretely (at certain points) and is reproducible (waste-dumping grounds, waste bins, places where people throw food, feeding by people). The use of such food requires the breaking of the barrier of anthropophobia. This phenomenon has been widely reported in the literature. The distribution and kind of food forces a change in the strategy of feeding. This change is evidenced by observations of birds passively waiting for people feeding them made in Poznań and in other cities (GRODZIŃSKI 1971, GRÜLL 1981, JADCZYK 1994) and a common sight in the Central and Eastern Europe of the birds gathering at waste grounds and especially at waste dumping places (i.a. BAUMANIS 1981, GÓRSKA & GÓRSKI 1980, SCHRAMM 1974, 1985, TIKHANSKIJ & NOVIKOV 1982, VALJUS et al. 1981). The use of the expectation strategy is confirmed by the evident increase in the number of motor-inactive Rooks (Fig. 6) and the results of detailed observations in Poznań (section IV). The energetic effects of this strategy undoubtedly increase after the earlier recognition of the sites and times of food appearance by the birds. The process of learning to identify and use such food resources was mentioned by GRODZIŃSKI (1971) and GRÜLL (1981). This process is long lasting. GRÜLL (1981) showed that the first Rooks penetrating into the city of Vienna at the beginning of winter are those three years old or older, these being followed after some time by the two-year olds and finally at the end of winter young birds appear. The earlier recognition of the optimum feeding grounds in specific cities is probably the reason of considerable fidelity of the Rooks to once found feeding grounds. For example individually recognized birds were noted on the same feeding grounds in Vienna for 3 and 4 subsequent winters while among many cases of high winter filopatry in former Czechoslovakia the record was 7 seasons (GRÜLL 1981, HUBALEK 1983).

The size of the winter assemblages of the Corvids can be related to the size of the cities which in winter become the main feeding grounds for Rooks and Jackdaws. Since the size of the assemblage is established even before the peak of winter, it should be assumed that a significant number of birds have recognized the local feeding conditions in previous seasons.

IV. FEEDING STRATEGIES OF ROOKS DURING WINTERING IN URBANIZED HABITATS OF POZNAŃ

A. Methods

The study was conducted from November 1983 to March 1984. In the aspect of atmospheric conditions (temperature and snow cover) the winter of 1983/84 was average (Fig. 2). On the basis of experience from the trial season of 1982/83 the following methods of field observations were assumed.

- Regular visits were paid to 12 areas (Fig. 8) which represented the main types of habitat in the city. Besides the areas of different degree of urbanization, the non-urbanized habitats and municipal waste-dumping ground were checked (Table I). All these areas, except waste dumping grounds – WS, and arable fields – P1 and P2 (7–10 km from the roost), were not farther than 5 km from the roost.

- Each area was checked once in ten days during wintering thus during the time of function of the wintering roost (November – March) (see Fig. 9). No check was made in the second ten days of December, one check of allotment gardens – OD area in the third ten days of November also being missing.

- The parameters noted during the controls were: the number of Rooks in the area (birds in transit flight were neglected), the number of young (one year old; see GRÜLL 1981) individuals, the type of behaviour of each bird at the moment it was first spotted.

- The number of Rooks in the areas checked was expressed as density (Number of individuals per 10 ha).

- The working area of the waste dumping ground (WS) changed. The large number of Rooks and their great activity in this area prevented the calculation of density and statistical description of

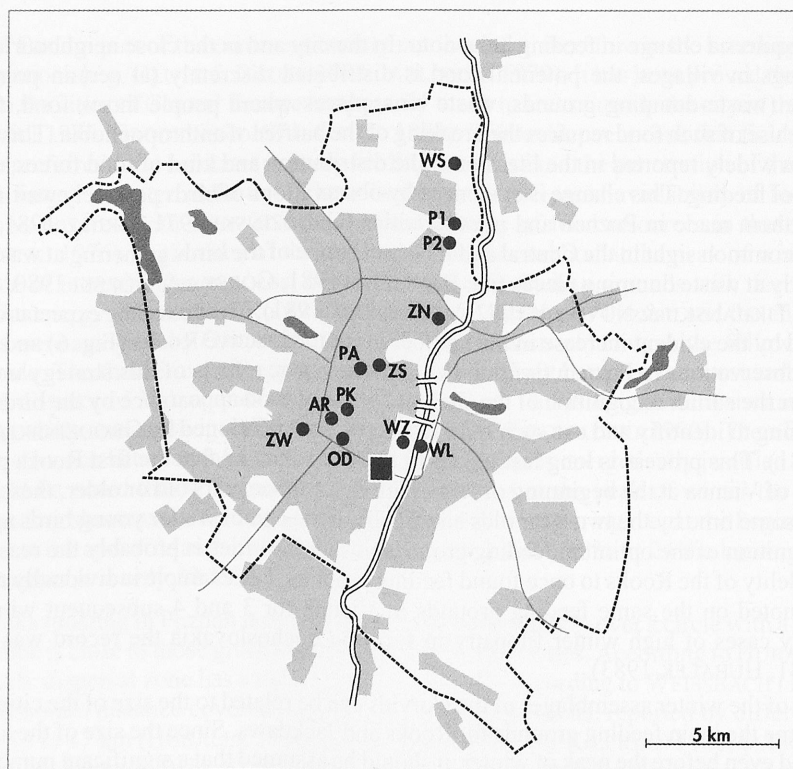


Fig. 8. Localization of the check areas in Poznań and the basic wintering roost „Warta”. The abbreviations are explained and characterization of the areas is given in Table I.

behaviour. Thus, the only result from this area is the absolute number of birds, data from this area having been excluded from detailed analyses.

– Two indices were used to characterize the behaviour of Rooks and their energy expenditure. The activity index (A) defined as:

$$A = N_a \times 100\% / N$$

where N is the number of Rooks in the area and N_a the number of motor-active Rooks in the area, e.g. feeding, showing comfort or mating behaviour, flying within the area.

The index of mean energy expenditure (M). The value of the index was calculated on the basis of the data reported by DOLNIK (1982) on energy expenditure on different forms of behaviour of birds whose size corresponded to that of the Rook. Assuming the energy expenditure during sleep as 1, the values assigned to other forms of activity were:

- day rest 1.12
- pedal activity 1.60
- flight 12.00

According to these assignments, the mean level of energy expenditure M for the Rooks in a given area was calculated from the formula:

$$M = 1.12 N_1 + 1.6 N_2 + 12 N_3 / N$$

Where: N_1 is the number of motor-inactive individuals, N_2 – the number of individuals showing all kinds of pedal activity, N_3 – the number of flying individuals and N – the total number of individuals in a given area, $N = N_1 + N_2 + N_3$. During daylight the values of M index must fall in the range 1.12 to 12.0.

Table I

Characterisation of the study plots

	Name	Size (ha)	
[1]	ZS	25.6	City. Old densely arranged many-storey buildings from the 19 th and the beginning of the 20 th century. high traffic
	ZW	17.2	A settlement of detached and semi-detached houses surrounded by gardens and orchards ("Ostroróg").
	ZN	18.4	A new housing estate on the border of compact city structure, a large number of high blocks of flats, surrounded by some green areas. Squares, not much traffic ("Osiedle Kosmonautów").
	PA	15.3	A series of old inner-city parks in the neighbourhood of busy streets (parks: "Moniuszki", "Wieniawskiego", "Mickiewicza", "Słowackiego", and "Marcinkowskiego").
	PK	5.6	An old, well taken care of, park in the neighbourhood of houses built in the mid – 20 th century ("Park Wilsona").
	OD	7.9	A complex of allotment gardens, orchards, and vegetable gardens (near "Osiedle Hetmańskie").
	AR	23.4	A complex of open sports grounds: sports stadium, swimming pool, green squares, sparse trees ("Park Kasprowicza").
	WL	21.3	Semi-natural old bog-alder forest, converted into a park, near a housing estate (between the River Warta and "Osiedle Piastowskie").
[2]	WZ	38.6	Periodically flooded mown grasslands along the River Warta (between the "Przemysł Bridge" and „Królowej Jadwigi Bridge").
	P1	20.6	A large complex of arable fields near sparsely distributed buildings ("Naramowice").
	P2	36.8	A large complex of arable fields near the urbanized area ("Osiedle Władysława Łokietka").
	WS	0.5-2.0	Communal waste-dumping grounds in the vicinity of fields and groups of trees of varied area. At present does not exist ("Umultowo").

[1] – urbanized habitats. [2] – non urbanized habitats.

B. Results

The dynamics of the Rook numbers in the areas observed is expressed in terms of density changes, and only for WS area in the absolute number of individuals (Fig. 9). As follows from the data collected, the areas were not used to the same degree. Differences were noted in the regularity of visits, mean density, maximum density and trends in the changes of the number of birds (Table II). A particularly great number of Rooks were observed in the city parks (PK, PA, AR), in garden allotments (OD), and in the urbanized areas outside the city (ZW, ZN). In these areas the number of the birds was observed to increase successfully, reaching a maximum at the peak of winter, and then decrease. The number of Rooks in park riparian tree stands (WL) and in periodically flooded grassland (WZ) was smaller. The fields surrounding the city (P1, P2) were irregularly visited by a small number of Rooks. The city (ZS) was visited by a small number of Rooks but regularly. The waste-dumping grounds (WS) were visited regularly by a large but varied number of Rooks. The significance of this area is indicated by the fact that the total number of Rooks noted there at all checks was almost 21 thousand individuals, while in all the other 11 areas the total number of Rooks was 13.5 thousands.

An independent set of data collected concerned the number and contribution of young (one year old) birds, Table III. The presence of young Rooks was noted only in seven study areas. They were

Table II

Characteristics of the Rooks' occurrence in the selected study plots.

	Study plots										
	P1	P2	ZS	WL	WZ	ZN	ZW	OD	AR	PA	PK
Total number of individuals	368	219	494	1053	2120	1293	1335	698	2649	1993	1290
Mean density	7.2	7.6	14.1	35.3	39.2	50.2	55.4	68.0	80.9	93.0	164.5
Maximum density	49.7	30.6	20.3	74.2	65	127.7	111.6	155.7	169.7	156.9	330.4
Mean activity (A)	96.7	95.4	36.9	67.0	90.8	71.1	25.4	51.4	51.5	63.2	30.3
Mean energy expenditure (M)	1.58	1.60	3.39	3.06	1.71	2.44	2.42	2.13	1.65	1.84	1.64

Table III

The contribution (%) of young Rooks in the groups occurring in particular study plots

10-day periods	study plots							
	WS	ZN	WL	WZ	OD	ZW	P2	P1, ZS, AR, PA, PK
XI-1	+	—	—	—	—	—	—	—
XI-2	1.0-2.0	1.5	1.0	—	—	—	—	—
XI-3	1.0-2.0	—	1.1	1.1	—	—	—	—
XII-1	2.0-2.5	—	—	—	—	—	—	—
XII-3	2.0	8.3	—	1.1	—	—	—	—
I-1	+	0.9	—	—	—	—	—	—
I-2	—	—	—	0.4	—	—	—	—
I-3	1.0-2.0	—	—	—	—	—	—	—
II-1	+	—	—	—	—	—	—	—
II-2	1.0	—	1.9	—	—	—	—	—
II-3	1.0	1.7	—	—	—	—	—	—
III-1	1.0-2.0	1.3	—	—	1.8	—	—	—
III-2	1.0-2.0	1.4	—	—	—	1.6	—	—
III-3	83.3	80.0	4.0	—	—	—	100.0	—

+ no quantitative data, — no young birds.

regularly spotted on the waste-dumping grounds (WS) where their contribution ranged from 1.0 to 2.5%, and the irregularly appeared at a new housing estate in the peripheries of the city (ZN). In the other 5 areas in the least urbanized habitats, they were sporadically observed, most often at the end of winter. The high contribution of young birds in the third decade of March was above all the result of a significant decrease in the number of adult individuals which were leaving the wintering roost (Fig. 9). Particularly interesting was the noted absence of young birds in the city, both in the old city urbanized area (ZS) and in the city parks (AR, PA, PK). The contribution of young birds in the assemblage studied was 5-7% (4.5 – 6 thousand individuals; section V), hence the results indicate that in winter young Rooks use the feeding grounds outside the city.

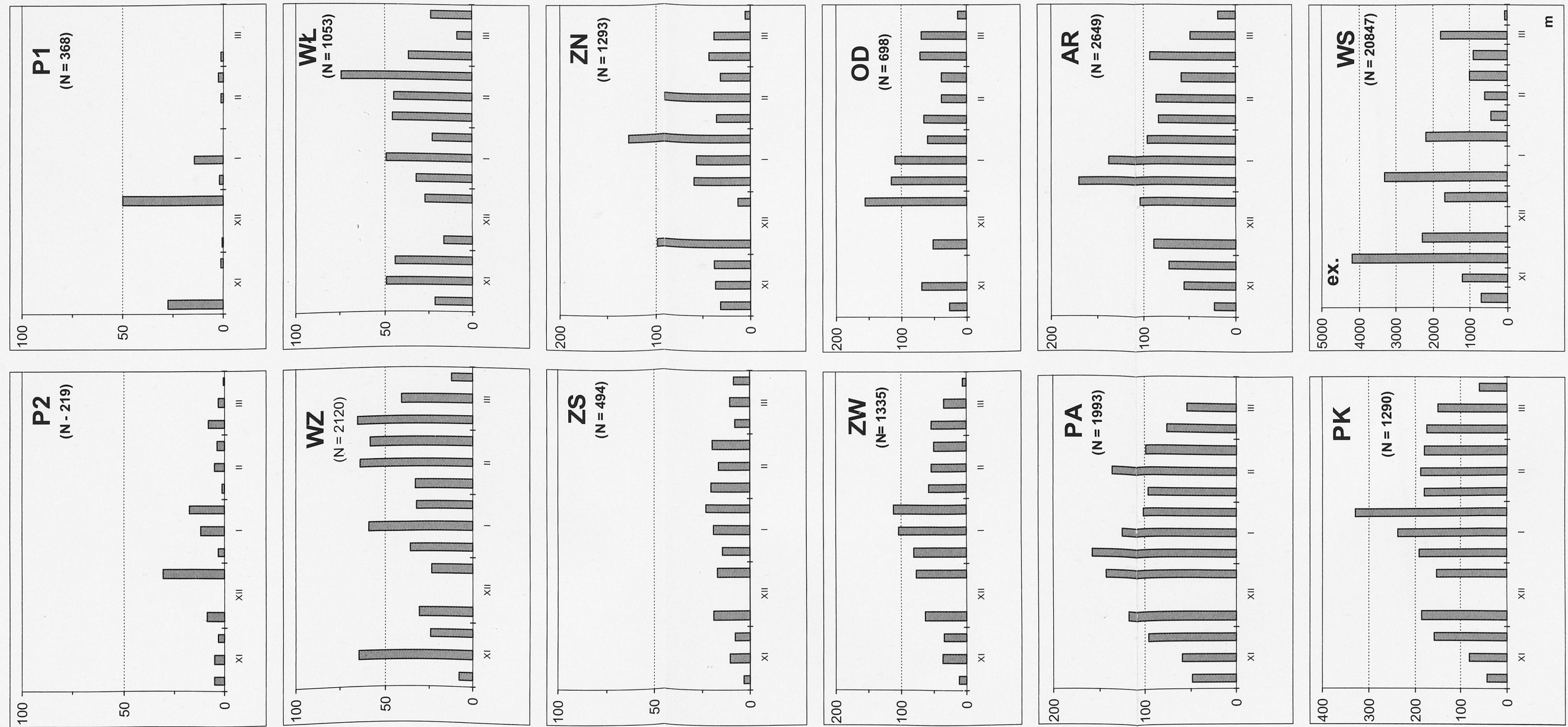


Fig. 9. Changes in the density of Rooks (indiv. per 10 ha) in the areas studied; for the area WS changes in the absolute number are given (ex.). The abbreviations are explained in Table I.

The behaviour of the Rooks in the areas studied and within one area was diverse. Besides the motor-active birds there were inactive ones sitting motionless on the ground, on trees, or on roofs. During each check the level of activity was described by the index A, see "Methods". Analysis of the mean values of the index (Table II) shows that the birds in the non-urbanized areas (fields and meadows P1, P2, and WZ) were highly active (A90%). The lowest values of bird activity (A(%)) were noted in the city (ZS, ZW, and PK).

No relationship between the activity of Rooks in the feeding grounds in the city and the atmospheric conditions was found (Fig. 10). The independent variable was either the minimum mean day temperature in the 10 days or the total for a period of 10 days snow precipitation. The dependent variable was the activity of Rooks on the 11 areas studied (without WS), obtained as the average for a 10 day period. In both cases the relationships are statistically non-significant, ($p > 0.05$). This is one more premise to relate the Rooks' activity with the structure of habitats and the biology of the species.

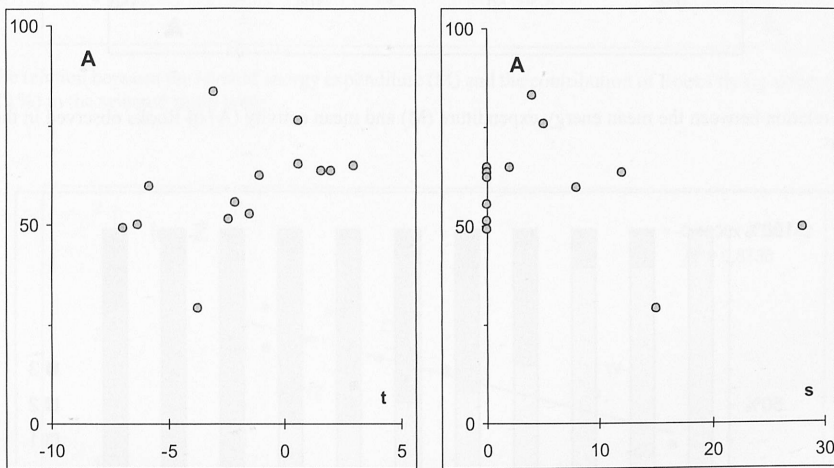


Fig. 10. The relationship between the Rooks' activity (A,%), the minimum day temperature ($t^{\circ}\text{C}$), and thickness of snow cover (S, cm).

Different forms of bird activity require different energy expenditure. This aspect is particularly important in low temperatures or in the case of scarcity or inaccessibility of food. For each visit to a study area, except WS, the energy expenditure of the Rooks observed was estimated using the index M, see „Methods". The mean values of M for the areas studied differed greatly, (Table II). Relatively low values of M were obtained for open agrocenoses (P1, P2, WZ) and in parks (PK, PA, AR). The highest values were those for urbanized areas, in particular ZS, and in a riverside park WL. The coordination between the mean M and A values was found to be statistically non-significant, $p > 0.05$ (Fig. 11). Hence, the energy budget of the Rooks is not a simple derivative of the contribution of motor-active and inactive birds. By definition the values of M are highly dependent on the contribution of flying birds since this activity demands the greatest energy. This is confirmed by the data on the forms of Rook activity in the areas studied (Fig. 12). The decisive affect of flying on the energy balance of Rooks is best illustrated in Fig. 13. The relationship between the mean M values and the contribution of flying birds is exact and statistically significant ($p < 0.001$).

In the context of the above results it may be assumed that an increase in energy expenditure (M) may reduce the attractiveness of potential feeding grounds. Consequently, a decrease in the number of Rooks with increasing M would be expected. However, the correlation of these two parameters for the 11 study areas analysed was statistically non-significant ($p > 0.05$, Fig. 14). This can be ex-

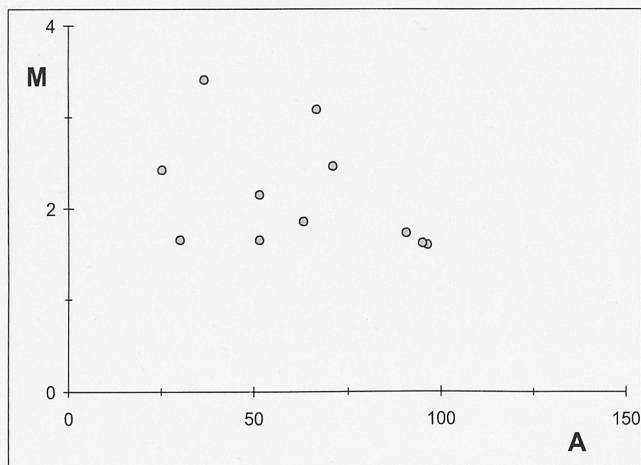


Fig. 11. The relation between the mean energy expenditure (M) and mean activity (A) of Rooks observed in the selected study areas.

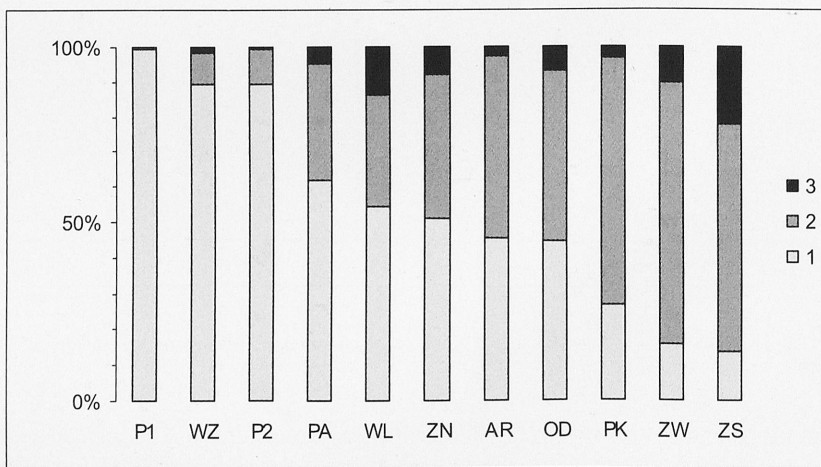


Fig. 12. The contribution of birds showing particular forms of behaviour in the study areas; 1 – actively foraging birds, 2 – motor-inactive birds, 3 – birds flying at the time of observation; area abbreviations are explained in Table I.

plained when taking into regard a variety of density values (the minimum in P1 and the maximum in PK) obtained for the areas of the lowest M index.

In order to analyse the results, each of the study areas was characterized by three parameters (Fig. 15). Besides the energy expenditure (M) and mean density of birds (Z), a third parameter was introduced – the mean for the area percentage contribution of feeding Rooks (F). There are two reasons for introducing this parameter. The first is the significant differentiation of the contribution of this category of birds in the areas studied (Fig. 12), and the second is the fact that the Rooks belonging to the assemblage studied assume two feeding strategies – an active search for food and passive expectation of food. In the three areas representing agrocenoses (P1, P2, WZ) the Rooks assume the strategy of active search for food which requires low energy expenditure, Fig. 12. In the fields the lowest density of birds was noted, which may be a result of decreasing density of the population and

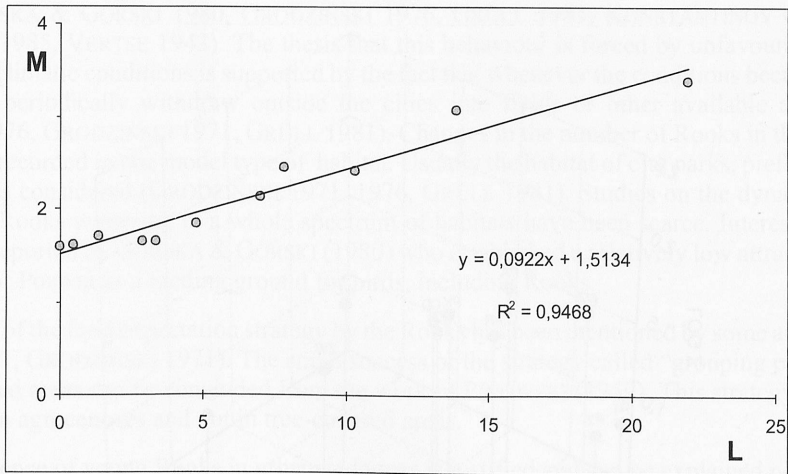


Fig. 13. The relation between the level of energy expenditure (M) and the contribution of Rooks flying at the time of observation (L%) in the selected study areas.

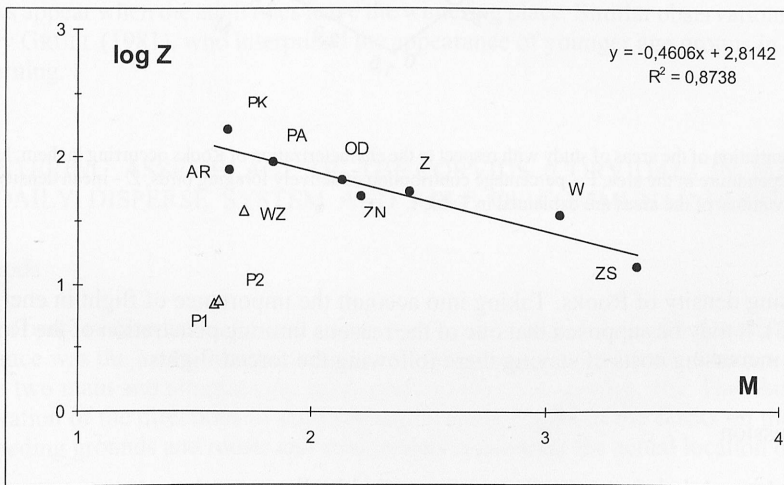


Fig. 14. The relation between the mean energy expenditure for given areas (M) and mean densities of Rooks in them (Z). Points – areas representing urbanized habitats, triangles – areas representing agrocosenes. The value of the determination coefficient and the regression equation refer only to the 8 urbanised habitats studied.

irregularity of appearances in certain fragments of these habitats (Fig. 9). The other areas represent urbanized habitats with a different degree of urbanization in which the contribution of actively feeding birds was intermediate or low, indicating more frequent assumption of the food expectation strategy (Fig. 12). In these areas the contribution of the flying birds was considerable. When the three areas representing agrocosenes are excluded from the analysis, a new interpretation of Fig. 14 is possible. The correlation between the mean density of Rooks and the level of their energy expenditure in the 8 urbanized areas is exact ($r = -0.9348$) and statistically significant ($p < 0.001$). The highest density at the lowest energy expenditure is characteristic of parks (PK, AR, PA), and the increasing degree of urbanization (towards the city) is related to an increase in the energy expenditure

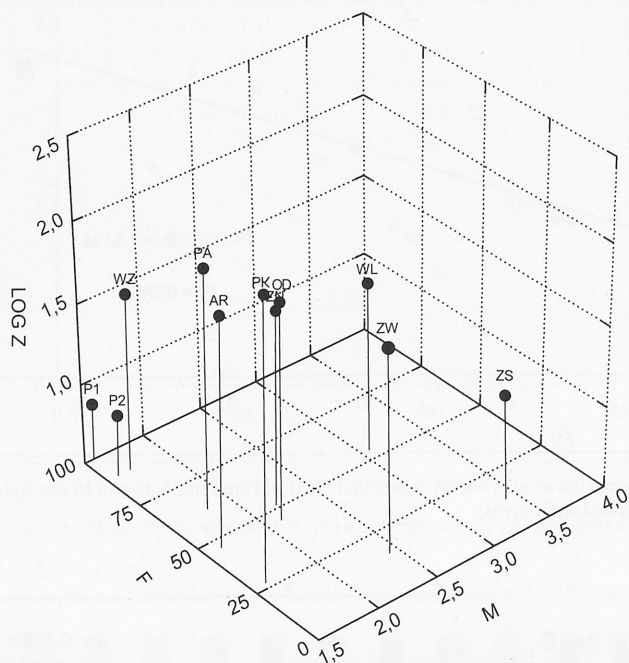


Fig. 15. Differentiation of the areas of study with respect to the characterization of Rooks occurring in them; M – mean level of energy expenditure in the area, F – percentage contribution of actively foraging birds, Z – mean density of Rooks per area. Abbreviations of the areas are explained in Table I.

and decreasing density of Rooks. Taking into account the importance of flight in energy expenditure (Fig. 13), it may be supposed that one of the reasons limiting penetration of the Rooks into the city are the increasing costs of staying there following the forced flights.

C. Discussion

The results and their interpretation are supported by literature data. Agrocenoses are the basic feeding habitats of Rooks not only in the breeding season and during migrations, but also in wintering places in Europe in the mild Atlantic climate (e.g. GLUTZ & BAUER 1993, JABŁOŃSKI 1979). In these habitats the strategy of active search for food or the optimum foraging strategy are used, the latter being particularly effective when feeding in flocks (CHANTREY 1982, HÖGLUND 1985, LOMAN 1980, PINOWSKI 1959). When analysing the role of the flock for the effectiveness of feeding, some authors have suggested its threshold maximum size. An increase in the size of a feeding flock may reduce the effectiveness of feeding because of increasing competition and level of aggression (ALRAMSON 1979, BALPH et al. 1979, CARACO 1979, FEARE 1978, INGLIS & LAZARUS 1981, LEJEUNE 1980). The observed strong variations in the number of Rooks at the waste-dumping grounds are most probably the result of the flock having reached over-threshold size. Similarly as in Poznań, waste-dumping grounds are a very attractive source of food for the Rooks in the whole of Central and Eastern Europe and are sites of the formation of the greatest feeding concentrations (BAUMANIS 1981, GÓRSKA & GÓRSKI 1980, GRÜLL 1981, SCHRAMM 1974, 1985, TIKHANSKIY & NOVIKOV 1982, VALJUS et al. 1981). The penetration of Rooks into cities has been described by many authors, who emphasize that this was particularly intense during the hardest winters (GÓRSKI

1976, GÓRSKA & GÓRSKI 1980, GRODZIŃSKI 1976, GRÜLL 1981, KONSTANTINOV et al. 1982, SCHRAMM 1985, VERTSE 1943). The thesis that this behaviour is forced by unfavourable atmospheric and climatic conditions is supported by the fact that whenever the conditions become milder, the Rooks periodically withdraw outside the cities into fields or other available agrocenoses (GÓRSKI 1976, GRODZIŃSKI 1971, GRÜLL 1981). Changes in the number of Rooks in the city were most often recorded in one model type of habitat. Usually the habitat of city parks, preferred by the species, was considered (GRODZIŃSKI 1971, 1976, GRÜLL 1981). Studies on the dynamics of the number of Rooks wintering in a whole spectrum of habitats have been scarce. Interesting results have been reported by GÓRSKA & GÓRSKI (1980) who established a relatively low attractiveness of the centre of Poznań as a feeding ground for birds, including Rooks.

The use of the food expectation strategy by the Rooks has been mentioned by some authors, (e.g. GRÜLL 1981, GRODZIŃSKI 1971). The small success of the strategy called "grouping pulsation" in the urbanized areas can be concluded from the work of PINOWSKI (1959). This strategy was noted only in open agrocenoses and not in tree-covered areas.

The absence of young Rooks in urbanized areas is justified and can be explained not only by a small contribution of this age group in the assemblage studied (5-7%). Another reason may be the inability of young individuals to obtain food by expectation strategy. Even in the preferred agrocenoses the feeding success of the young is poorer than that of the adults (HÖGLUND 1985). Moreover, the effect of food competition within age groups cannot be excluded. This may explain the fact that young Rooks appear when the adult ones leave the wintering place. Similar observations were made in Vienna by GRÜLL (1981), who interpreted the appearance of younger age groups in the city as a result of learning.

V. WINTERING ASSEMBLAGE OF THE CORVIDS (CORVIDAE) IN POZNAŃ, DAILY DISPERSE SYSTEM AND ROLE OF COMMUNAL ROOST

A. Methods

The main body of data was collected during the carefully planned checks described below. Of key importance was the location of the authors' dwelling and place of work, which were halfway between the two main and alternatively used roosts of the Corvids (Fig. 16). This fact facilitated daily observation of the directions of morning and evening flights of the flocks on the routes between the feeding grounds and roosts and conclusions concerning the actual location of the roost.

1) Evening checking of the roosts

The current roost was checked at least once in ten days during the winter of 1983/84, 1984/85, and 1985/86. Each check began about 30 minutes before the arrival of the birds and ended about 15 minutes after they had settled. The observer was at the observation point ensuring good visibility of the flocks arriving from the sites of pre-roosting concentration. During a check the observer estimated the size of the flocks, noted the directions from which they came, and in selected flocks estimated the contribution of Jackdaws and Carrion Crows. The first checks were made at the post-breeding roost localized in the centre of the city and began in August 1983, July 1984, and August 1985. After dissolution of this roost at the turn of October and November, the checks were made at the wintering roost until its dissolution in the first ten days of April. Whenever the roost location changed, the abandoned roost and the current roost were checked. The aim of the checks was to determine the location of the roost, estimate the number of roosting birds, and species composition of the assemblage, and identify the sites of pre-roosting concentration points. The estimations of the size of assemblages were continued in the seasons 1986/87, 1987/88, and 1988/89.

2) Morning checks of the roosts

In the winter of 1984/85 (December – February) 10 checking visits were paid to the roosts. Their aim was to establish the way in which the birds were left the roosts in the morning.

3) Checks of pre-roosting concentration points

Fifteen such checks were made in the winters of 1983/84 and 1984/85. The checks began with the arrival of the first birds and ended when the last birds left the point flying to the roost. The number of birds, the species composition of the assemblage and the contribution of young Rooks were estimated. The contribution of Jackdaws and young Rooks was assessed on the basis of calculation in 10 randomly selected groups of approximately 1000 birds. In view of the impossibility of determination of the species-composition structure and age structure of the Corvids assemblage at the roost and the non-representative character of data collected on the feeding grounds (MAZGAJSKI et al. 1997), this method was assumed as the optimum.

4) Checking of the evening and morning routes of flights between the roosts and feeding grounds

The routes were determined on the basis of planned observations from high points on the highest floors of the highest buildings at a few sites in the city. The checks were made in the winters of 1983/84 and 1984/85 at least once or twice a week. The observations were supplemented by the results of the evening and morning checks at the roosts and concentration points, as well as some incidentally collected information. During the evening flights in the winters of 1983/84 and 1984/85, the observer walked along a constant route of about 3 km (Fig. 17). The route crossed those of daily flights of Rook flocks to the roost called Warta, localized about 3 km to the east of the city. The checks were made 2-3 times a week.

5) Assessment of the daily changes in the number of Rooks on feeding grounds

In order to describe the time of stay, changes in number and flock size of Rooks on the feeding grounds, in 1984 a single check was made of 3 areas in Poznań. These were: the old city urban area of 25.6 ha denoted as ZS, meadows on the River Warta of 38.6 ha – WZ, and the bog alder forest on the River Warta converted into a park of 21.3 ha – WL (Fig. 8). Each area was checked every hour, the checking started before the arrival of the birds from the roosts and ending after the birds had left for the roosts. The counting on ZS area was performed on 7th December 1984 and on the adjacent areas WZ and WL on 22nd November 1984.

6) Assessment of the intensity of autumn and spring migration

At the turn of October and November 1983 and 1984 as well as at the turn of March and April 1984 and 1985, observations of bird flights were carried out at least 3-4 times every day in the noon hours. The frequency and size of migrating flocks of Rooks and Jackdaws were noted. A subjective classification into weak, intense, highly intense, and no migration was made. The information was fed into database, which also contained incidental reports of other people.

B. Results

After the breeding season, the Rooks nesting in the area of Poznań every year roosted in an inner-city park (Fig. 16). This post-breeding roost from July to the beginning of the winter hosted about 2-3 thousand Rooks and Jackdaws. The Rooks constituted about 80% of the assemblage. The appearance of the wintering roost was noted on Oct. 22nd, 1983, Oct. 24th, 1984 and Oct. 24th, 1985. On the same days the post-breeding roost was observed to dissolve. The final number of the Corvids (about 100 thousand birds) on the wintering roost was established within a few days. The appearance of the wintering assemblage coincided with the time of intense migration of mixed flocks of

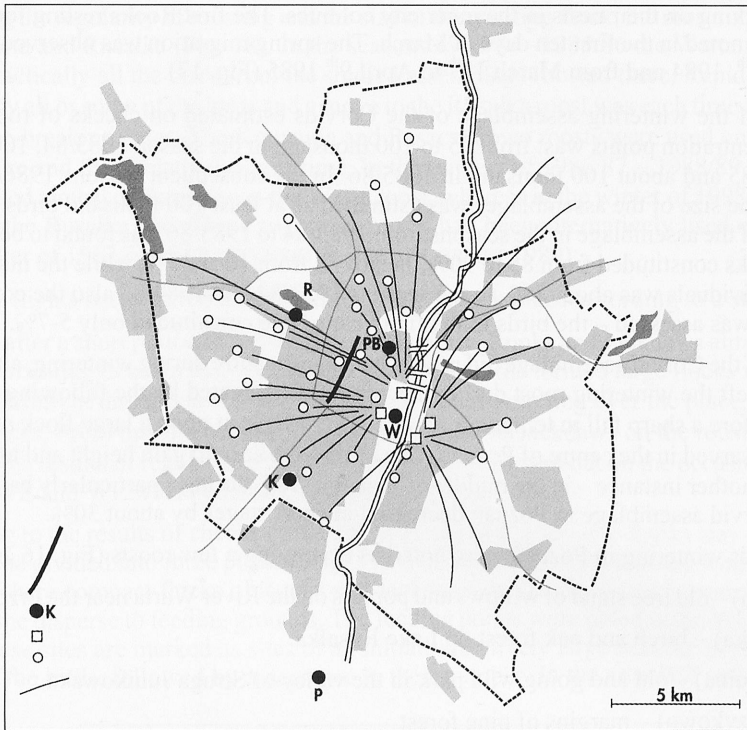


Fig. 16. Selected elements of the system of flights of the Corvids wintering in Poznań. PB – post-breeding roost, W and R – main wintering roosts „Warta” and „Rusalka”; K, P – wintering satellite roosts „Kopanina” and „Puszczykowo”; open dots recognized sites of post-feeding concentration, squares – pre-roosting sites at the „Warta” roost, lines – routes of the evening flights during the time of functioning of Warta roost. The bold line marked is the route of evening controls.

Rooks and Jackdaws in the W and SW directions. The autumn migration was observed from Oct. 21st to Nov. 3rd, 1983 and from Oct. 24th to Nov. 5th, 1984 (Fig. 17).

A notable decrease in the size of the wintering assemblage was noted in the middle of March in the years 1984-1986, and the last few Rooks were seen on the wintering roost on April 1st, 1984, April 9th, 1985, and April 9th, 1986. These observations coincided with the beginning of the spring migration and the breeding season. As soon as in the first ten days of February individual Rooks

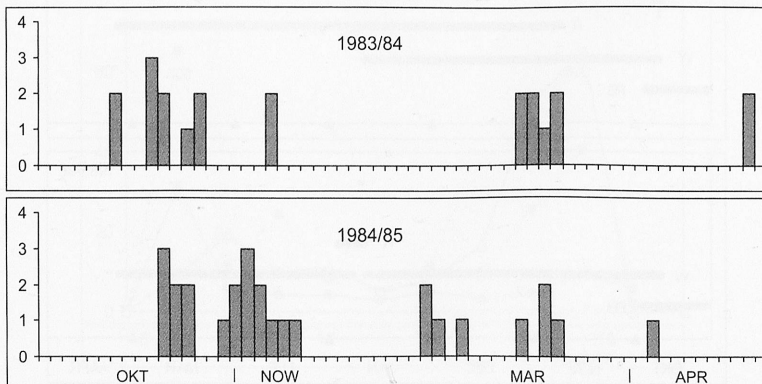


Fig. 17. Intensity of flights of the Corvids in autumn and in spring of 1983/84 and 1984/85 in the vicinity of Poznań; classes of intensity: 0 – no flights, 1 – sparsely observed, 2 – intense, 3 – very intense.

were seen working on their nests in the inner city colonies. The first Rooks resting for the night in the nests were noted in the first ten days of March. The spring migration was observed from March 21st to April 9th, 1984 and from March 13th to April 9th 1985 (Fig. 17).

The size of the wintering assemblage of the Corvids estimated on checks of roosts and pre-roosting concentration points was: from 95 to 100 thousand in the season 1983/84, 100–110 thousand in 1984/85 and about 100 thousand in 1985/86. In the subsequent seasons 1986/87, 1987/88 and 1988/89 the size of the assemblages was estimated as at least 100 thousand birds. The species composition of the assemblage in the seasons from 1983/84 to 1985/86 was found to be more or less the same: Rooks constituted from 85 to 90%, Jackdaws from 10 to 15%, while the number of Carrion Crow individuals was about 200. In the seasons 1983/84 and 1984/85 also the contribution of young Rooks was assessed – the birds in the first year of age constituted only 5–7%.

The size of the Corvid assemblage did not change significantly during wintering, although some of the Rooks left the wintering roost during the winter, as indicated by the following observation. On the day before a sharp fall in temperature (Feb. 18th, 1986), at noon a large flock of about 2500 Rooks was observed in the centre of Poznań. The birds were seen to gain height and turn decidedly to the west. Another instance – in the middle of January 1987, during a particularly hard winter, the size of the Corvid assemblage in Poznań decreased in short stages by about 30%.

The Corvids wintering in Poznań were noted as occupying a few roosts (Fig. 16 and Fig. 18):

- W (Warta) – old tree stand of willows and poplars on the River Warta near the Przemysł bridge
- R (Rusałka) – birch and oak forest on Lake Rusałka
- K (Kopanina) – old and going wild park in the valley of Struga Junikowska
- P (Puszczykowo) – margins of pine forest

Small groups of birds were sporadically observed to roost in other places, such as city parks.

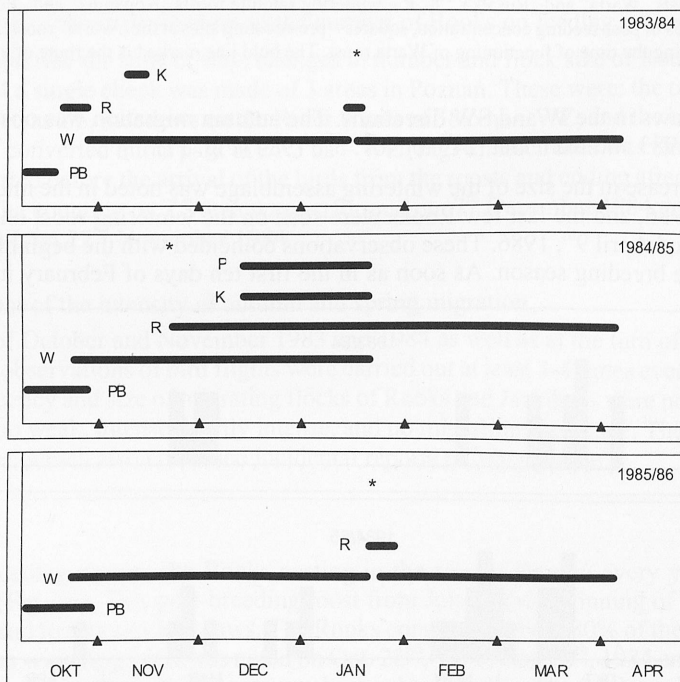


Fig. 18. The periods of the roost use in three winter seasons: PB – post-breeding roost, W – “Warta” roost, R – “Rusałka” roost, K – “Kopanina” roost, P – “Puszczykowo” roost; * – time of occurrence of gales.

Regarding the regularity of roosting and the size of the roosting flock, the most important are the two sites Warta and Rusalka (Fig. 18). In the seasons 1983/84 – 1985/86 the Warta roost was preferred and practically all the birds from the studied assemblage roosted there. Rapid abandonment of this roost by all or some of the birds and a move to the Rusalka roost was each time a consequence of strong, tree-breaking gales. The Kopanina and Puszczykowo roosts were used only by a part of the assemblage and for a relatively short time. In the winters of 1986/87 – 1988/89, the wintering Corvids roosted almost exclusively on the Warta roost, whereas in the winter of 1998/99 almost exclusively on the Rusalka one. These two main roosts had been alternatively used earlier, at least from the winter of 1967/68 (BERESZYŃSKI & ŻOŁĄDKOWSKI 1980).

The daily flights between roost and feeding grounds took place according to a strict schedule.

At dawn, after a short period of increased vocal activity, Rooks and Jackdaws almost simultaneously left the roosting trees. In the vicinity of the roost the birds formed large flocks which flew off in definitely different directions. The undecided individuals, circling over the place, finally joined one of the flocks. From this moment no presence of Rooks or Jackdaws on the roost was noted, as indicated by the results of regular checks of the Warta roost carried out on the occasion of the visits to the areas WZ and WL where counting of the Corvids took place.

According to the results of checks of the ZS, WZ, and WL areas, the Rooks stay on the feeding grounds can be divided into three phases (Fig. 19). The first is the arrival at the feeding concentration points, where compact flocks of Rooks and Jackdaws do not show much motoric activity and after some time disperse to feeding grounds. The feeding points were noted in the WL and ZS areas. In Fig. 19 these sites are marked as sites of an initially relatively large number of individuals and flock size of the birds, followed by a decrease in their number. In the area WZ only the arrival of

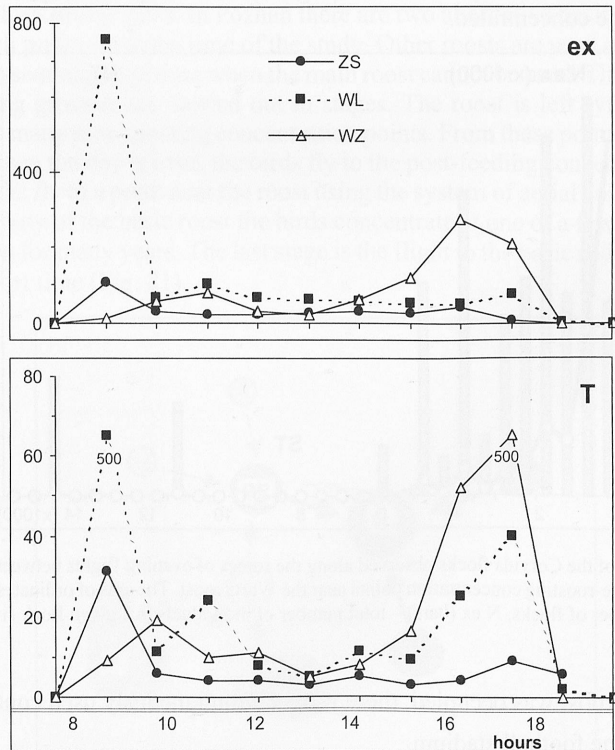


Fig. 19. Changes in the number (ex) and maximum size of flocks (T) of Rooks in the three areas studied (ZS, WL, WZ) in the cycle of hours.

birds which had gathered earlier at a concentration point outside this area was noted. Analogous, for some time permanent concentration points were also spotted at many sites in Poznań. The second phase is the actual stay on the feeding grounds. At this time no significant changes in the number of birds or in their flock size were noted. The third phase is the concentration of birds at post-feeding points near the feeding grounds, such a point being identified in the WZ area (Fig. 19). At these points an increase in the number and flock size of the birds was noted; in the WL area only local concentrations of birds which then flew off this area were observed. The formation of analogous concentration points, at which up to a few thousand birds were counted, was observed at many sites of the city.

The Corvids left the post-feeding concentration points flying in flocks to the roost. Many times the birds were observed to land at certain and the same sites along the route to the roost. At these sites flocks coming from different directions joined together. The location of such intermediate points is shown in Fig. 16. The size of the flocks flying towards the roost was characterized on the basis of the data collected on many control visits along the constant route (see "Methods", entry 4). From a few thousand reports randomly selected data on 250 flocks (Fig. 20), were analysed. The information on flocks smaller than 10 individuals was disregarded, although from 10 to 20% observations were those of small flocks. This decision followed from the finding that in the majority of cases these small flocks were actually the front or back of larger ones. The mean size of the flock from the selected sample of 250 flocks was 1140 birds (median 650). The majority of the flocks were of less than 1000 birds (69%), although those of up to 5000 Rooks and Jackdaws were regularly spotted. The largest flocks in the group analysed were of 11 and 14 thousand individuals. The largest flocks were observed to be formed from many smaller ones combining into one during the flight. The mornings as well as the evening routes were found to form a system of aerial corridors fixed in time. The destination sites of the above-described star-like flight system were pre-roosting concentration points in the vicinity of the roost (Fig. 16), at which practically all the birds belonging to a given assemblage concentrated.

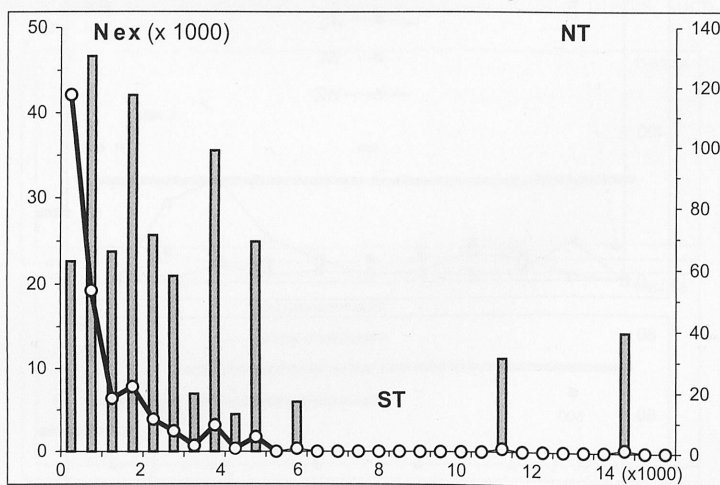


Fig. 20. Characterization of the Corvids flocks observed along the routes of evening flights between the post-feeding concentration points and pre-roosting concentration points near the Warta roost. The axis of ordinates – classes of flock size, NT (points) – the number of flocks, Nex (bars) – total number of individuals in a given flock size class.

When the Warta roost was occupied, there were 4 simultaneously used concentration points:

- at and around the football stadium
- groups of trees, gardens, and idle land on the margin of a new housing estate,
- fields and idle land on the margin of a housing estate,

– avenues, orchards, and idle lands.

When the Rusalka roost was occupied, there were 3 regularly used and one temporary concentration points:

- grass-covered airport grounds and idle lands,
- vast old park,
- sports stadium and groups of trees surrounding it,
- frozen lake (temporary point).

The pre-roosting concentration points in the vicinity of the Rusalka roost had not changed since the winter of 1970/71 (BERESZYŃSKI & ŻOŁADKOWSKI 1980).

All the birds concentrated at the 3–4 concentration points around the currently used roost. The maximum concentration at one of the points was estimated as 55 thousand individuals. The concentration points were definitely left by all birds 60 to 80 minutes from the arrival of the first birds. The process of leaving occurred synchronically at nightfall. The flight to the current roost and occupation of the roost trees took only 10 minutes. After this time only small groups of birds which did not stop at the concentration point flew in sporadically.

The results can be summarised as follows. The assemblage of Rooks and Jackdaws wintering in Poznań tends to roost at one basic roost. The location of the roost is permanent in a cycle of many years. Its abandonment in a given winter, either temporary or definitive, is forced by unfavourable external factors such as strong gales. In Poznań there are two alternative basic roosts, of which the Warta one was much preferred at the time of the study. Other roosts are used only periodically and only by part of the assemblage at a time when the main roost cannot be used. The flights between the roost and the feeding grounds are carried out in stages. The roost is left synchronically and the flocks of birds fly to many post-roosting concentration points. From these points they disperse to the feeding grounds. When the day is over, the birds fly to the post-feeding concentration points. From these points the flocks fly to a point near the roost using the system of aerial corridors fixed in space and time. In the vicinity of the basic roost the birds concentrate at one of a few pre-roosting points, which are permanent for many years. The last stage is the flight to the basic roost, which is synchronous and takes a short time (Fig. 21).

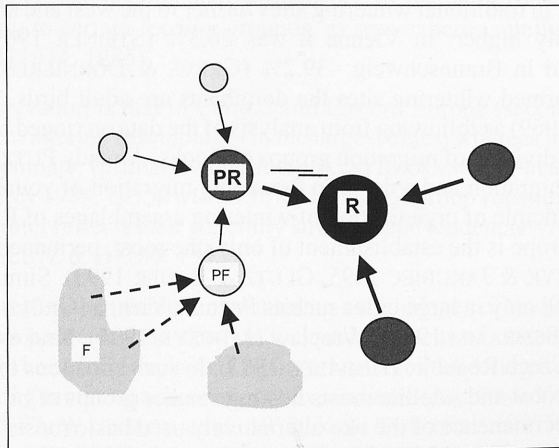


Fig. 21. Model of the system of flights of the Corvids: F – feeding grounds, PF – post-feeding concentration points, PR – pre-roosting concentration points, R – roost.

C. Discussion

The results of the observation of the wintering assemblage of the Corvids in Poznań are in many aspects consistent with those obtained by other authors. Similarly as in observed in Poznań, wintering assemblages of Rooks and Jackdaws in Central and Eastern Europe concentrate around cities, (e.g. ALLEN & YOUNG 1982, GLUTZ & BAUER 1993, HUBALEK 1983, JADCZYK & JAKUBIEC 1995). Some tens of the largest wintering assemblages of 100 thousand or more birds were noted only in the vicinity of large urban agglomerations (GLUTZ & BAUER 1993, GRODZIŃSKI 1971, GRÜLL 1981, HUBALEK 1980, 1983, JADCZYK 1994, JADCZYK & JAKUBIEC 1995, STORK et al. 1976, STORK & JÄNICKE 1977, SCHRAMM 1974, VARSHAVSKIJ et al. 1984). It is also a rule that Rooks and Jackdaws winter in one roost and form mixed flocks on feeding grounds (e.g. ALLEN & YOUNG 1982, GLUTZ & BAUER 1993, JADCZYK & JAKUBIEC 1995). This may be explained by the greatest similarity of the foraging niches of these species of all European Corvids (LOMAN 1980, WAITE 1984).

The wintering of Rooks and Jackdaws in Poznań described in this paper does not differ from the phenological data collected from other sites in Europe (e.g. BERESZYŃSKI & ŻOŁĄDKOWSKI 1980, GRÜLL 1981, HUBALEK 1979, WACHSMUTH 1935, WEISSBACH 1978), while the dates of the beginning and end of wintering coincide with those of migrations (BUSSE 1969, LANOVENKO 1983, PUTZIG 1937, WATERHOUSE 1949). In Poznań, an increase in the size of the wintering assemblage of the Corvid was noted from about 28-30 thousand at the beginning of the 70s (BERESZYŃSKI & ŻOŁĄDKOWSKI 1980) to about 100 thousand in the 80s. A similar increase in the size of the Corvids assemblage in the last decade was also observed in Wrocław (JADCZYK 1994). The shift of the winter area of these species is confirmed by the appearance of new roosts in Eastern Europe, e.g. in Lithuania (PIATRAJTIS et al. 1976) or even in Moscow (KONSTANTINOV et al. 1982). This evidence corroborates the thesis of BUSSE (1969) that the Corvids, and particularly Rooks, show a strong tendency to shorten the routes of migration and thus to settle. The novelty of this phenomenon is indirectly confirmed by the fact that the roosts are abandoned by some of the birds as a result of deterioration of the atmospheric conditions, this having been observed not only in Poznań but also in Braunschweig (GREVE 1983) and Basel (BÖHMER 1973). A periodical decrease in the size of wintering populations of Rooks during hard winters has also been noted in the eastern part of Germany (PRRILL et al. 1985).

The appearance of wintering sites closer to the breeding sites explains the unequal contribution of young Rooks in different wintering assemblages. In the 80s the contribution of young Rooks in the wintering assemblage in Poznań was only 5-7%, while in Wrocław the corresponding value was 5-6% (JADCZYK 1994). In traditional wintering sites further to the west and south, the percentage of young Rooks is notably higher. In Vienna it was 26.3% (STEINER 1969), in Saxony 38.2% (BÄHRMANN 1960) and in Braunschweig –39.2% (GREVE & DORNIEREN-GREVE 1982). This means that in newly formed wintering sites the dominants are adult birds. This finding was also mentioned by BUSSE (1969) as following from analysis of the data on ringed birds. It is undoubtedly connected with the age division of migration groups of Rooks. Already PUTZIG (1937) reported the earlier time of winter migration and a delay in the spring migration of young Rooks in relation to those of adults. The principle of organization of wintering assemblages of Rooks and Jackdaws in Central and Eastern Europe is the establishment of only one roost, permanent for many years (e.g. HUBALEK 1983, JADCZYK & JAKUBIEC 1995, GLUTZ & BAUER 1993). Simultaneous use of a few roosts has been observed only in large cities such as Poznań, Vienna (GRÜLL 1981), Berlin (STORK et al. 1976), Hanover (SCHRAMM 1974), Wrocław (JADCZYK 1994), Kraków (GRODZIŃSKI 1971) and a few cities in the Czech Republic (HUBALEK 1983). In such situations the authors reported the formation of the basic roost and satellite roosts hosting smaller groups of birds, appearing in a different frequency. The permanence of the two alternatively used basic roosts in Poznań, for at least 30 years, is not surprising. The oldest of the known wintering sites in Europe have been used for over 100 years, and many others have been functioning for a few tens of years (e.g. GRÜLL 1981, HUBALEK 1983, MUNRO 1975). Rarely encountered small assemblages are characterized by low

time and space stability (HUBALEK 1983), indicating a significant winter-site fidelity at least in some of the Rooks and Jackdaws. This fidelity has been confirmed by sightings of individually recognized Rooks at certain wintering sites e.g. in Vienna for 4 winters (GRÜLL 1981), and at a site in the Czech Republic for 7 winters (HUBALEK 1983). Similar fidelity was noted in some of the Rooks as far as their Rookeries are concerned (e.g. ENA 1984, PATTERSON & GRACE 1984, RICHARDSON et al. 1979).

The location of the two alternatively used basic roosts in Poznań – in the tree stand on the river and in the lake valley – fully corresponds to the observations of other researchers. The location of roosting places of Rooks and Jackdaws near reservoirs, and especially in the river valleys, is almost a rule (e.g. EGGERS 1968, GRÜLL 1981, GRODZIŃSKI 1971, JADCZYK 1994, LÜCKER 1975, GLUTZ & BAUER 1993). This location is undoubtedly related to the specific mild microclimate in the vicinity of water. The land depressions occurring naturally near water reservoirs are in our climatic zone overgrown with deciduous forests, especially willow-poplar and alder or, less frequently, oak-hornbeam and light oak forests (MATUSZKIEWICZ 1993). The problem much discussed in literature of preferences for particular tree species (mainly deciduous forest) is, according to the present author, of secondary importance. It has been established that Rooks do not avoid roosting in pine tree stands – such observations have been reported not only from Poznań (GRÜLL 1981, HUBALEK 1983, SOKOŁOWSKI 1936).

The system of star-like daily flights (Fig. 21) is composed of a few elements stable in time and space: the centrally located basic roosts, a locality of feeding grounds, the flight routes connecting them forming a system of aerial corridors and rest sites on the routes. In the evening these rest sites are post-feeding concentration points, intermediate points, and pre-roosting concentration points, and in the morning pre-feeding concentration points.

A similar organization of winter assemblages of the Corvids has been described by other authors, particularly worth emphasising being the studies of GRÜLL (1981), JADCZYK (1994), STORK & JÄNICKE (1977), and STORK et al. (1976). Similarly in Poznań, the departures of birds from the roost were synchronous (the so-called “Katapultenstart”, ASCHOFF & HOLST 1958), the birds gathered at the pre-roosting concentration points and the time of the flight to the roost very short. In some assemblages local modifications in the system of flights were observed. For example, in Wrocław, after leaving the roost, the birds stopped at the point of the evening pre-roosting concentration (JADCZYK 1994). Independently, there was a correlation between the time schedule of flights between the roost and feeding grounds and the intensity of light (e.g. HUBALEK 1978a, b, STORK & JÄNICKE 1977). The documented permanence of the daily routes of flights is a consequence of Rook fidelity to certain feeding grounds, as was experimentally shown by e.g. GRÜLL (1981) and SCHRAMM (1974, 1985).

An interesting observation is that in Central and Eastern Europe (secondary wintering places) the Corvids form large wintering assemblages in the largest cities, whereas in Western and Southern Europe with a milder climate, (primary wintering places) Rooks winter near the breeding colonies (e.g. COOMBS 1978, ENA 1984, GOODWIN 1976). The fact of group roosting and feeding of Rooks and Jackdaws in the winter reflects their generally strong social tendencies, revealed also during migration and nesting (GLUTZ & BAUER 1993).

Despite much interest in the problem of wintering assemblages of the Corvids, the reasons for their formation, and in particular the reasons for establishment of communal roosts (ALLEN & YOUNG 1982), have not been fully explained. Many advantages following from group roosting have been indicated, including minimisation of energy expenditure (ALLEN & YOUNG 1982, GAVRILOV 1979a, SWINGLAND 1977, WARRILOV et al. 1978, YOM TOV et al. 1977) and protection against predators (ALLEN & YOUNG 1982). It has also been suggested that the roost is a centre of information concerning food (WARD & ZAHAVI 1973, LOMAN & TAMM 1980, YDENBERG et al. 1983 and also ALLEN & YOUNG 1982).

On the basis of the results of this study and other works, it may be supposed that the main reason for establishment of communal roosts by Rooks and Jackdaws is their role as an information centre. This supposition is supported by the following premisses:

- there is a strong tendency for the formation of only one roost as a centre of the system of flights to the feeding grounds,
- the organization system, including the location of the roost, flight routes, intermediate points, and at least partly the feeding grounds, is characterized by considerable stability in time and space in the seasonal and many-year aspects,
- the roost is shared by those species showing the greatest similarity of foraging niches.

According to some authors, assumption of the hypothesis on the communal roost role as the information centre requires assumption of the altruistic behaviour of the birds (WEATHERHEAD 1983). In the context of the above results, this assumption is absolutely unnecessary. The stability of the roosts in time and space indicates that the choice of the site is made by the most experienced individuals, who have been wintering in the region for a few seasons. The repeatability of the flight routes to the feeding grounds also reflects the earlier experience. Sharing the information about the best feeding grounds with inexperienced individuals is not altruistic behaviour, as follows from the arguments below. The first is that the effectiveness of foraging increases when food is searched in groups (CHANTREY 1982, HÖGLUND 1985, LOMAN 1980, PINOWSKI 1959). It has been experimentally shown that among Rooks (DUVALL 1980, RØSKAFT & ESPMARK 1984) as well as Jackdaws (LORENZ 1931) there is a strict hierarchy and Rooks of lower status in the hierarchy have poorer food success (HÖGLUND 1985).

This poorer food success may be a consequence of increased competition and aggression (BALPH et al. 1979, CARACO 1979, FEARE 1978). LACK (1954) proved that in low temperatures the level of aggression in Rooks increases. The second reason is that in primary feeding grounds (agrocenoses) in winter food is irreproducible and periodically inaccessible, so that even the most experienced individuals may have to be forced to change their feeding ground. The existence of a central roost facilitates the change simply by joining another group of birds flying to a different feeding ground. An additional profit for the informers is an increase in survival during roosting. It has been found that individuals at a high level in the hierarchy occupy the space in the centre of the roost where the temperature is highest and predator pressure lowest (GAVRILOV 1979a, b, SWINGLAND 1977). The location of the roost is of secondary importance in view of its role as the information centre. The location in the city is dictated by decreased energy expenditure during a hard winter when the birds withdraw from far-off feeding grounds and change their feeding strategy, penetrating an urban environment. The roost location in tree stands near reservoirs, in river or lake valleys at the lowest altitude, is dictated by the favourable microclimate at these sites.

The role of the roost as the information centre is also indicated by the stability of large roosts and instability of small ones (e.g. HUBALEK 1983), this most probably being a consequence of the weak information power of the latter. An analogous mechanism has been noted in Rooks in the breeding season (JÓZEFIK 1976). The present author has proved that the homeostasis of the breeding populations of Rooks is the result of two coupled factors: prointegration tension and increased competition. In consequence, small breeding colonies quickly undergo disintegration and in the too large ones weaker individuals are forced out to suboptimum habitats.

The formation of breeding colonies and wintering assemblages by Rooks stems from the same reason – a high social character of the species and significance of the cooperation among individuals. The wintering place can be considered as a substitute for a breeding colony as indicated by the fact that in the milder climate of Western Europe Rook wintering places are in the vicinity of breeding colonies.

VI. CONCLUSIONS

The wintering assemblage of the Corvids in Poznań, in which Rooks are absolute dominants, is representative of assemblages described in other cities of Central and Eastern Europe.

The period of existence of wintering assemblages of the Corvids in Central and Eastern Europe is delimited by the dates of the birds' migration. They function on the basis of roosts stable in time and space, located in large cities. As a rule the assemblage comprises Rooks and Jackdaws. The Rooks are absolute dominants in the assemblages, and the contribution of one-year-old individuals is much smaller than in the wintering places localized more to the west or the south. This is a result of the tendency to shorten the routes of migration to wintering places revealed by the Rooks from the East European populations and separate migration of these birds from different age groups.

The stability of wintering roosts of the Corvids over many years ensures the existence of a repeated in time system of flights to feeding grounds. This system is composed of the roost and aerial corridors with intermediate points along them. The main role of this system is as the centre of information concerning food resources. The secondary energy saving role follows from the optimum location of the roost. The communal roost also facilitates protection against predators, this being reflected by the way of arrivals and departures from it. When the dark falls the birds arrive synchronously at the roost, having earlier gathered at pre-roosting concentration points. The departures are also synchronous and occur in a very short time.

The assumption of the hypothesis concerning the communal roosts playing the role of information centres does not imply the necessity of assuming an altruistic behaviour of the birds. The roosting of groups of birds of a similar food niche reflects the tendency to forage in flocks. In view of the decreasing amount and deteriorating availability of food during particularly cold periods in winter, the informer birds gain information on new and better feeding grounds. The information receivers – the youngest birds having the lowest social status – are made to occupy the peripheries of the roosts and form the energetic and antipredatory shield of the assemblage.

The wintering roosts of Rooks are localized in the immediate neighbourhood of large cities, this being particularly well evidenced for the largest assemblages. During daylight the birds are regularly dispersed over, sometimes distant, feeding grounds. Similarly as in the seasons other than winter, at the beginning and the end of winter the Rooks prefer country agrocenoses and apply there the innate feeding strategy of an active group search for food. At the peak of winter they abandon this type of feeding grounds and move into the neighbourhood of human dwellings (in the city and villages). There they use the strategy of food expectation which requires earlier recognition of food resources and the learning of certain behaviour. For this reason the Rooks penetrating the cities at the peak of winter are not the youngest and least experienced ones.

Withdrawal from agrocenoses and feeding in urbanized habitats at the peak of winter is evidenced by the shortening of routes of daily flights and the concentration of birds in the city and its immediate vicinity. The reasons for the above behaviour are: reduced availability of food in agrocenoses, irreproducibility of food in these habitats, decrease in the energy costs of flights, and shortening of the effective time of feeding (short daylight).

The size of the wintering assemblages of the Corvids is related to the size of the cities, whereas the size of the daily dispersal zone is related to the size of the assemblage.

The penetration of the species into urbanized areas at the peak of winter is a phenomenon forced by external factors. The energy costs follow not only from the need for active searching for food, but also from daily flights between the roosts and the feeding grounds. The feeding in urbanized habitats is energetically justified when the roost is localized in the neighbourhood of the city. It requires a change in the feeding strategy to that of expecting food. The assumption of this strategy is related to breaking the barrier of anthropophobia and to individual recognition of local food resources in the process of learning. Presuming that the density of birds is an indicator of attractiveness of the feeding ground, the Rooks prefer sites with a low degree of urbanization in the city, such as parks, garden allotments, and a loose type of housing concentration, such as e.g., on some new housing es-

tates. A daily stay in these habitats requires energy expenditure close to that related to the stay in agroecosystems. Penetration into the city causes an increased energy loss, mainly due to much energy-consuming flights forced by stressful traffic. A relatively large number of Rooks at the waste-dumping grounds indicates its high attractiveness as a source of food. Great changes in the number of birds in this habitat may be a consequence of periodical variations in the amount of food and increased competition in obtaining it.

The effectiveness of the strategy of food expectation depends on the experience of the birds (learned behaviour), which explains the absence of young birds in the winter in urbanized environment.

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Repeatability of size and shape of eggs in the urban Magpie *Pica pica* (Passeriformes: Corvidae) population

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Abstract. This study was conducted over four breeding seasons, 1986, 1987, 1998 and 1999 in Zielona Góra, western Poland. Repeatability patterns for length, breadth, volume index, and elongation index are presented (based on 234 Magpie eggs from 42 clutches). Mean repeatability estimates were 0.63, 0.59, 0.60, 0.64 for length, breadth, volume and elongation index, respectively. These data suggest that in the Magpie population in Zielona Góra variation between clutches both in the size and shape of eggs is dependent on the body condition and physiological limitations of the female.

Key words: Magpie, eggs, repeatability, female quality.

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I. INTRODUCTION

The Magpie *Pica pica* (LINNAEUS, 1758) is a common bird in the Palearctic (GOODWIN 1986), which has been the subject of many biological, ecological and behavioural studies (see reviews in BIRKHEAD 1991, TROST 1999). There have been a number of papers concerning variation in egg dimensions but most of them concentrate on descriptions of egg size for specific populations (MAKATSCH 1976, SMETANA 1978, KELLER 1979, ARIAS DE REYNA et al. 1984, BIRKHEAD 1991). It is known, however, that eggs in a single clutch of any individual female may differ strongly (BIRKHEAD 1991). To date, there has been no quantitative description of the variation in egg dimensions within clutches. The best method of describing such variation is that of repeatability which is useful in separating the variation in egg dimensions within a clutch into its genetic and environmental components (BOAG & VAN NORDWIJK 1987, FALCONER 1989, BAŃBURA & ZIELIŃSKI 1998).

Both breeding success and egg size are correlated with many factors including female quality and territory quality. However, CLARKSON (1984) suggested that the strongest effect in the Magpie is the "female factor", although this is still not clear. Using the repeatability method arguments are put forward in favour of one of these hypothesis.