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The Urban Population of the Woodpigeon *Columba palumbus* Linnaeus, 1758, in Europe — its Origin, Increase and Distribution

[Pp. 585—632 and 6 text-figs.]

Populacja miejska grzywacza *Columba palumbus* Linnaeus, 1758, w Europie — jej powstanie, wzrost liczebny i rozprzestrzenienie

Городская популяция вяхиря *Columba palumbus* Linnaeus, 1758, в Европе — её возникновение, рост численности и распространение

Abstract. The history and course of the expansion of the urban Woodpigeon population in the European mainland has been reconstructed on the basis of literature and the latest data. The paper comprises detailed data on the present state of this population in towns of the border zone of its range and its density in three types of habitats, i.e. in a forest, an open area and a town. The laws of expansion of a new population in the area already occupied by this species have been formulated and a hypothesis concerning the mechanism of urbanization of the Woodpigeon is put forward. Arguments pointing to the non-hereditary nature of changes, which result rather from an increase of the whole population of this species in size, are presented.

CONTENTS

I. INTRODUCTION

The literature on the synanthropization and urbanization of birds suggests that, beside the *Turdidae* and *Corvidae*, also the family *Columbidae* shows a strong tendency to colonize towns. The pigeons have even a better chance in this respect than the other two families, since they nest in the crowns of trees, unlike the originally low-nesting *Turdidae*, and are better tolerated by man than are the *Corvidae*. All the species of the European pigeons already enter towns; they are *Columba livia*, *Columba palumbus*, *Streptopelia decaocto*, *Columba oenas* (e.g. in London — HOMES et al., 1964) and *Streptopelia turtur* (I have recorded single pairs in town parks at Augustów, Lublin and Rzeszów in Eastern Poland). In Asia, in addition to the species mentioned for Europe, the Palm Dove *Streptopelia senegalensis* also nests in towns. In North America the Mourning Dove *Zenaidura macroura* occurs in towns commonly and the White-winged Dove *Zenaida asiatica* and Inca Dove *Scardafella inca* in places (PETERSON, 1960; HAVERSCHMIDT, 1969; MAUERSBERGER, 1971). These facts permit the admission of the statement as to the pre-adaptation of pigeons to life in towns as proved.

Most detailed aspects of the synanthropization and urbanization of birds have hitherto been investigated on one model species, i.e. on the Blackbird *Turdus merula*. With all its advantage, this course of action creates danger of incorrect generalizations. For this reason in the present work the conclusions drawn during the study of the urban Blackbird population have been checked by the adoption of the analogous method of analysis for the Woodpigeon *Columba palumbus*. This is, after the Blackbird and Mistle Thrush *Turdus viscivorus*, a third closely investigated example of the expansion of a different population within the breeding area already occupied by the species (HEYDER, 1955; PEITZMEIER, 1957; PEUS, 1958). As regards the Woodpigeon, in some cases we can eliminate the part played by food resources utilized by different populations, which made it difficult to draw conclusions in the case of the Blackbird. This facilitation results from the following specific characters of the Woodpigeon:

a) the extensive range of foraging activity of breeding specimens permitting them to utilize food resources situated even more than 15 km from the nest;
b) the territorial behaviour evolved by the Woodpigeon under the influence of the necessity of scattering the nests in order to avoid the pressure of predation, but irrespective of food resources;
c) nesting in tree crowns and not like Blackbirds chiefly in shrubs, which are usually few in intensely urbanized places. Thus, the nests of Woodpigeons are less exposed to destruction from man.

II. HISTORY OF THE SYNANTHROPIZATION AND URBANIZATION OF THE WOODPIGEON IN EUROPE AND THE RANGE OF THE URBAN POPULATION

As in HEYDER'S (1955) study of the Blackbird, a survey of available data illustrating the historical and geographical aspects of the formation of the urban

Woodpigeon population in Europe is given below *. To make comparisons easier a scale of grades of the intensity of changes in the mode of occurrence of the species in the habitat has been established. The following stages of changes have been distinguished arbitrarily:

Stage O. Initial state — nesting in forests and mid-field copses, far from human settlements.

Stage I. Nesting of small numbers of birds in peripheral parks, near houses, chiefly adjoining to villages or in quiet little towns, and the occurrence of single pairs in large, less urbanized parks of big cities.

Stage II. Nesting in town parks and cemeteries at a higher density than that observed in forests.

Stage III. Not infrequent nesting in closely built-up areas (in streets) and fairly frequent in town parks.

Stage IV. Common and fairly numerous nesting in streets, not infrequent on buildings, and very numerous in town parks.

Finally, in some very extensive towns there may appear a new quality, the utilization of food which is easy of access in them, e.g. taking of bread.

Stage I covers the phase of initial synanthropization and the other three stages embrace synanthropization proceeding in town areas, further referred to as the urbanization of the species (acc. to the definition given in a previous study — Tomiałojć, 1970).

Under original conditions the Woodpigeon was an eurybiontic bird of deciduous, mixed and coniferous forests nearly all over Europe. In these habitats it is still observed in Northern Scandinavia (Merikallio, 1957; Lack 1966) and in the vast area of the U.S.S.R. (Dementyev et al., 1954; Ptushenko and Inozemtsev, 1968). These populations are mainly associated with the there prevailing coniferous forests. The opinions differ as to the changes in the size of these populations; a shift of their range to the north has been reported from Finland, which would indicate an increase in the number of Woodpigeons in that country (Kalela, 1949; L. Saari, in litt.), whereas a progressive fall in their number has been noted in the U.S.S.R. in the present century (Dementyev et al., 1954; Ptushenko and Inozemtsev, 1968). The Woodpigeons are there extremely shy and occur in small groups, e.g. flocks of 10 specimens are rarely met with in the Moscow region. They nest in single pairs at the edge of old

* Bird observation carried out by the author in Polish towns was subsidized by the Committee of Ecology, Polish Academy of Sciences. In addition to the data obtained from literature, I received much valuable information imparted by letter from different European towns, for which I am greatly thankful to the following correspondents: S. Anioła (Poznań), M. Czajkowski (Lyon), W. J. Doude van Troostwijk (Hague), B. Frochot (Dijon), D. Goodwin (London), W. Górski (Koszalin), G. Grempe (Rostock), P. Hald-Mortensen (Copenhagen), K. Hudec (Brno), Z. Kwiatek and A. Kulczycki (Kraków), W. Kalbarczyk and M Luniak (Warsaw), A. Le Toquin (Paris), Z. Lewartowski (Poznań), L. Pomarnacki (Radom), F. Purroy (Madrid), A. K. Randik (Bratislava), E. Schmidt (Budapest), H. Scotte-Møller (Aarhus), Z. Szymusik (Gliwice) and P. J. Zomerdijk (Alkmaar).

pine-oak forests or pine-oak forests with spruce and forage partly in the forest and partly in cultivated fields. Personally, I know a similar state of the population of densely wooded areas in eastern Poland, such as the Augustów and Białowieża Forests in the Białystok Province and the Solska Forest and the forests of the Roztocze Mts. in the Lublin Province, where the density of the population is generally 0.1—0.5 pair per 10 hectares of wood.

As regards Central Europe, reports of the original stage of the Woodpigeon population still appeared in publications at the beginning of the nineteenth century, e.g. NAUMANN (1833) and GLOGER (1834) laid stress on the dependence of the Woodpigeon on the crops of seeds of forest trees (spruce, beech and oak) and on its great shyness. Nevertheless, as early as 1822 BREHM knew instances of the nesting of single pairs in proximity to villages and a year earlier UECHTRITZ (1821) reported their breeding in human settlements (towns?) in Saxony. The earliest record pointing to stage II of urbanization was published by GLOGER (1834). In his work on the birds of Europe he wrote that the Woodpigeon sometimes „grosse Garten und Baumparthieen in den grössten und lebhaftesten Städten brütend bewohnt". It may be supposed that he meant Paris, for before 1841, and so not long later, a Pole K. TYZENHAUZ (1843—1846), to his surprise, found some very tame Woodpigeons breeding in the Tuillerie and Luxemburg Gardens in Paris, which was next corroborated by TACZANOWSKI (1882). In French literature the earliest record of Woodpigeons in Paris was not published until 1874 (N. QUÉPAT).

Very early, since during the eighteenth century, the original state of these birds underwent a disturbance in southern England and at the turn of the century the Woodpigeon became a pest to crops (MURTON, 1965). It should be stressed that its increase in number took place only in the farming scenery and was not noted in London before 1883. Although several pairs of Woodpigeons nested in the large Kensington Gardens at least from 1834, they remained at the same level in respect of number for a long time (FITTER, 1949). This is confirmed by the fact that there is no record of urban Woodpigeons in a number of books entitled „A History of British Birds" (MAC GILLIVRAY, 1837; 1940; MORRIS, 1851—57; YARRELL, 1841). Their authors emphasized the extreme shyness of Woodpigeons, and listing their nesting habitats did not name town parks and, in general, human settlements. Even SEEBOHM (1884) who mentioned not very shy Woodpigeons in the Botanical Gardens in Paris and Berlin, did not report their occurrence in any of the English towns.

Thus, stage II (nesting less shy Woodpigeons in town parks at an increasing density) was first attained in Paris (about 1830—1840), then one of the biggest cities in Europe, with its human population of 548000 in 1801 and 785000 in 1831 *. In London (about 1 000 000 inhabitants in 1800 and 2 000 000 in 1835) this stage manifested itself only about 1883 (HOMES et al., 1964) and thus later than in towns of Holland and in Berlin.

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* Numerical data acc. to DORST (1971) and BEAUJEU-GARNIER and CHABOT (1971).

The differences shown between these two big capitals of Western Europe, Paris and London, may have resulted from different areas of these cities. About 1840 in Paris, the closer and smaller of them, Woodpigeons could forage in adjacent cultivated fields. On the other hand, London with its 1—2 million inhabitants was too extensive and the small population of these birds from the Kensington Gardens was presumably doomed from the very beginning to the food available within the town area. It began to grow rapidly only after the birds had got rid of their shyness and thus dared to use food given them by man. Then, within about 10 years this population expanded and even colonized the built-up area of the City.

Further data concerning the urbanization of the Woodpigeon in the European mainland are as follows:

1851 — nesting in human settlements in Lusatia, situated between Saxony and Silesia (TOBIAS, 1851).

1853 — nesting in promenades in the town of Oldenburg in Lower Saxony (NEGELEIN, 1853).

1857 — regular nesting in the Botanical Gardens of Wrocław (GÖPPERT, 1857, quoted after PAX, 1925), which were then situated in the periphery of this largest town of Silesia (about 140000 inhabitants).

1865 — occasional nesting in single trees in streets at Görlitz (TOBIAS, 1865); — a nest outside a much frequented café near Münster in Lower Saxony, a „widely known" phenomenon (ALTUM, 1865).

1870—1880 — a conspicuous increase in the number of reports indicating the territorial expansion of the phenomenon and an increase in the size of the urban population. Woodpigeons were reported to breed in Dutch towns (Thijsse, 1923 — acc. to ZOMERDIJK), at Münster in 1874 (PEITZMEIER, 1969), in the regions of Leipzig and Dresden (CABANIS, 1870), in Berlin (SCHALOW, 1876, 1877) and, in small numbers, at Wismar in 1875 (GREMPE, in litt.) and Stuttgart in 1879 (FRIEDRICH, 1905).

SCHALOW's (o.c.) information is particularly important; according to him, at that time in Berlin Woodpigeon nested not only in parks (e.g. in the Thiergarten, which was then situated on the outskirts of the city) but also in closely built-up areas, e.g. in Leipziger Platz. PFANNENSCHMID (1876) wrote that then the Woodpigeon also nested in the busiest streets of the little town of Emden in the Oldenburg Province. These records indicate that stage II and even the beginning of stage III had already been attained in Berlin, Emden and Görlitz.

1881—1882 — increase in number in the towns of Lower Silesia and the first nest near the University in the centre of Wrocław (KOLLIBAY, 1906); similarly, the first nest on a building at Görlitz (TOBIAS, 1881). It was therefore the beginning of stage III.

— first breeding birds in the parks of Rotenburg and Stade near Friedeberg in Hessen (GEBHARDT and SUNKEL, 1954) — stage II.

1883—1890 — a marked increase in the number of birds in London (FITTER, 1949) — attainment of stage III; a considerable increase in number in

Dutch towns of eastern Friesland, e.g. as many as 80 pairs in the elms by the market in the little town of Norden and at Braunschweig (BÄSECKE, 1941; LEEGE-JUIST, 1905; PRÖLSS, 1956); frequent nesting in streets at Niesky and Görlitz (BAER, 1898).

— colonization of Milan, before 1886 (MOLTONI, 1953).

1890—1900 — the Woodpigeon became one of the commonest birds of London; they colonized the centre of this city about 1900 (FITTER, 1949; HOMES et al., 1964) and reached stage IV of urbanization.

Recapitulation. The years 1870—1890 were a period of Woodpigeon's penetration into towns of the north-western and central lowlands of Europe and the appearance of a separate focus of urbanization in the Plain of Lombardy (Milan) — Fig. 1. Signs of a marked increase in the number of these birds were noted in Paris, towns of Holland and Lower Saxony, England, Berlin and towns of the Silesian lowlands (Görlitz and Wrocław). During the first 7 decades of Woodpigeon's encroachment on towns (1830—1900) it occupied the towns in the most fertile, most densely populated and at the same time most disafforested plain regions of Europe. Relatively very early this phenomenon reached its extreme town in the east, Wrocław. It may even be supposed that Wrocław was an independent centre of the development of the urban population of this bird.

The dates presented indicate that, in fact, the penetration of towns by the Woodpigeon occurred than earlier than their colonization by the Blackbird. SCHNURRE (1921) and PAX (1925) pointed at this fact, without presenting any evidence.

A close analysis of the map in Fig. 1 shows that during the next 7 decades (1900—1970) further colonization of towns proceeded not only towards the east, but in many directions, the southern direction being even prevalent. This is chiefly true of more hilly or piedmont regions, which have worse soil conditions and are decidedly better wooded (20—40% of the area). Here, too, the towns situated in woodless river valleys were colonized earlier than those in the adjacent uplands. This can be exemplified by the present state of the urban population in Baden-Württemberg (Hölzinger et al., 1970), where Woodpigeons occur in the valleys of the Rhine and other rivers, i.e. at Donaueschingen, Heilbronn, Karlsruhe, Ludwigsburg, Waiblingen and also Mannheim and Stuttgart (though in small numbers), but still avoid the towns of the well-wooded areas of Swabian Jura and Schwarzwald, such as Freiburg, Tübingen, Villingen and Ulm. Even in Munich, with a population of 2000000, surrounded by wooded piedmont areas, the Woodpigeon still occurs in very small numbers in hardly several places of the city (WÜST, 1970) and shows the signs of stage I of urbanization. Similarly, the appearance of urban Woodpigeons in Luxemburg, situated on woody hills, was not noted until the beginning of the twentieth century (HULTEN and WESENICH, 1960—1961) in spite of the close neighbourhood of the Belgian and Dutch lowland populations, at that time urbanized for a long time.

I have at my disposal a huge amount of information concerning the period after 1900, illustrating the intensification of the process under study. As early as 1915 the Woodpigeon nested in great numbers in Berlin, where specimens taking food from a man's hand were seen occasionally and in the Zoo (Thiergarten) 8 breeding pairs were observed in an area, 20 steps in diameter (SCHALOW, 1919). The expansion spread also on Jutland, where the first signs of nesting in the little town of Storeheddinge (south-east Zealand) were observed about 1900 and in 1913 Woodpigeons were already present in the central parks of Copenhagen (ARCTANDER, 1916; FLØYSTRUP, 1920, 1925, after SKOTTE-MØLLER). It is only then that they appeared in the towns of Schleswig-Holstein (e.g. a nest on a building at Kiel-Studnitz in 1921), and at Wilhelmshaven the first nest was observed in 1919 (KROHN, 1924; RIESE, 1954). The Woodpigeon began to nest in trees in frequented streets at Halle and Leipzig about 1925 (SCHÖNBRODT, 1970) and so later than in the towns of Lower Silesia. In these last towns large numbers of Woodpigeons were noted as early as about 1920 — Görlitz, Żagań, Bolesławiec, Legnica, Świdnica and Wrocław (HÄRTER, 1922; PAX, 1925; PURMANN, 1922). The third decade of this century brought also an increase in their number in the towns of Hesse (GEBHARDT and SUNKEL, 1954), the onset of colonization of Swiss towns (RIGGENBACH, 1949, GLUTZ v. BLOTZHEIM, 1962) and the colonization of Szczecin (ROBIEN, 1920).

The colonization of the towns of the Ruhr Basin began as late as 1935, e.g. at Dortmund in 1936 and at Padeborn in 1948 (PEITZMEIER, 1969). There was a marked rise in number in the towns in Belgium (Brussels and Antwerp) and Holland in the forties (KESTELOOT, 1956) and in the centre of Wilhelmshaven in the fifties of this century (REISE, 1954).

The latest decades (after 1945) have been characterized by a further, although slow, expansion of the process, which covers the territories of Sweden, Poland, Austria, etc. These data illustrate the present range of the urban population of the Woodpigeon in Europe.

III. THE STATE OF THE POPULATION IN TOWNS NEAR THE LIMIT OF THE RANGE OF THE URBANIZED FORM

In the case of such a long-lasting process of urbanization changes it is extremely important to leave detailed data from chosen towns, recorded in publications, so that it shall be possible in the future to compare the state observed then with the present — day situation, for the process of increase of the size of the urban Woodpigeon population does not seem to run smoothly and continuously. It will be particularly instructive to investigate in the future what influence will be exercised by the colonization of towns by more slowly urbanized birds of prey and *Corvidae*, especially *Corvus corone*, upon the size of the urban Woodpigeon population.

Denmark

Thisted (pop. 10000). Woodpigeon in urbanization stage IV. On May 19, 1965 84 nests were occupied in the Christiansgave Park (about 6 hec. in area) inside the town, the density being about 140 nests per 10 hec. (HALD-MORTENSEN). This park, founded about 1850, consists chiefly of *Ulmus glabra* and *Fagus silvatica* and is much frequented by people. As at Legnica, at Thisted the birds forage in the neighbouring barley fields; the nearest forest lies 4—5 km from the town. Fairly many Woodpigeons of this population have already got over their shyness to the extent that they collect food in the lawns of the park. In the last few years the size of this population, like the size of the whole population of Denmark, has somewhat decreased. The density of nests is here the second highest reported from the European mainland (inferior to that of Legnica — TOMIAŁOJĆ, 1970).

Aarhus (pop. 200000). Small numbers of Woodpigeons occur in parks, e. g. about 5 pairs in the University Park, 12—15 hec. in area (SKOTTE-MØLLER).

Copenhagen (pop. ca 1000000). It has been present in the wooded areas of the since about 1905, but for some time in very small numbers only. E. g. one pair nested in Østre Anlaeg (13 hec.) in 1914—1916 (FLØYSTRUP, 1920, 1925), whereas in 1972 there were about 20 pairs there (HALD-MORTENSEN).

Sweden

Malmö (pop. ca 250000). The Woodpigeon has inhabited the parks since about 1938. Recently 20 pairs have been noted in a 40-hectare park, which makes 5 pairs per 10 hec. Moreover, an urban population occurs also at Lund (JERDEN, after TENOVUO, 1967; LJUNGGREN, 1968).

Poland

Out of the Polish towns, Legnica (pop. 90000*) has the highest density of Woodpigeons, 157 pairs per 10 hec. (TOMIAŁOJĆ, 1970), and Wrocław (pop. 525000) comes in second, 71 pairs per 10 hec. Detailed data concerning these towns will be published in a separate paper on the there conducted study of the ecology of reproduction of the urban and farmland population (TOMIAŁOJĆ, in press).

In addition to the towns of Lower Silesia colonized as early as the nineteenth century and Szczecin colonized in the twentieth century, fairly numerous urban populations have recently been discovered in other towns of western and central Poland, which now mark out the eastern boundary of the range of the urbanized population. These towns are as follows: Koszalin (W. GÓRSKI), Stargard Szczeciński (J. NOSKIEWICZ), Poznań, Gniezno, Inowrocław, Kalisz,

* The data on the population of the Polish towns refer to the state in 1970 (Rocznik Statystyczny, 1971).

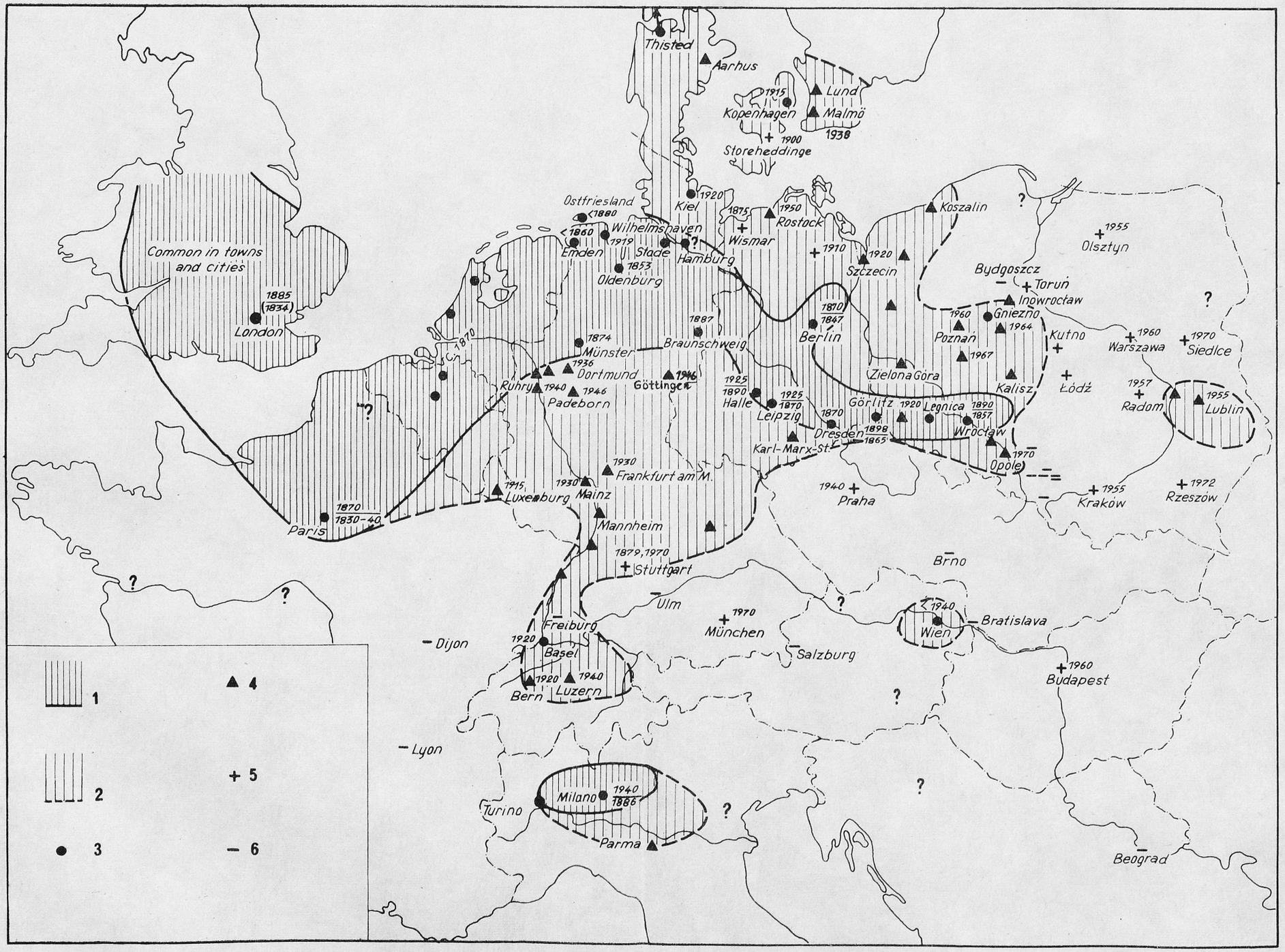

Fig. 1. Range of urban Woodpigeon populations in Europe. The dates placed beside the marks indicate the first record of nesting in the town (single date or that under line) and the outset of the period of intense growth of the population in number (date over line). Designations: 1 — area occupied to 1900; 2 — area occupied in 1900—1970; 3 — towns with large Woodpigeon population; 4 — towns with small Woodpigeon population; 5 — towns with single breeding pairs (chiefly in periphery); 6 — towns without breeding Woodpigeons

Wrocław, Brzeg and Opole. A separate centre of urbanization has arisen also at Lublin (Map—Fig. 1). The survey of the situation in these towns will be begun with Zielona Góra, as a rather exceptional town situated far to the west.

Zielona Góra (pop. 73000). Urbanization stage III. Here the Woodpigeon inhabits not only parks but also nests in streets, even in the very centre of the town. The density is however very low. On April 28, 1971 I counted 17 breeding pairs in the central part of the town and the adjacent parks and residential quarters (about a half of the town area), which constitutes approximately two-thirds of the later breeding population. In the Park Tysiąclecia (Millenium Park, 8.12 hec.), which up to 1966 had been an unutilized area left over from a former cemetery, there were 8 pairs (7 nests) on May 27, 1972, the density of population being about 10 pairs per 10 hec. The cause of this low density may be the close neighbourhood of forests and/or the uncommonly high number of *Corvidae*, for in this town I found a nest of the Hooded Crow *Corvus corone*, so far unfrequently inhabiting Polish towns, and such a high number of Magpies *Pica pica* as has never been noted in any other Polish town. On April 28, 1971 I found 36 occupied nests of Magpies against 17 Woodpigeons' nests in the study area of the town (about half its area).

Koszalin (pop. 65000). Urbanization stage III. According to the data presented by W. Górski (in litt.), in 1972 the Woodpigeon occurred in fairly large numbers in two old parks, abounding in limetrees and chestnuts and rather much frequented by people. In the park situated nearer the centre of the town there were 14 pairs in an area of 12.2 hec. and in the other one (a former cemetery) 20 pairs in 7.3 hec., thus the density being respectively 11.5 and 26.6 pairs per 10 hec. and so fairly high as for Polish towns. The Woodpigeon inhabits also the residential and villa districts of Koszalin (1.6—1.9 pairs per 10 hec.), not excluding the central part (0.7 pairs per 10 hes.).

It also occurs at Sławno (pop. 10000), where there are single pairs of this species in larger parks and in the whole seaside zone they live in little towns (Mielno, Łazy, Darłowo, etc.) 2—5 pairs in each (Górski, in litt.).

Poznań (pop. 470000). Urbanization stage I. The lack of an actually urbanized population in this town was greatly enigmatic. Breeding was noted only in peripheral wooded areas and sporadically in down-town parks, e. g. a pair in the Marcinkowski Park in 1920—1925 (Sokołowski, 1957), a rather shy pair in the Zoo (Mroczkiewicz, 1962) and in the Moniuszko Park (Graczyk and Bereszyński, 1974). It is only recently that an increase in number has been observed on the outskirts of the town, e. g. in the Maltański Klin Zieleni (Malta Green Area — Bednorz, 1970), Botanical Gardens (Anioła) and at Sołacz and Golęcin (Graczyk and Bereszyński, 1974). In 1972 the density found in the 10-hectare park of the Citadel was 2 pairs per 10 hec. (Z. Lewartowski). The highest density was observed in the Sołacki Park (12 hec.), situated on the outskirts of the town but fairly much frequented by people. On May 26, 1973 I recorded 8 breeding pairs (5 occupied nests) in it, the density being therefore 6.6 pairs per 10 hec. It is interesting that the first breeding

Woodpigeons were not seen in this park until 1965 despite close observations carried out before (GRACZYK and BERESZYŃSKI, 1974). It is worth mentioning that in 1973 in the Sołacki Park there were also 2 breeding pairs of Hooded Crows *Corvus cornix*, 1 pair of Jays *Garrulus glandarius* and 1 pair of Magpies *Pica pica*, i. e. the species which can effectively impede the growth of the population of Woodpigeons.

The foregoing data show that Woodpigeons colonize Poznań by degrees, from its periphery towards the centre.

The hundred-year retardation of the commencement of urbanization of the Woodpigeon at Poznań in comparison with not very distant Berlin and Wrocław deserves special consideration. The causes are certainly complex. The earlier appearance of breeding *Corvidae*, especially of the Hooded Crow, in this town may have had an inhibitory effect. This cause could however act only in the latest period. In the past the process may have been prevented by the small proportion of green areas and their young age, because Poznań was a Prussian stronghold up to the beginning of the twentieth century, and it is only in the last decades that the town included many wooded areas (KOŚCIELNY and STECKI, 1959; PTASZYCKA, 1950). The most important factor that caused the retardation of urbanization of the Woodpigeon, and also of the Blackbird (HAMMLING, 1933; PAX, 1917) seems to have been the situation of Poznań on the Warta, where it breaks through the unfertile morainic hills. The soils are clearly less fertile here than in the region of Legnica and Wrocław, which can be seen, if not from other things, from the dominance of pine forests and not forests of the *Querco-Carpinetum* type in the vicinity of the town. There are also more forests in the Poznań region (about 15% of the area) — than in the environs of Wrocław (5% — cf. Fig. 6).

For a long time, therefore, the low trophic value of the soils and at the same time the abundance of breeding sites were unable to produce the surplus of birds fit for reproduction, which would have exerted pressure on the non-colonized gap such as this town was within the breeding area. Now we should investigate the course of the colonization of the town: will the birds colonize it gradually, starting from the periphery (as indicated by the data from the past) or will pluckier specimens colonize the down-town parks rapidly at a certain moment? Another possibility, though little probable, is the origin of the population which colonizes Poznań from another town.

Gniezno (pop. 52000). Advanced stage II of urbanization. The density of the breeding population in this town is unexpectedly high in view of the conspicuous retardation of this process at Poznań, a considerably larger town and situated further to the west. On April 26 and May 25, 1973 I observed as many as 38 pairs of Woodpigeons in the Świerczewski Park (13.7 hec.), lying in the central part of the town (Fig. 2), and thus their density was at least 28 pairs per 10 hec. However, LĘGAS (in litt.), who made observations in this park sporadically, informed me that in 1972 the Woodpigeons were still more numerous and that there happened to be two nests occupied in one tree. The

census of 1973 gave a lower number because of the cold spring of that year, the effect of which I also noted on the materials from Legnica and Wrocław.

In addition, at Gniezno I saw single nests of Woodpigeons in other wooded areas of the town, e. g. outside the railway station, but not in the streets. As in the towns of Lower Silesia, at Gniezno the Woodpigeons are not very shy and forage in the neighbouring cultivated fields.

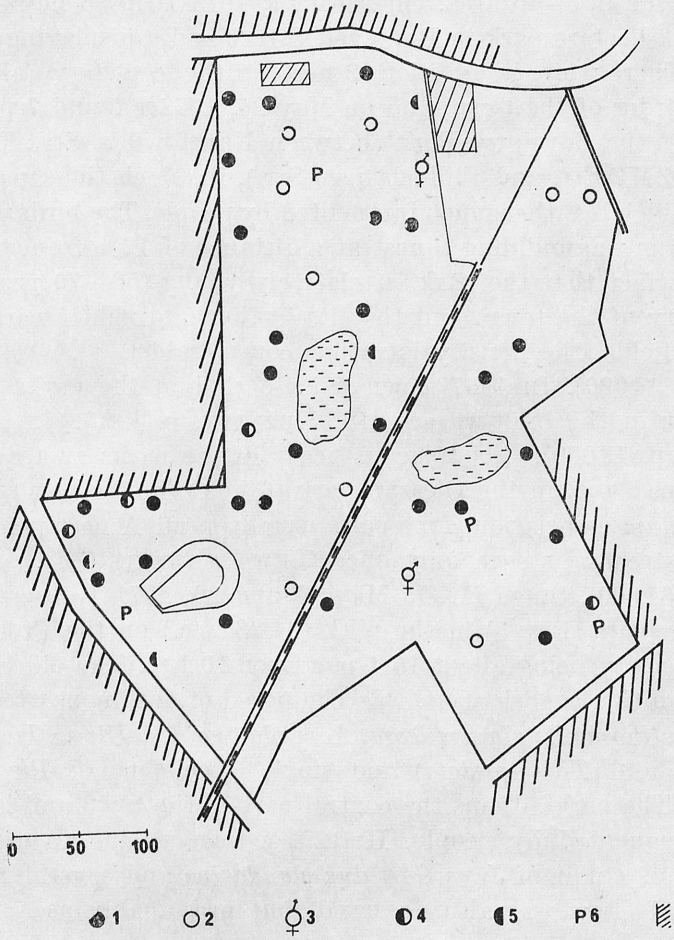

Fig. 2. Distribution of Woodpigeons and Collared Turtle Doves in the Świerczewski Park at Gniezno. Designations: 1 — nest of Woodpigeon occupied on May 25, 1973; 2 — nest of Woodpigeon occupied on April 26, 1973, destroyed later but the birds present in its vicinity; 3 — breeding pair of Woodpigeons (May 25, 1973); 4 — occupied nest of Collared Turtle Dove (May 25, 1973), 5 — a pair or a displaying male of Collared Turtle Dove (May 25, 1973); 6 — nest of Magpie; 7 — built up area

Several pairs of Magpies *Pica pica*, which may destroy Woodpigeons' nests, and a colony of 163 nests (and further 130 in the adjoining wooded area) of Rooks *Corvus frugilegus*, which may attract Woodpigeons, occur in the park under observation.

Mogilno (pop. 6000). The nesting of a small number of not very shy Woodpigeons was observed on May 24, 1973 (a nest near the railway station and another in the Krasicki Park, both placed close to the colonies of Rooks). The trees of this park are not suitable to hide nests in — they are mostly young and not very branchy poplars.

Inowrocław (pop. 55000). Early stage II. Woodpigeons occur still only sporadically within the built-up area. On April 27, 1973 I saw 3 nests of not very shy birds in a 3-hectare park in Roosevelt Street and a displaying bird in Mickiewicza Str. There were, in addition, 2 nests in the cemetery (about 10 hec) lying at the border of the town, and on May 25, 1973 I found 7 pairs in a 10-hectare area of the Zdrojowy Park (between Narutowicza Str., Przy Stawku Str., outlet of ZMP Str. and Wilkońskiego Str.), in which the sanatorium buildings lie and which is rather much frequented by people. The birds were not very shy and one pair was building a nest at a distance of 12 m from the observer. In view of the fact that the park is relatively young (50—70 years), situated in the periphery of the town, and that its farther and wilder parts neighbour on cultivated fields, the density is rather considerable.

Leszno (pop. 34000). In 1967 seven pairs nested in the parks of the town and other four in the built-up area (S. KUŹNIAK, in litt.).

Września (pop. 16000). Woodpigeons occur in the parks at a density of 6.5 pairs per 10 hec., e. g. in the Oleszyn park (6 hec.), in the nature of the thin *Querco-Carpinetum* association, four pairs usually nest. A nest placed in a tree growing in a street was seen only once (LEWARTOWSKI).

Kalisz (pop. 81000). Stage II. On May 25 and 26, 1971 I observed as many as 38 breeding pairs (Fig. 3) in the park (24.28 hec.) on the Prosna, founded in 1798, the density being about 16.4 pairs per 10 hec. The old stand of the park, laid out in the English style, was composed of deciduous tress, 25—35 m high (*Alnus glutinosa*, *Betula verrucosa*, *Acer platanoides*, *Ulmus laevis*, *Aesculus hippocastanum* and *Tilia cordata*) and single specimens of *Picea abies* and *Pinus strobus*. The park adjoins the central part of the town and is moderately numerously frequented by people. Here Woodpigeons' nests are exposed to destruction from a pair of Jays *Garrulus glandarius* and several Magpies *Pica pica*. A Hooded Crow was also observed, but presumably as a visiting bird only.

Three male Woodpigeons occur in the small cemetery (3.86 hec.) in Górnośląska Str., but there are none in the built-up area.

Opole (pop. 87000). Stage II. Woodpigeons do not, as yet, occur in small downtown wooded areas, but 10 pairs (8 nests) nest in the small cemetery (6 hec.) in Wrocławska Str., which till not long ago lay at the border of the town. All the 8 nests observed on April 27, 1972 were placed in conifers, like *Thuja* sp. and *Pinus strobus* or in the ivy *Hedera helix*, which is connected with the strong pressure exerted by nest destroyers in these, mostly deciduous trees, from where 3 pairs of Magpies, 1 pair of Jays and 1 pair of particularly formidable Hooded Crows have been recorded.

The density of Woodpigeons in the Nadodrzański Park is somewhat increased (4 pairs in an area of about 6 hec.).

Lublin (pop. 236000). Early stage II. Lying amidst a woodless and fertile loess region, Lublin, with its old park now surrounded by built-up areas, becomes an independent centre of urbanization of the Woodpigeon. As early

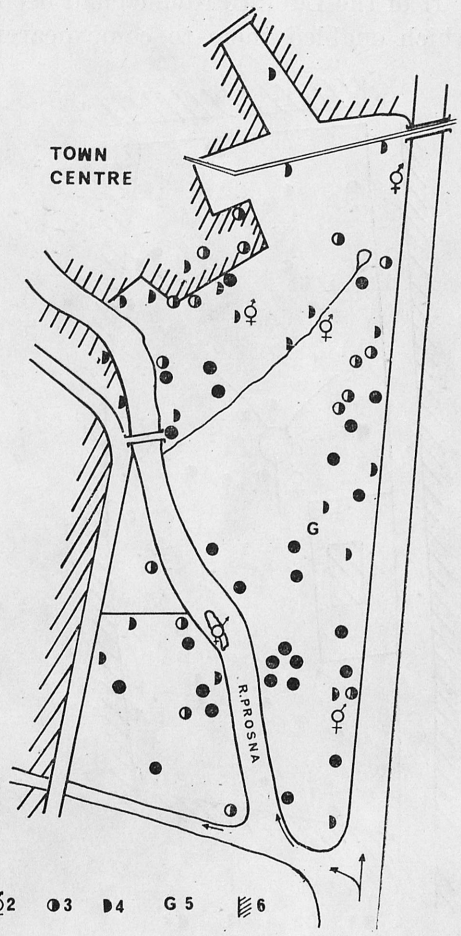

Fig. 3. Distribution of Woodpigeons and Collared Turtle Doves in the Municipal Park at Kalisz. Designations: 1 — nest of Woodpigeon; 2 — breeding pair of Woodpigeons; 3 — occupied nest of Collared Turtle Dove; 4 — a pair or a displaying male of Collared Turtle Dove; 5 — breeding pair of Jay; 6 — built up area

as the fifties of this century a few pairs nested in the periphery of the town (Riabinin, 1959). The park named Ogród Saski (14.5 hec.), lately cut off by an urban built-up tract, became a breeding site of fairly numerous Woodpigeons. On June 24, 1971 I found 9 breeding pairs in it, the density was therefore 6 pairs per 10 hec. (Fig. 4).

The observations made in the Lublin region as early as 1850—1860 showed that „in the areas poor in forests single pairs settle... in gardens and build their nests close to houses" (Taczanowski, 1882). In 1911—1914 Woodpigeons nested in large numbers in the park, situated among the fields, attached to

the Uher estate near Chełm (FUDAKOWSKI, 1933). In 1967 rather numerous nesting birds were observed in small gardens and in much frequented squares at Nałęczów (health resort) near Puławy (SZYMUSIK, in litt.). These birds, while building nests, let the observer take photographs at a distance of 12 m, which indicated that they had overcome their shyness to some extent. The foregoing fact suggest that for a long time the field population of the central part of the Lublin Province had been showing some changes in their behaviour, which enabled them to come nearer to man.

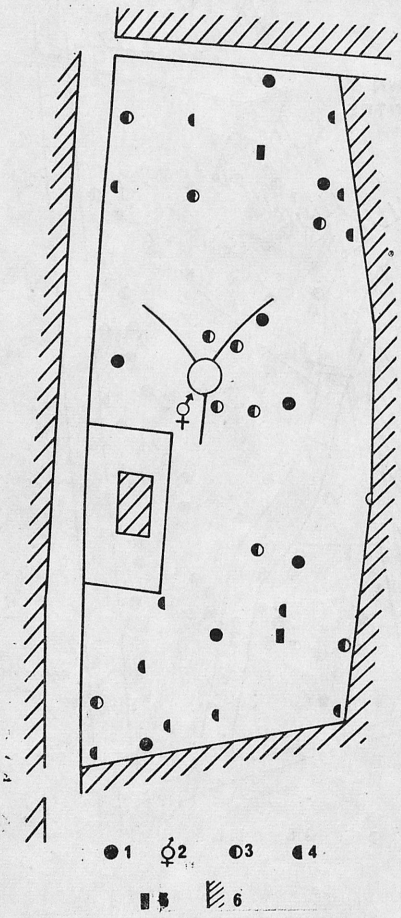

Fig. 4. Distribution of Woodpigeons, Turtle Doves and Collared Turtle Doves in the Saski Park at Lublin. Designations: 1 — nest of Woodpigeon; 2 — breeding pair of Woodpigeons; 3 — occupied nest of Collared Turtle Dove; 4 — a pair or a displaying male of Collared Turtle Dove; 5 — displaying pair of Turtle Doves; 6 — built up area

Other Polish Towns

In other Polish towns the nesting Woodpigeons, if there were any, were usually represented by single pairs inhabiting wooded areas in their poorly urbanized districts. In these cases we may not, as yet, speak about the existence of an urban population. The situation corresponds with stage I of the process discussed.

Olsztyn (pop. 94000). In this town 7—9 nests of Woodpigeons were found

in 1956—1957, 3—5 of them in the streets of the central part abounding in green areas. No increase in their number was observed until 1968 (Okulewicz, 1971). Until recently Olsztyn was a small town (45000) with very many wooded areas of the semi-forest type. The town is surrounded by forests and not very fertile cultivated fields. Presumably, this will not favour the progress of urbanization of the Woodpigeon. It should be added that the first records of single pairs of Woodpigeons in the Mazurian towns — Lidzbark Warmiński and Bartoszyce — come from the thirties of this century (Tischler, 1941).

Toruń (pop. 130000). Woodpigeons occurred here in small numbers in the peripheral parks of the town (2—6 pairs in an area of 24 hec.) and in 1953—1956 there was one pair in the centrally situated park in Rapacki Str. (Dubicka, 1957; Strawiński, 1963). At an inspection on April 27, 1973 I found no Woodpigeons in this park, more than ten hectares in area and now marked by heavy traffic in the streets that cross it. The situation of Toruń on river-side dunes, covered by dry pine forests in the past, and the fact that it is surrounded by forests (Fig. 6) do not favour the urbanization of the Woodpigeon.

Kutno (pop. 30000). On May 24, 1973 I noted one occupied nest in the Park Wiosny Ludów (17.85 hec.), lying at the border of the town and still of the semi-forest type with a relatively young oak stand (50—70 years). In this park there lived extremely numerous Collared Turtle Doves (about 70 males). The lack on an urbanized population of Woodpigeons in spite of the agricultural surroundings of Kutno needs an explanation. It may be supposed to be due to the nearly complete absence of old trees from the agricultural landscape, which made it impossible for the field population to develop and thus isolated the forest population from the town. The lack of old parks within the town area was also of essential importance.

Łódź (pop. 762000). Only single pairs of Woodpigeons occur in its peripheral parks, which in their nature resemble forests (Graczyk, 1962; Markowski, in litt.; author's own observations). The marked spatial isolation of the central parks of this city from fertile fields is probably responsible for this situation. Łódź borders upon poor pine forests, at least on the northern side, and large areas in the outskirts are occupied by orchards of dwarf trees unfit for nesting, allotments and suburbs. Łódź seems to have become too extensive before the suburban Woodpigeons had attained a suitable degree of preadaptation for town colonization.

Warsaw (pop. 1300000). Stage I. Signs of a slight increase in the number of Woodpigeons have recently been observed in Warsaw. Although as early as 1920 single nests were seen in the Rakowiecki Cemetery and before 1940 in the Łazienkowski Park, these were then peripheral wooded areas, weakly influenced by the town (Luniak, Kalbarczyk, Pawłowski, 1964). Now Woodpigeons nest in several large parks, e. g. 6—10 pairs in the Łazienkowski Park (73 hec. in area), but are still absent from centrally situated parks and gardens, e. g. the Saski Gardens (Kalbarczyk and Luniak, in litt.). The low density (up to 1 pair per 10 hec.) in the Łazienkowski Park coincides with the occurrence

of very many Hooded Crows (18 pairs) in it (KALBARCZYK, in litt.). The situation of Warsaw in poor sandy and even dune country does not favour the urbanization of Woodpigeons. To the north of the city there are extensive poor pine forests (Kampinoska Forest). More fertile soils occur only in the region of the Łazienkowski Park, which having been surrounded with urban buildings might become a centre of development of an urban population. The earlier colonization of the city by the Hooded Crow, which nests even in its centre, in E. Plater Str., may appear an important factor inhibiting the penetration of the Woodpigeon.

Kraków (pop. 585000). Here the Woodpigeon nested sporadically: in 1949 and 1966—1967 a pair in the Jordan Park, in 1951—1953 and 1961 a pair in the Botanical Gardens and in 1955 a pair in the Planty (wooded tract surrounding the town centre) — (FERENS, 1957; ŚMIAŁOWSKA, 1970; TOMEK, 1969). In KWIATEK'S (in litt.) opinion, a few Woodpigeons pairs nested in the Planty in the post-war period, from where they have recently with-drawn. In 1966 the number of Woodpigeons in the whole area of Kraków was estimated at 13—15 pairs (KULCZYCKI, in litt.).

Judging from the size of the town and its situation in a river valley, at the border of a fertile loess region, we may suppose that an urban population of this bird will develop in Kraków soon.

Rzeszów (pop. 82000). On June 23, 1972 I noted only one nest of the Woodpigeon, namely, in the old cemetery (3.9 hec.) on the River Wisłok, i. e. in group of trees neighbouring on the suburban environments. The lack of old parks and the great density of the Collared Turtle Dove in the town. e.,g. 25 pairs (17 nests) were counted in the Waryński Park (4.5 hec.), may have prevented its colonization by Woodpigeons, despite the agricultural character of its environs.

Czechoslovakia

So far no typical urban populations of the Woodpigeon have been reported from Czechoslovakia, only single pairs being recorded in the peripheral zones of some tows. However, the first nests in trees in streets were observed in two small places in Moravia: at Havlickuv Brod in 1952 and Dasice in 1956 (HLADIK et al., 1959). Also in Slovakia the Woodpigeon becomes more and more numerous and nests close to human habitations, especially in parks, e. g. at Zeliezovce (FERIANC, 1964).

Prague (pop. 1100000). The Woodpigeon does not nest in the city itself. Single pairs have been noted only in the outskirts (WAHL, 1944; BAUM, 1955; Hudec, in litt.). This is probably due to the hilly and not very fertile environs of the town.

Brno (pop. ca 350000). No urbanized population; only single pairs seen within the town area (HUDEC, in litt.).

Bratislava (pop. ca 300000). The Woodpigeon is a rare visitor and supposedly nests sporadically, e. g. in the Patrzalsky Park (RANDIK, in litt.).

Austria

Vienna (pop. 1700000). An urban population of the Woodpigeon existed here even before 1940 (BAUM, 1955). Now it is a very common bird (HUDEC, in litt.), even though sure enough not very numerous, as GOODWIN (oral information) failed to observe it during his visit in August. Vienna seems to be an independent centre of urbanization of the Woodpigeon, because none of the nearest big cities (Prague, Bratislava, Budapest, Belgrade, Salzburg and Munich) has an urban population of this species.

Hungary and Yugoslavia

Budapest (pop. above 2000000). Supposedly stage I of changes. Small numbers of Woodpigeons nest in peripheral parks. Several pairs occur also in parks on Margaret Island (SCHMIDT, in litt.).

Belgrade (pop. 745000). The Woodpigeon has not, as yet, been recorded from this town (VASIĆ, 1970).

Italy

Milan (pop. 1700000). The colonization of this town, situated in the most fertile region of Italy, by the Woodpigeon took place before 1886 (MOLTONI, 1953), when it had about 470000 inhabitants. This was undoubtedly an independent urbanization centre, very distant from other areas with the urban population. Woodpigeons occur also in other big towns of the fertile and almost woodless northern part of Italy, e. g. in Turin, Parma and also in Florence (ARRIGONI, 1929; TORNIELLI di CRESTVOLANT, 1965). The occurrence of Woodpigeons in Rome is not clear. It was mentioned by Arrigoni, but BLANCHET (1948) claimed that no nesting of Woodpigeons had been found in this city.

Spain

Madrid (pop. 3600000). As in other Spanish towns, there is no typical urban population in Madrid. However, in 1973 the nesting of 6—10 pairs of Woodpigeons was observed in the Retiro Park (about 130 hec.), situated near the town centre (PURROY, in litt.). The density of this population still corresponds with the original state of Woodpigeons in European forests.

Iraq

The centre of urbanization of the Woodpigeon in Iraq is completely separated from the European centres. The Woodpigeon is known to occur in the following Iraqi towns: Bagdad, Basra, Fao and Kazimain (ALLOUSE, 1953). It has not been observed in Teheran-Iran (SCHÜTZ, 1957; EICHLER, 1968), Bagdad (pop. 1800000). Woodpigeons inhabit mostly the border zones of this very extensive town, where however they are not rare at all (SCHÜTZ, 1957; EICHLER, 1968).

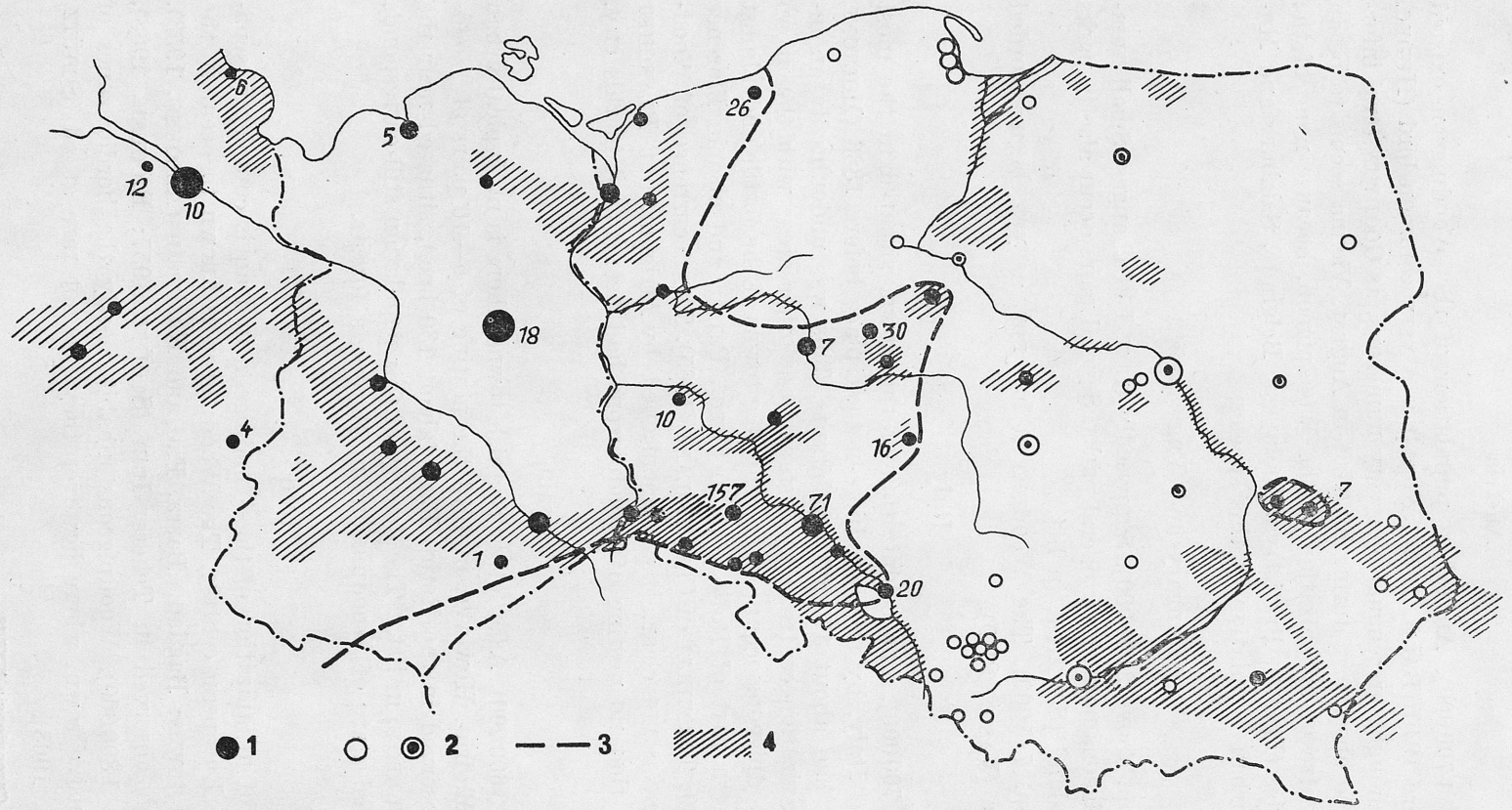

Fig. 5. Towns with or without Woodpigeon populations against the background of the distribution of fertile wheat-and-sugarbeet lands and barley lands (data acc. to Atlas świata, Warsaw, 1962). The figures represent the highest density of Woodpigeons in the town (in pairs per 10 hec.). Designations: 1 — towns with large population: 2 — towns with no or only single pairs of Wood-pigeons; 3 — range limit of urban populations; 4 — fertile wheat-and sugarbeet lands and barley lands

IV. LAWS OF EXPANSION OF THE URBAN POPULATION

In analysing the material presented above we can perceive several deviations in the process of urbanization of the Woodpigeon from the laws formulated for the analogous process of the Blackbird (cf. HEYDER, 1955, 1969). Characteristics of pioneer towns. A common characteristic of the towns in which the urban population of Woodpigeons developed first is usually their fairly considerable size and a great change in the surrounding landscape. Generally, such populations first arose in towns situated in early deforested fertile areas turned into cultivated fields (fig. 5). Both these factors—the magnitude of the town and the deforestation of its environs — notably favour the increase of the spatial isolation which loosens the contact between the forest population and the one colonizing the town. This is well exemplified by the history of colonization of both Paris and Wrocław, Milan and, recently, Kalisz or Lublin.

On the other hand, towns lying in more intensely wooded areas and/or on poor soils were colonized with a marked delay — evidently with difficulty. In such cases the factor of the trophic value of the environment acted together with the other inhibitory factors. The appearance of Woodpigeons in the towns of the Ruhr Basin may be an example, since these towns were colonized in 1936—1940, while Münster, situated in their neighbourhood but among fertile fields, was colonized as early as 1874 (PEITZMEIER, 1969). Similarly, the Woodpigeon is wanting in the greatest urban agglomeration in Poland, i. e. in the towns of Upper Silesia, like Gliwice (SZYMUSIK, in litt.), Katowice and Pyskowice (PROFUS, in litt.) and also in Bielsko-Biała (RAKOWSKI, 1965) and Częstochowa (MARKIEWICZ, 1969, author's own observations). These towns are mostly situated on very poor soils occupied by pine forests, which, in the form of a sometimes wide ring, separate them from agricultural regions.

This relationship is also perceptible, if the highest values of density of the Woodpigeon population in a given town are compared with the differentiation of towns in respect of their environs and geographic situations. A series of maps (Fig. 6) show that the highest values have been obtained from towns of western Poland and that these values decrease as we move to the east (comparison of maps in level). However, the differences between the nearby towns of the same order of magnitude but differing in the proportion of wooded areas and the fertility of soils in their neighbourhood are equally well seen (comparison of maps in vertical). The fourth pair of towns — Kalisz and Opole — needs a comment. In this case, exceptionally, the town surrounded by more forests, Opole, has also a slightly higher maximum density of the Woodpigeon population. This may be explained by different degrees of isolation of these two towns from the towns colonized earliest in the fertile Silesian Lowlands. Opole is not separated by an ecological barrier from Wrocław or Brzeg, which has also an urban population. On the other hand, Kalisz lies outside the intensely wooded (about 30% of area) regions of Trzebnica, Syców, Milicz and Ostrów Wielkopolski, which constitute the ecological barrier preventing

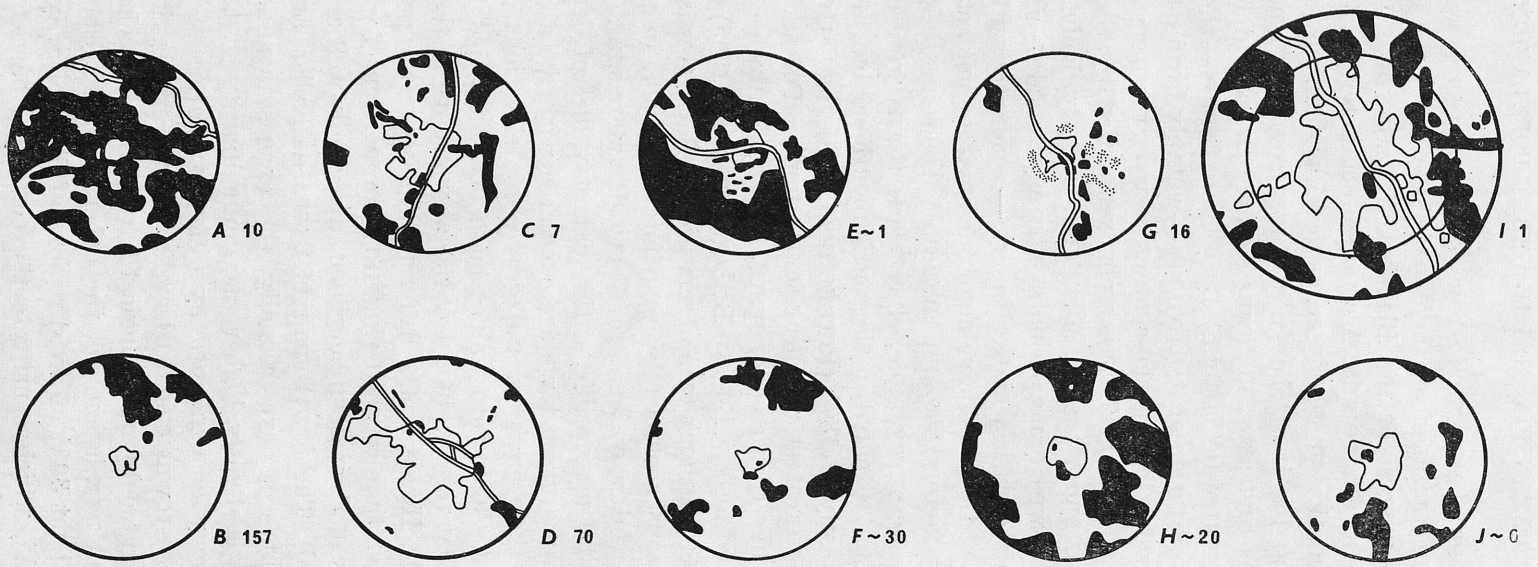

Fig. 6. Maps shoving the forest coverage (black patches) within a radius of 15 (20) km from the town centre. The figures given beside indicate the highest density of breeding Woodpigeons found in wooded areas of the given town. A — Zielona Góra, B — Legnica, C — Poznań, D — Wrocław, E — Toruń, F — Gniezno, G — Kalisz (additionally orchards marked by stippling), H — Opole, I — Warsaw, J — Lublin

this phenomenon from expanding. In addition, the soils in the Kalisz region are poorer (rye-potato soils) and to a large extent put under orchards of dwarf fruit-trees. Thus, this case does not deny the regularity discussed.

No relationship was found between the time of origin of the urban Blackbird population of a town and both the fertility of soils and the degree of deforestation of its region. However, there seems to be a number of particular facts that suggest that also in this case such a relationship plays some part. The nature of the town environs exerts an influence on the trophic conditions (at any rate, in the period when Blackbirds leave the central parts of towns after breeding — cf. ERZ, 1964) and also on the spatial isolation from the initial population.

Characteristics of the occurrence of the urban population. The Woodpigeon populations of most European towns are still migratory. In the towns of the German Democratic Republic, Denmark and Poland, in spite of their characteristic symptoms of advanced urbanization, these birds still form typical migratory populations. Moreover, even the populations of towns in Western Europe do not usually winter within these towns but move to the neighbouring agricultural areas, where they occur beside the forest specimens. Sometimes they return to the towns only for group roosting, in which they resemble the *Corvidae*. E. g., the breeding Woodpigeons in Paris, at least 1000 to 3000 pairs, nearly all leave this city in autumn to return in February. At most several tens of specimens winter in the town (LE TOQUIN, in litt.). In London, too, part of the population stay out of town in autumn and winter (GOODWIN, 1960). Even in Milan, the town situated in the zone of winter quarters of the Woodpigeons from North Europe, the possible competition with the northern migrants does not stop the town birds from spending the winter in flocks out of town (MOLTONI, 1953). Only in Holland, some areas of which are like one extensive town, the Woodpigeons forage chiefly in urbanized areas even in winter (DOUDE van TROOSTWIJK, in litt.).

Therefore, the earlier attainment of sedentariness is not a necessary condition of the origin of an urban population. In the Woodpigeon sedentariness is a rare result of urbanization, manifesting itself in very extensive European towns, and not its cause.

Directions of expansions.

The data presented in the text and in Fig. 1 show that during the first 70 years of the urbanization process of the Woodpigeon, this phenomenon expanded mostly to the east and even to the south-east. On the other hand, the spring migrations of the North-East-European populations, which winter in the Iberian Peninsula, southern France and northern Italy, have a north-eastern direction (RENDAHL, 1965; GOETHE and GOERTZ, 1968; LEBRETON, 1969). The divergency of these directions denies HEYDER'S (1955) hypothesis based on the material concerning the Blackbird (N. B. not quite evident even from this material) that the main direction of expansion of the urban population coincides with the route of its spring migrations. Thus, the role of the prolon-

gation of spring migrations (SVÄRDSON and DURANGO, 1951) in the phenomena of expansion of the urban population is not confirmed, which agrees with the qualifications made by NOWAK (1971).

The main direction of expansion of the urban Woodpigeon population is determined above all by the distribution of optimum environments, i. e. low-lying fertile woodless areas with numerous large towns. This regularity is well illustrated by Fig. 5, which shows the distribution of the towns with rather numerous Woodpigeon populations against the regions of wheat-sugar beet and barley crops in Poland. These regions have at the same time a forest coverage of less than 10 per cent.

It was not until the optimum environments had been colonized that the urban population began to form in less convenient areas, occupying higher regions of Europe, areas with more forests and those with fewer large towns.

This generalization agrees with MAYR's (1963) ecological rule, according to which the areas having the greatest density of optimum biotopes are colonized by a given species most rapidly. Thus, the expansion or formation of urban Woodpigeon populations in areas inhabited by this species for a long time is based on the same rule. Ecological expansion proceeds like geographical expansion.

Winter quarters and origin places of urbanization. It is rather generally accepted that the urbanization of birds started in Western Europe, because it is there that the winter quarters of North-East-European populations lie. This is thought to cause the congestion of birds and deficiency of food in winter, owing to which the birds are compelled to enter human settlements (STEINBACHER, 1942).

In the case of the Woodpigeon however the penetration of towns occurs in the breeding season and not in winter. Moreover, there is another fact that disagrees with the above opinion. The winter quarters both of the Woodpigeon (RENDAHL, 1965; GOETHE and GOERTZ, 1968) and of the Blackbird, Song Thrush and other *Turdinae* (ASHMOLE, 1962; GROMADZKI, 1964) lie chiefly in South-West Europe, where there are no urban Woodpigeons at all, and the beginnings of urbanization of the *Turdinae* were also observed elsewhere, either in England or on the southern coast of the North Sea.

The commencement of the urbanization process of birds was noted in the parts of Europe which show the greatest and oldest antropogenic changes in the landscape, i. e. those being most densely populated now. The very close contact of many English birds with man suggests that there we should seek the main focus of transformations. It should be kept in mind that Great Britain, especially England, was practically woodless in the eighteenth century and it was later that the project of reforestation was put in execution. In 1949 woodland constituted 5.8% of the area in England, 6.2% in Wales and 6.6% in Scotland (YAPP, 1962; WILLIAMSON, 1970). Similarly, the present forest coverage in France (20.7%) is a secondary situation. In the initial period of urbanization of the Woodpigeon, about 1850, the forest coverage of France

was hardly 16.8%, many areas, including the regions of Paris and Lille, being still poorer in forests (DORST, 1971). The same is true of many adjacent territories.

The observations of the migration routes of the Woodpigeon in France (LEBRETON, 1969) and the results of ringing (RENDAHL, 1965) indicate that birds belonging to very remote breeding populations have their winter quarters in common. The Central-European, Scandinavian and Russian birds all winter in the same areas and are exposed to the same winter conditions. Hence it follows that the differences that they show in the process of urbanization must result from differences occurring in the breeding areas.

Change in shyness. A decrease in shyness from man is one of the most important conditions of urbanization. However, in the Woodpigeon this decrease in shyness does not proceed in such a simple way as was suggested for the Blackbird. Anyway, it has not been proved even in the Blackbird that specimens which leave the centre of a town maintain the same low degree of shyness. In the Woodpigeon the situation is similar to that found in Mallards *Anas platyrhynchos*, which lose shyness in the central parts of towns and are very cautious whenever they fly out of town (LUNIAK, KALBARCZYK, PAWŁOWSKI, 1964; SOKOŁOWSKI, 1973). Woodpigeons which nest in the centres of towns are very tame. While foraging in park lawns, which is still a rare occurrence in the Polish towns, they can be approached at a distance of 10 and sometimes 5 m, and the brooding birds in their nests at a distance of 2 m. Foraging in fields out of town, the same birds behave almost like wild birds, being flushed when approached at a distance of 40—50 m (author's own repeated observations in the regions of Wrocław and Legnica.) Throughout their stay in a town for breeding (from the end of March till the beginning of October) adult birds fly to neighbouring fields everyday, whereas juveniles of the first brood leave the town forever as early as June and stay in large flocks in the fields. They are very shy, often notably shyer than are the adult birds. This is not only the result of their gregarious ways of life, since I observed the great shyness of juveniles immediately after their leaving the nest and mastering flight*.

The decrease in shyness from man is not a simple and mechanical reaction in Woodpigeons. It is distinctly differentiated according to the place in which the birds are staying at the moment. This is thus an acquired reaction (based on experience) and not a genetically coded one, which GRACZYK (1963) sug-

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* I noted repeatedly at Wrocław and Legnica that well flying young birds flushed from trees when approached at a distance of 20—30 m, while the adult birds were building nests, displaying or resting at a distance of 8—10 m. On May 27, 1973 in the park of the health resort of Inowrocław I observed adult birds building a new nest and picking twigs about 12 m away from me, while their young ones from the first brood (I had known this nest before), sitting at a height of about 15 m, began to be uneasy when I was at a distance of 20 m from the tree and finally flew over to the next tree. My observations are therefore inconsistent with the generally held opinion that young birds are less shy. As regards Woodpigeon, only ZHELNIN (1959) mentioned a concrete situation in which young birds were found to be less shy than adult ones.

gested on the basis of certain data concerning the Blackbird. This is not the simple natural selection of hereditarily less timid specimens, but rather the favouring of birds fit to learn different reactions to man in and out of town. There are many detailed observations, both published in literature and made by the author of this paper, which indicate that adult Woodpigeons learn to stay in the close neighbourhood of man and even choose this neighbourhood actively for their being less accessible to their natural enemies.

V. MECHANISM OF URBANIZATION

STEINBACHER'S (1942) interpretation of the course of colonization of towns by the Blackbird cannot be applied for the Woodpigeon, since it does not concern the winter season. In addition, it can be seen from numerous data, among others those concerning Polish towns, that the nesting of single pairs in towns is often only an unsuccessful trial for urbanization of the species. Such cases, preceding the origin of the proper urban population by several tens of years, are known from London, Poznań and Warsaw. Some conditions, other than the incidental appearance of the first breeding pairs in towns, must therefore be fulfilled.

The colonization of a town by Woodpigeons seems to be preceded by initial changes in the farmand population. These changes are their more and more frequent nesting in roadside trees, in parks situated close to human settlements and next in clumps of trees in villages and small towns marked by little traffic. Such symptoms were reported in the past (see the Section on the history of synanthropization and urbanization) and are noted now, e. g. in eastern Poland (TOMEK, 1973; KULCZYCKI, in litt.; author's own observations in the north-east of Poland), in Slovakia (FERIANC, 1964) and in the steppe areas of the Ukrainian S. S. R. (KISTIAKIVSKIY, 1957). Moreover, the observers suggest a certain rise in the numbers of Woodpigeons in these territories. Similarly, an increase in the number of specimens had been observed as regards Blackbirds (LIEBE, 1879, after HEYDER, 1955; KAYSER, 1920;) before the first signs of urbanization. This would confirm PEUS'S (1958) view that the colonization of new anthropogenic environments is induced by the overcrowded state of initial populations. Nowadays we already know many instances of the overcrowded state of populations inhabiting optimum environments, as evidenced by the occurrence of an excessive number of birds fit for reproduction but non-territorial, numerous evidences have been presented by BROWN (1969) and CARRICK (1972) for different bird species.

I think that the suburban Woodpigeon populations, too, are deficient in breeding sites for their members displaying territorial behaviour. This excess of birds is necessary for the frequency of their penetration into a town to reach a critical level. Furthermore, it is only when the population of a given town exceeds a certain „critical" number that the acceleration of transformations

is possible. The insufficient number of breeding sites around the town is usually caused by great anthropogenic changes followed by the reduction of wooded areas.

The question arises why Woodpigeons have not, as yet, colonized the towns situated in the practically woodless regions of Eastern Europe, e. g. the Lublin Province, where, as may be supposed from TACZANOWSKI'S (1882) and FUDAKOWSKI'S (1933) remarks, the insufficiency of breeding sites in the agricultural landscape has occurred for a long time. It seems that the conservatism of birds (MALCHEVSKIY, 1968), also termed „ecological inertia" (PEITZMEIER, 1942), should be taken into account in this interpretation. The colonization of a town demands from the birds to overcome many primitive reactions of the species. This is facilitated by the occurrence of intermediate situations, i. e. the intensification of the human penetration of environments inhabited by wild populations (forests, groups of trees among fields), however, this is not the case in the European regions that are characterized by a low density of human population. A similar role is played by another precondition, the presence of areas with threes in the given town, which areas, in their general nature, would resemble the environment inhabited by the birds originally, so that their reactions of settling down in them shall be triggered (cf. HILDEN, 1965). At the same time, only the parks that are well isolated spatially from more natural environments (chiefly by urban built-up areas and worse by treeless fields) make the later rapid increase in the number of birds possible, as this isolation limits the exchanges of specimens and hinders predators from getting to them. And so, e. g., Lublin, the parks of which were situated only in the outskirts of the town until not long ago, did not fulfil these conditions.

The farmland Woodpigeon populations inhabiting the forests in the vicinity of Moscow or Leningrad have still more distinct conservative characters, such as great shyness, a narrow range of tolerances shown in occupying breeding sites and a low number. These are typical characters of populations which constitute the periphery of the geographical range of a species and whose small intrapopulational variation is a well-known biological quality (MAYR, 1963). It is therefore evident that in those regions the Woodpigeon is one of the first birds to leave tree groups as they become engulfed and transformed by the growing town. Evidence of this is provided by BELAYEV (1937) and FLINT and KRIVOSHEYEVA (1962) as regards Moscow and BOZHKO (1957) for Leningrad.

Finally, an important part is played by the fertility of fields surrounding the town, which fertility, being the main attribute of optimum environments, attracts the birds and, as the breeding sites are insufficient in number (few tree groups), leads to the gathering of an excessive number of specimens fit for reproduction. Some of these birds may settle down in a nearby marginal environment such as the town is primarily, together with its noise and the presence of people. Thus, at the initial stage the penetration of birds into the town may be a forced process. As the time passes, after the birds have sur-

mounted their shyness, the urban environments sometimes appear to be optimum breeding sites. Since then the tendency for birds to stay and breed in towns has become a character favoured by natural selection.

Summing up, it may be stated that the urbanization of the Woodpigeon started in the quantitative centre of its range. The question that remains not quite explained is to what degree this centre is natural and to what degree it is secondary — a result of anthropogenic changes in the landscape of Western Europe.

The Distinctness of the Urban Population from the Non-urbanized Population — the Significance of Spatial Isolation

The main problem connected with the urbanization of birds is that of the distinctness (genetic) of urban populations from the neighbouring non-urbanized ones. Most authors are inclined to accept the thesis on the distinctness of these populations and usually assume that formation of the urban population of a species is a single act (HEYDER, 1955, 1969; ERZ, 1966; GRACZYK, 1959, 1963; LUNIAK, 1970; STRAWIŃSKI, 1971). These opinions were based on studies on the Blackbird *Turdus merula* and especially under the impression of the expansion of the range of its urban population, including more and more towns, which was believed to suggest the actual movement of these birds from town to town.

However, an analysis of the data concerning the Woodpigeon in this respect undermines this opinion. It seems that, at least in this species, the existence of constant though quantitatively limited exchange between the two populations, the urban and the nonurban, is very probable. This theory is supported by the following arguments:

a) The coincidence of the local abundance in the forest-field environment with that in the nearby town, as can be seen from the comparison of data in Tables I—III. Thus, the density of birds in groups of trees among fields in Western Europe and some regions of Central Europe (Silesian Lowland, Wielkopolska) is distinctly higher than the corresponding data for mid-field environments surrounding towns without urban populations. On the other hand, the lack of urban populations in the towns of the U. S. S. R. concurs with the small size of the natural population.

b) Woodpigeons do not spend all time within towns but fly out into cultivated fields, where they may come into contact with the birds which breed in forests and wooded areas. It is therefore possible that a bird that has lost its partner may mate with a specimen belonging to a different population. The movement of urban birds to the forest is particularly probable, whereas the birds living in the wild may be stopped from moving in the opposite direction by their fear of the town noise.

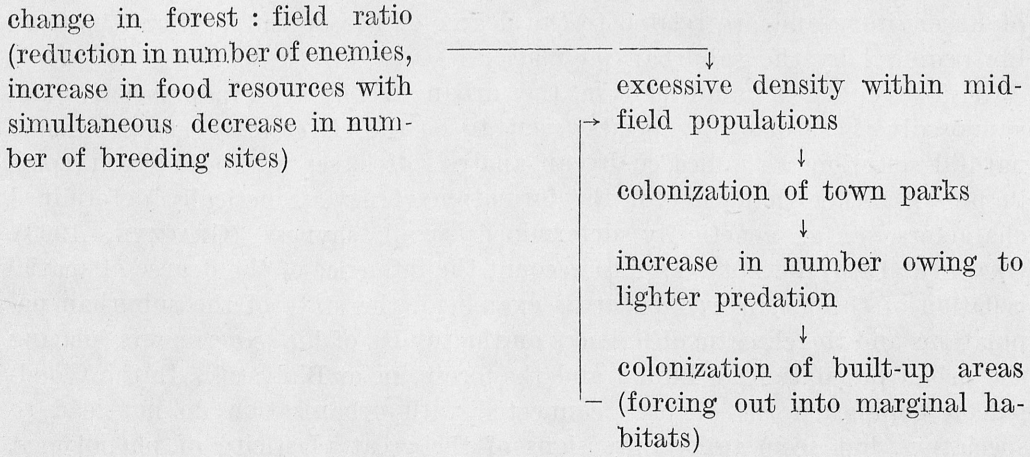
c) Soon after mastering flight, young Woodpigeons leave the town to spend autumn and winter in fields, where they may mix with the wild population. So far no differences in shyness have been observed between winter flocks and

so it may be supposed that both populations have common winter habits and that their members may form common flocks. The formation of mixed pairs is particularly probable (in the light of the calculus of probability) in the period when the urban population is in its initial stage and „dissolves" in the flocks of wild birds. This probably impedes the quantitative growth of the urban population in its initial stage.

d) The degree of spatial isolation between the two populations may be different in particular towns. The spatial isolation may be conditioned by two factors: the extensity of the town area and/or the width of the zone of fields separating the town from rather large forests. In both cases between the distinctly urbanized town population and the primary forest population there is usually a zone where both these populations mix and form a peripheral population of the town and/or a suburban population of the mid-field groups of trees. The size of this intermediate fraction is various. Sometimes it may be very large and in the landscape markedly changed by man, e. g. in England or Holland, it may nearly completely replace the forest population over large areas of the country.

In very big towns the very extensiveness of the built-up area becomes an increasing impediment in the contacts with non-urbanized population. This makes the inbreeding of the urban population more and more probable and leads to the fixation of the habits that are adaptations to the new habitat and after some time even to the fixation of some new genetic arrangements. A flow of genes seems however to persist owing to intermediate populations and the dispersal of juvenile specimens. As for now, the chances are against the interruption of this exchange of genes between the urban and forest populations.

Supposedly there is a constant or at least periodical interaction of the two populations. One may imagine the mutual stimulation of these populations by their growth in size induced by the man-made great transformation of the European landscape as a circular system:



The possibility of exchange between the urban and forest populations does not however mean that these are parts of the same local population (deme). In this case the degree of contacts and genetic exchange would probably be much more limited than it is between any other neighbouring demes. The distinction of two separate populations differing in a number of characters is here fully justified. Further studies of this question would demand the ringing of birds carried out on a wide scale to make it possible to prove the existence of exchange in both directions or in one direction beyond doubt and calculate its magnitude.

The existence of regular exchange between the urban and suburban populations of the Blackbird has been demonstrated by ERZ (1964), who has refuted the opinion that there are no contacts between them. My observations made at Wrocław and Legnica incline me to think that a high percentage of young Blackbirds leave the town area right after the breeding season and presumably fly away. The assumption that the urban population of the Blackbird is entirely sedentary in Poland is arbitrary, not supported by any sufficiently reliable facts.

e) There is a series of indirect evidences that the origin of the urban Woodpigeon population was not one single act. Now we know two very remote centres of urbanization of this bird, in Western and Central Europe and in Iraq, in which two subspecies are involved, *Columba palumbus palumbus* LINNAEUS, 1758 and *C. p. iranica* ZARUDNY, 1913. It may also be supposed that the urban population in so remote towns as Lublin and Vienna and, especially earlier, Paris, London, Milan and Wrocław arose independently of each other. Naturally, this does not exclude another possibility, namely, that many towns situated near each other and not separated by ecological barriers (extensive forests, mountains, areas in which there are no sufficiently large towns, etc.) have been colonized by the birds descending from the population which developed in only one of them. Surely, in such cases the differences in the time of appearance of the urban population in a given town are the resultant of the distance from the town already occupied, the size of the town and the nature of its environs and are related to the degree of the „preadaptation" to town life acquired by the suburban population.

f) The changes manifested in the urban Woodpigeon populations (and supposedly those of other species) seem to be the effect of the weakening of natural selection, as indicated by an analysis of losses in broods (TOMIAŁOJĆ, in press), rather than that of the formation of new, genetically determined characters, e. g. genetically determined small shyness (GRACZYK, 1963). GRACZYK (1963) did not take into account the influence of the degree of spatial isolation of the urban wooded areas examined, the state of the suburban populations and the climatic differences on the results of his experiments (placing the urban population at Lublin and the forest one at Białystok). In the Woodpigeon population the changes connected with urbanization do not lead to speciation, but seem to be only signs of the great plasticity of phenotypes,

especially as regards behaviour. STEINBACHER (1942) has already expressed a similar opinion on Blackbirds, emphasizing the role of individual experience and imitation of other birds in the modification of the behaviour of a specimen.

VI. RATE OF EXPANSION OF THE URBAN POPULATION

The only case in which the rate of expansion of an urban population in areas inhabited by the same species has been calculated is that of the Blackbird (HEYDER, 1955). The urban population of these birds shifted its eastern limits of occurrence by over 1000 km in a hundred years, averaging 10 km yearly. In the last decades this rate seems to have decreasing very clearly, as the population in question has entered the areas with a thick snow cover even in towns, which makes it difficult for the birds to find food.

As can be seen from the map (cf. Fig. 1), it is difficult to carry out an analogous calculation for the Woodpigeon, because the shape of the distribution area is greatly differentiated. During the first 70 years this population occupied (or arose in) a narrow tract from Paris to Wrocław, extending over about 1250 km. Assuming that the origin of this population occurred as a single act and only in Paris and that the corresponding stages with respect to size were attained in Paris in 1860 and at Wrocław in 1890, we obtain the rate of expansion of about 41 km per year and thus four times as fast as that of the Blackbird. The foregoing assumptions however seem to be poorly grounded all the more so because in the second period — better known — the rate was quite different. During the next 80 years (1890—1970) the eastern boundary moved only about 100—150 km, i. e. by 1.2—2 km yearly. In this case the set-back of the expansion is still more distinct than in the Blackbird.

More exact data are obtained by calculating the area of the region occupied by this population using a method like that applied by NOWAK (1971) for expanding species. The British Isles have been excluded from the present calculation because I had not at my disposal sufficiently detailed data concerning them in the past. During the first 70 years the towns that were occupied in the continent were scattered over an area of 220000 sq. km, i. e. it increased by 3140 sq. km per year. During the next 70 years the additional area occupied was 410000 sq. km, i. e. 5860 sq. km per year. The area occupied in the second period is twice as large as that of the first period. However, keeping in mind the fact that at that time the expansion proceeded in many direction unlike the one-direction expansion in the preceding period, we can easily find that the rate of expansion of this phenomenon was in fact reduced. This might be calculated using such units as the number of square kilometres of newly occupied areas per year falling to 100 km of the front-line, but this computation would provide no new elements.

It is worth while to compare the figures obtained now with the rates of

expansion of the species presented by NOWAK (1971) over new areas. In all the eight species discussed by him this rate was at least twice as high as in the urban Woodpigeon population. Its values range from 10000 sq. km per year in *Dendrocopos syriacus* to 77000 sq. km per year in *Streptopelia decaocto*. The value obtained for *Serinus serinus* was above 14000 sq. km per year. It should be emphasized that in their progress these species had to overcome, among other obstacles, the climatic barriers that separate the Mediterranean climate from the Central- and North-European one. The urban Woodpigeon population met with no such obstacles. Finally, it may be added that the mammals (except the notably sedentary wild rabbit) and nearly all insect species discussed by NOWAK (1971) showed still higher values than those given for the birds.

Against the background of the foregoing data the relatively very slow rate expansion of the urban population of the Woodpigeon is striking as for a species whose reproductive rate is nearly identical with that rate of *Streptopelia decaocto* and which nests in the same habitat, i. e. human settlements, whereas in the mobility of specimens this migratory and, as a rule, not sedentary species greatly exceeds *S. decaocto*. Its rate of expansion is about a twelfth of the value obtained for *S. decaocto*. As can be seen from the linear measurements of the rate of expansion, the urban population of the Blackbird is also somewhat more expansive than the urban Woodpigeon population.

The conclusion that may be drawn here is that the urban population of the Woodpigeon and, to a somewhat smaller degree, that of the Blackbird are not completely isolated from the suburban populations of these species. The territorial expansion of this first species is not a direct result of its reproduction occurring in town habitats, because then it would be at least as rapid as it is in *Streptopelia decaocto*, but is inhibited by the action of the populations surrounding the town. The expansion of the urban population of the Woodpigeon and, probably, that of the Blackbird express the changes occurring in the whole population of the species in the given geographical region.

VII. DENSITY OF THE WOODPIGEON POPULATION IN DIFFERENT HABITATS

Density is one of the basic criteria which permit the determination of the degree of changes in the state of an animal population. It has been shown that in the course of urbanization of the Blackbird in town habitats there was a tendency towards the manifold increase of the density of its population in relation to the values known for the initial populations. This increase is of the order of 2.5 times (TOMIAŁOJĆ, 1970), 4 times (HAVLIN, 1963), and even up to 16 (DYRCZ, 1963, 1969) and 22 times (CAMPBELL and SNOW, cit. after DYRCZ, 1963).

In the case of the Woodpigeon this phenomenon is much more complicated. It has not been analysed in detail hitherto and the materials presented in Tables 1—3 for the first time allow a fairly close analysis. Three types of environ-

Table I

Density of the Woodpigeon in European forests

Habitat	Region	Size of plot in ha	Density in pairs/10 ha	Author
1	2	3	4	5
A. Deciduous or mixed-deciduous forests				
Light oak-wood	Switzerland	?	**4—5**	Glutz (1962)
Different d. forests	„	?	1.0—2.0	„
Mixed f., mainly deciduous	Westfalen	34.2	**3.5—5.0**	Thiemann (1958)
Mixed-deciduous f.	Schleswig-Holstein	26.8	2.9	Puchstein (1962)
Beech-woods of different age	Brandenburg	?	0.6—2.3	Flössner (1964)
Beech a. alder woods	prov. Poznań	32+14	1.2—1.4	Bednorz, Bogucki (1964)
Oak-hornbeam wood with lime	n. Magdeburg	5.1—12	1.8—2.5	Ulrich (1970)
Oak-hornbeam f.	n. Frankfurt a. M.	25+18	1.2—1.5	Pfeifer, Keil (1958)
Oak-hornbeam f.		25.2	1.9	Niebuhr (1948)
Oak-hornbeam f. with beech	n. Haldensleben	10.8	1.8	Brennecke (1971)
Asch a. elm forest	n. Leipzig	80.75	1.5—1.6	Erdmann (1970)
Oak-hornbeam wood amidst meadows	prov. Poznań	28	**5.0**	Z. Lewartowski
Oak-hornbeam forest	„ „	30.4	2.0	„
Oak-hornbeam forest	„ „	400	0.6	„
Oak-hornbeam a. alder f.	n. Legnica	55.9	0.18	Tomiałojć (1974)
Oak-hornbeam f.	n. Wrocław	49.7	0.5—1.0	Tomiałojć, Profus (in print)
Oak-hornbeam f.	Slovakia	?	1.7	Turček (1951)
Deciduous f. (different method !)	Finland	140.7	0.14	Merikallio (1946)
B. Coniferous forests				
Pine a. mixed-pine f.	Lower Saxony	1822	1.47	Oelke (1968)
Old pine forest	n. Halberstadt	166	1.1	König (19.68
Pine a. oak-pine f.	n. Zerbst	16.8+22.5	0.4—0.6	Dornbusch (1971)
Spruce f. (65 years)	n. Worbis	10.57	2.8	Pomrehn (1972)
Pine a. pine-oak f.	prov. Poznań	400	0.15	Z. Lewartowski

Table I (cont.)

1	2	3	4	5
Pine-oak a. pine f.	n. Legnica	71.5	0.56	Tomiałojć (1974)
Spruce f.	Slowakia	?	0.35	Turček (1956)
Spruce-pine f.	Masuria	?	0.4	Steinfatt (after Tischler 1941)
Spruce-deciduous f.	Byelorussia	100	0.6	Fedyushin, Dolbik (1967)
Diff. types of coniferous forests	South Sweden	533	0.33	Karvik (1964)
Coniferous f.	Finland	231.2	0.04	Merikallio (1946)
Old (100—120 years) pine f. amongst young plantations	prov. Poznań	6.5	**6.0**	Z. Lewartowski
„ „ „	„ „	5	**14.0**	„

ments inhabited by the Woodpigeon in the breeding season have been assumed for working purposes: forests, mid-field groups of trees and towns.

Forests.

Wooded areas exceeding 10 hectares are included in this category. Parts of considerably larger forest complexes were usually investigated. In Europe the density of the breeding Woodpigeon population in deciduous forests and in mixed ones in which however deciduous trees prevail ranges between 0.18 and 5.0 pairs per 10 hec. (Table I), i. e. the highest value is 25 times as large as the lowest one. The low values were generally obtained in large study areas and the values approximating to the upper limit in small forests neighbouring upon fields. This is a classical example of the influence of „edge effect" and of the size of area on the result of measurement. No clear gradient of changes can be distinguished in the density of the European population, either in the north-south or the west-east direction. Very low values predominate only in the north of Scandinavia and in the U.S.S.R., which however may be connected with the nearness to the boundary of the breeding range marked out by any other factor than the nature of the biotope.

This variation is somewhat better seen in the material from coniferous forests, for which the data from north-eastern Europe are somewhat lower. The population density ranges from 0.1 to 2.8 pairs per 10 hec. in these forests. However the materials are still too poor to allow any far-reaching conclusion.

The values obtained in small (5 and 6.5 hec.) „islands" of *Pino-Quercetum* stand growing among extensive young stands and forest clearings are exceptional (Lewartowski, in litt.). The density of 6.0 and even 14.0 pairs per

10 hec. is unique and points to a very strong effect of the island-like position, and this seems to be made up of both the lack of breeding sites and the time-spatial isolation, which makes it difficult for the predators to come at the birds. These areas should therefore be considered together with the mid-field groups of trees.

Mid-field groups of trees

In order to avoid the divergencies resulting from the differentiation of wooded areas with respect to size, clusters of trees from 2 to 10 hec. in area are regarded as mid-field groups of trees. In some cases Table II gives the mean values from several small groups of trees.

The density of Woodpigeons in this habitat is greatly differentiated, from 0.5 to 279 pairs per 10 hec., the uncommonly high values (above 30 pairs per 10 hec.) being known only from eastern England and the north-western part of the German Lowland. In the other areas it rarely exceeds 5 pairs per 10 hec. This usually happens when the structure of the stand resembles a park rather than a forest and the very group of trees is situated near the houses of a village. As there are no data available from the U.S.S.R., the geographical variation of the density of this species in mid-field tree groups cannot be determined.

In exceptional cases in Poland the density of populations in mid-field groups of trees also reaches considerably higher values, e. g. in a pine grove, several hectares in area, situated among fields near Ostrów Wielkopolski in the Poznań Province, the number of breeding Woodpigeons was estimated at 40—50 pairs (WIATR, 1970) and thus the density would be about 100 pairs per 10 hec. In the grove there was an abandoned colony of Rooks, in which 12—15 and, in some years, up to 25 pairs of Kestrels *Falco tinnuculus* nested. Cases in which Woodpigeon colonies were found in aggregation of other species (*Corvus frugilegus*, *Falco tinnunculus*) were reported from the Poznań Province also by CZARNECKI (in litt.). I think that in these cases the Kestrels or Rooks played the same role as does the presence of people in towns, i. e. they protected the Woodpigeons' nests from enemies. From the biological point of view such cases should be analysed together with the material from urban habitats.

Town areas

Three degrees of intensity of the phenomenon have been distinguished within the category of towns: towns inhabited by Woodpigeons, including built-up areas, towns of which only parks are inhabited fairly numerously, and towns with still very small population of Woodpigeons, occurring chiefly in peripheral parks or those in poorly urbanized areas inside these towns.

Table III shows that the average values given for towns lie within the limits of the values met with in mid-field tree groups, 0.2 to 14.0 pairs per 10 hec. Considerably higher values were obtained only from parks and ceme-

Table II

Density of the Woodpigeon in mid-field wooded areas of Europe

Habitat	Region	Size of censussed plot in ha	Density in pairs/10 ha	Author
A. East Anglia				
Small copses in farmland	Cambridgesgeshire	total 15 and 24.6	93—100	MURTON (1965)
,,		?	279	COLQUHOUN (a. CRAMP, 1958)
B. European continent				
Mid-field woods	Westfalen	5.08	33.0	PEITZMEIER (1969)
,, ,, ,,	,,	total 50	6.8—10.0	,,
,, ,, ,,	,,	7.86	11.4	,,
,, ,, ,,	n. Dortmund	?	0.9—1.8	,,
,, ,, ,,	n. Köln	12.0	0.8	MILDENBERGER (1950)
,, ,, ,,	n. Magdeburg	11.3	4.4	HERDAM (1967)
,, ,, ,,	n. Lund	13.0	3.0—4.6	ENEMAR (1966)
,, ,, park	n. Poznań	10.8	2.0 (3.0)	CZARNECKI (1956)
,, ,, cemetery	,, ,,	4.2	2.3—7.1	,,
,, ,, parks	prov. Poznań	2—4	7.0—10.0	Z. LEWARTOWSKI
,, ,, ,,	,, ,,	7	3.5	
Suburban park amidst fields	n. Warszawa	15	1.3	TRUSZKOWSKI (1963)
Mid-field park	prov. Poznań	5	6.0—15.0	MICHOCKI (1967)
,, ,, ,,	n. Legnica	12.2	9.8	TOMIAŁOJĆ (1970)
,, ,, lime-wood	,, ,,	8.4	2.3	,,
Mid-field parks near villages	n. Wrocław	10+7	5.0—7.1	author
,, ,, woods (ash-elm with spruce)	,, ,,	6.8—3.0	2.9—4.8	,,
,, ,, wood (ash a. elm)	,, ,,	10	1.0	,,
C. Mosaic of fields and wooded areas "Knicklandschaft"	Schleswig-Holstein	80	1.1—1.7	HAHN (1966)
Farmland with 4% of wooded areas	n. Wrocław	1180	0.13—0.14	author

teries situated inside towns. In the peripheries of towns the density is usually much lower and rather smoothly passes into the value equal to those given for mid-fields groups of trees.

Table III

Density of the Woodpigeon in European towns

Town and kind of urban development	Size of censussed plot in ha	Density in pairs/10 ha	Author
1	2	3	4
London — Inner London	10.450	1.2—1.6	Cramp, Tomlins (1966)
— suburbs (Dollis Hill)	220	1.8	Simms (1962)
Basel — neighbourhood of ZOO	5	22.0—28.0	Glutz (1962)
Luxemburg — park in town			
— 1911	21.7	0.4	Schmitt (1964)
„ — 1961	21.7	5.0	„ „
Dortmund — city a. compactly built-up areas	72+168	0.2—0.4	Erz (1964)
— villa-quarters	33	3.0—4.0	„ „
— park in town centre	5.6	9.0—11.0	„ „
Oldenburg — city a. compactly built-up areas	750	av. 1.6	Prölss (1956)
Wilhelmshaven — whole town	3.500	0.47	Riese (1954)
— city	50	9.0	„ „
Stade n. Hamburg — whole town	241	1.4	Link (1958)
— old a. new built-up areas		1.1—2.1	„ „
— cemetery near the city	6	11.7	„ „
— other parks		2.6	„ „
Hamburg — city a. built-up areas	58+64	0.6—1.5	Mulsow (1968)
— villa quarters	12+45	4.0—5.0	„ „
— parks n. city	8+4.8	8.8—10.4	„ „
— peripheral park	22	2.2	„ „
Kiel — city a. built-up areas	32+214	0—0.8	Erz (1964)
— villa quarters	44	5.0—6.0	„ „
— park near city	8	5.0	„ „
Rostock — city a. built-up areas	975	0.26—0.27	Grempe (1967)
Rostock — cemeteries	37+24	3.5—5.0	Grempe (1967)
Göttingen — built-up areas	300	0.3—0.5	Heitkamp, Hinsch (1969)
— tree-belt around old town	15	4.0	„ „
— peripheral parks	total 38	3.2	„ „

Table III (cont.)

1	2	3	4
Berlin — built-up areas	?	8.7—13.9	Löschau, Lenz (1967)
— parks in the city	13+16	11.3—9.0	Lenz (1971)
— Zoo in the city	30	18.6	„ „
— Zoo on the periphery	180	0.8—2.7	Fischer (1963)
Karl-Marx-Stadt — built-up area	117	0.2	Saemann (1970)
— park n. city	9.2	1.1	„ „
— cemetery	39.2	0.7	Rinnhofer (1965)
Wrocław — built-up area	63	2.5—5.5	author
— park near the city	7	57.1—71.4	Tomiałojć, Profus (in print)
— part of larger park	17	15.9—22.3	„ „
— peripheral parks	24+25.5	2.9—4.7	author
Legnica — city a. built-up areas	112	8.7	Tomiałojć (1970)
— down town part of park	14	149.4—157.1	„ „
— another part of park	21	21.4—28.5	„ „
— peripheral parks	20+34	5.5—9.7	„ „
Thisted — park in town centre	6	c. 150	P. Hald-Mortensen
Towns and cities with Woodpigeons breeding only in parks			
Kopenhagen — park n. city	13	15.4	P. Hald-Mortensen
Malmö — park	40	5.0	Tenovuo (1967)
Koszalin — old parks	12.2+7.3	11.5—26.6	W. Górski
Poznań — park amidst villa quarters	12	6.6	author
— peripheral parks		0.5—3.0	J. Bednorz a. others
Gniezno — park n. city	13.7	27.0 (30)	author
Inowrocław — peripheral park	10	7.0	author
Kalisz — park n. city	24.3	16.4	„
Toruń — peripheral park	25	0.8—2.4	Strawiński (1963)
Warszawa — large urban park	73	1.0	W. Kalbarczyk (1959)
Radom — park n. city	7	1.4	L. Pomarnacki (1959)
Lublin — park n. city	14.5	6.0	author
Kraków — peripheral park	21	0.5	Tomek T. (1969)
Łańcut near Rzeszów — peripheral park	31	0.6—0.9	Kulczycki (1966)

Although the geographical variation of the density of urban populations is marked, yet it presents itself as a complicated phenomenon. In the towns of the western half of Europe it is conspicuously intenser than in Eastern Europe, where the Woodpigeon is usually absent from towns or occurs in single pairs. It is however striking that nearly all towns with high values (above 20 pairs per 10 hec.) lie in a relatively newly occupied zone situated close to the boundary of the range of the urban population (e. g. Thisted, Koszalin, Gniezno, Wrocław, Legnica and Basel). The high values in these towns are not correlated with their size, but seem to result from their different food resources and security against natural enemies. The presence of urbanized Hooded Crows *Corvus corone* in a great many western towns and their absence from many eastern towns seem to be here of great importance. This would therefore be an example of the temporary liberation of Woodpigeons from the pressure of predators. An attempt made to demonstrate in detail the influence of predation on the Woodpigeon population is presented in another paper (Tomiałojć, in press).

As regards the high densities of Woodpigeons in some towns and in places in the farmland of East Anglia (Murton, 1965), we may speak about nesting colonies. Their values, of the order of 150 or 280 pairs per 10 hec., approximate to other extreme values, those of the extinct Passenger-Pigeon *Ectopistes migratorius*. E. g., in 1871 a colony of this bird was estimated at 136 000 000 specimens inhabiting an area of 2200 sq. km, which averages about 300 pairs per 10 hec. (Schorger, 1955). This example illustrates the limits of possibility, which a Woodpigeon population might approach, if man destroyed its natural enemies, and this has almost been accomplished in East Anglia, where the following species are lacking: *Martes* sp., *Accipiter gentilis*, *Falco peregrinus*, *Bubo bubo*, *Corvus corone*, etc. The uncommonly high densities of Woodpigeons in some towns of Europe and in the farmland of England seem to have the common cause — the lack of its main natural enemies.

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STRESZCZENIE

Obok innych gołębi, grzywacz odznacza się silną tendencją do zasiedlania miast, wykazując przy tym szereg odmienności od innego modelowego pod względem poznania gatunku — od kosa. W tej pracy zostały zestawione dane literaturowe oraz uzyskane korespondencyjnie lub też zebrane osobiście, celem odtworzenia przebiegu i obecnego zasięgu urbanizowania się grzywacza. Dla ułatwienia porównań wyróżniono cztery stadia narastania zmian w urbanizującej się populacji. Wyniki przedstawiono w postaci mapy (Fig. 1), która wymaga uzupełnienia informacją, że inne samodzielne centrum urbanizowania się tego ptaka wykryto w Iraku w Bagdadzie, dotyczące zresztą odrębnego podgatunku *C. p. iranica* Zarudny. Najwcześniejsze dane o silnie zurbanizowanym grzywaczu pochodzą z lat 1830—1840 z Paryża (Gloger 1834, Tyzenhauz

1843—1846). Bardzo szybko zjawisko to zostało odnotowane także w miastach Holandii, w Berlinie, Halle, Lipsku i Wrocławiu. Do r. 1900 zostały opanowane miasta wielkich obszarów niżowych odlesionej i gęsto zaludnionej części północno-zachodniej i środkowej Europy, a w ciągu następnych 70 lat — także obszary mniej odpowiednie — silniej zalesione, pagórkowate, o uboższych glebach i z rzadko rozmieszczonymi miastami.

Przedstawiono także szczegółową charakterystykę i dane liczbowe dla miast leżących w strefie przy granicy obecnego zasięgu populacji. Dane te, ilustrowane przykładami rozmieszczenia grzywacza w parkach śródmiejskich Gniezna, Kalisza i Lublina (Fig. 2—4) umożliwią w przyszłości ścisłe zarejestrowanie dalszego przebiegu zjawiska.

Analizując reguły ekspansji nowej populacji zachodzącej w obrębie areału już zajmowanego przez gatunek wykazano, że przebiega ona zgodnie z regułami ekspansji całych gatunków na nowe tereny (por. Mayr 1963, Nowak 1971), tj. najszybciej tam, gdzie są skupienia optymalnych biotopów. Wykazano, że początek urbanizowania się odnotowano w najdawniej i najsilniej zmienionych częściach północno-zachodniej Europy, a nie wiąże się ono z położeniem głównych europejskich zimowisk, ani też proces ten nie przebiegał szybciej w kierunku zgodnym z kierunkiem wiosennej wędrówki gatunku. W odróżnieniu od kosa, populacje miejskie grzywacza nie wykazują skłonności do osiadłości, pozostają populacjami wędrownymi albo koczującymi.

Przeanalizowanie zmian w płochliwości grzywaczy, które codziennie wylatują za miasto po pokarm, a także całą jesień i zimę (ptaki dorosłe) oraz lato (ptaki młode z pierwszego lęgu) spędzają poza miastem, wskazuje, że nie występuje tu genetycznie zakodowana niska płochliwość (por. Graczyk 1963), lecz jedynie duża zdolność uczenia się różnego reagowania na obecność człowieka w zależności od miejsca aktualnego pobytu.

Mechanizm urbanizowania się grzywacza zdaje się polegać na powstawaniu przegęszczenia w śródpolnych środowiskach otaczających miasta, co szybciej następuje w terenach silniej odlesionych (mało wrogów naturalnych, mało miejsc lęgowych) i o wysokiej troficzności (rozległe, żyzne pola) przyciągającej ptaki (Fig. 5 i 6). Dodatkowym i zwykle późniejszym powodem wnikania do miast może być naśladownictwo innych osobników, które swą liczebnością i zachowaniem mogą wskazywać bezpieczne miejsca lęgowe, leżące w obrębie miast.

Przenoszenie się ptaków miejskich z miasta do miasta prawdopodobnie zachodzi regularnie tylko w przypadku bliskiego sąsiedztwa tychże. Nie wyklucza się, że i w niektórych innych przypadkach początek (przykład) dają osobniki przybyłe z innych miast. Lecz proces trwałego zasiedlania bywa pomyślny jedynie wtedy, kiedy populacja podmiejska dysponuje już nadmiarem populacyjnym preadaptowanym do zasiedlania miasta.

Zwrócono uwagę na rolę różnego stopnia izolacji przestrzennej populacji mielskiej od wyjściowej-leśnej w poszczególnych miastach (Fig. 5) oraz na prawdopodobne istnienie ograniczonej lecz stałej wymiany osobników między

obu populacjami. Brak zatem jeszcze przerwy, która mogłaby prowadzić do zainicjowania procesów mikroewolucyjnych.

Zestawione dane sugerują, że populacja miejska grzywacza w Europie nie jest tworem jednorazowego aktu jej powstania na zachodzie. Fakt istnienia ekspansji terytorialnej zdaje się być wynikiem ogólnych zmian w liczebności tego gatunku, osiągającego w Zachodniej Europie stan przegęszczenia (m. in. wskutek małej liczby wrogów naturalnych), który następnie „rozlewa się" na coraz dalsze obszary kontynentu, pociągając za sobą także ekspansję ekologiczną do miast.

Zestawienie danych o gęstości populacji (Tab. I—III) wykazuje, że we wszystkich trzech typach środowisk, tj. w lasach, zadrzewieniach śródpolnych i miastach, zauważa się na ogół wyższe wartości podawane dla zachodu niż dla wschodu Europy. Zaburzenie tej prawidłowości widoczne w miastach, gdzie najwyższe wartości pochodzą z centrum kontynentu (Dania, Polska), wydaje się być wynikiem wtórnego obniżenia zagęszczenia w miastach zachodnich, wskutek zasiedlenia ich przez niektóre drapieżniki, a zwłaszcza przez wronę. Szczegółowemu udokumentowaniu doniosłości presji drapieżnictwa na populację grzywacza będzie poświęcona oddzielna praca (Tomiałojć, w druku).

РЕЗЮМЕ

Рядом с другими голубями вяхирь проявляет сильную тенденцию к заселению городов, обнаруживая при этом ряд разновидностей от другого модельного, с точки зрения изучения вида — чёрного дрозда. В настоящей работе использовано данные из литературы, а также полученные на основании корреспонденции или собранные автором с целью отображения городского ареала вяхиря. Для облегчения сравнения выделено четыре стадии нарастания изменений урбанизирующейся популяции. Результаты представлено в виде карты (фиг. 1), которую следует дополнить информацией, что другой, самостоятельный центр урбанизации этой птицы обнаружено в Ираке, в Багдаде, касающийся отдельного подвида *C. p. iranica* Zarudny. Самые ранние данные по сильно урбанизованному вяхирю известны с 1830—1840 гг. из Парижа (Gloger 1834, Tyzenhauz 1843—1846). Это явление очень быстро было отмечено также в городах Голландии, в Берлине, Гале, Лейпциге и Вроцлаве. До 1900 г. были заселены города больших низменных, обезлесенных и плотно заселённых частей северно-западной и средней Европы, а в течение следующих 70 лет — также территории менее соответствующие, холмистые, с бедными почвами и редко распространёнными городами.

Представлено также подробную характеристику и количественные данные для городов лежащих в зоне у границы настоящего ареала городской популяции. Эти данные, иллюстрированы примерами распространения вяхиря в городских парках

Гнезна, Калиша и Люблина (фиг. 2—4) сделают в будущем возможным точную регистрацию хода этого явления.

Анализируя правила экспансии новой популяции в районе ареала уже занимаемого видом, доказано, что она проходит согласно с правилами экспансии целых видов на новые местности (ср. MAYR 1963; NOWAK, 1971), то есть вначале там, где имеются скопления оптимальных биотопов. Доказано, что начало урбанизации отмечено в наиболее сильно и давно изменённых частях северно-западной Европы и оно не связано с расположением главных европейских мест зимовки. Этот процесс не проходил быстрее в направлении весенней миграции вида. В отличии от чёрного дрозда, городские популяции вяхиря не проявляют склонности к оседлости; остаются миграционными или кочующими популяциями.

Анализ изменений пугливости вяхиря, который ежедневно вылетает за город питаться, а также всю осень и зиму (взрослые птицы) и лето (молодые птицы первого выводка) проводят за городом, указывает, что здесь не отмечается генетически закодированной низкой пугливости (ср. GRACZYK 1963), а лишь большая способность обучения различного реагирования на присутствие человека в зависимости от места актуального пребывания.

Механизм урбанизации вяхиря кажется состоит на образовании перенаселённости в межпольных средах, окружающих города, что происходит быстрее в обезлесенных местах (мало естественных врагов, мало выводковых мест) и с высокой трофичностью (просторные, урожайные поля) привлекающей птицы (фиг. 5 и 6). Добавочной и дальнейшей причиной проникновения в города, может быть подражание другим экземплярам, которые своей численностью и поведением могут указывать на безопасные гнездовия, лежащие в районе городов.

Кочевание птиц из города в город вероятно происходит регулярно лишь в том случае, когда города расположены на небольшом расстоянии друг от друга. Не исключена возможность, что в некоторых других случаях начало (пример) дают особи из других городов. Процесс постоянного заселения является удачным лишь тогда, когда пригородная популяция располагает популяционным излишеством заранее адаптированным к заселению города.

Обращено внимание на роль различной степени пространственной изоляции городской популяции от исходной-лесной в отдельных городах (фиг. 5), а также на вероятное существование ограниченного, но постоянного обмена между двумя популяциями. Отсутствует ещё перерыв, который мог бы привести к началу микроэволюционных процессов.

Сопоставленные данные подсказывают, что городская популяция вяхиря в Европе не является образованием разового акта её создания на западе. Факт существования территориальной экспансии кажется следствием общих изменений в численности этого вида, достигающего в Западной Европе состояния перенаселения (м. пр. в результате малого количества естественных врагов), которое затем „разливается" на дальнейшие пространства континента, вызывая также экологическую экспансию в города.

Составление данных по плотности популяции (табл. 1—3) показывает, что у всех трёх типов сред, т.е. в лесах, межпольных насаждениях и городах, наблюдаются

более высокие данные на западе чем на востоке. Нарушение этого правила наблюдаемое в городах, где самые высокие данные имеются в центральной части континента (Дания, Польша), является, вероятно, результатом вторичного понижения плотности в городах запада, в результате заселения их некоторыми хищными, а особенно вороной. Подробное обоснование влияния хищничества на популяцию вяхиря будет рассмотрено в отдельной работе (TOMIAŁOJĆ, в печати).

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