

<b>EKOLOGIA POLSKA</b> (Ekol. pol.)	<b>23</b>	<b>2</b>	<b>231–263</b>	<b>1975</b>
--	-----------	----------	----------------	-------------

Zbigniew GŁOWACIŃSKI

Nature Conservation Research Centre, Polish Academy of Sciences, Cracow

## SUCCESSION OF BIRD COMMUNITIES IN THE NIEPOŁOMICE FOREST (SOUTHERN POLAND)

**ABSTRACT:** Structural changes in avifauna in the succession from an old river bed to a climax oak-hornbeam forest (series A) are expressed in the progression of the number of species ( $N$ ) and their density ( $D$ ), and in the increasing and later fairly uniform course of species diversity ( $H'$ ). Under the study conditions the climax ending successional series of deciduous forests (series A) and coniferous forests (series B) may be the oak-pine forest stage. The bird community formed there reaches its highest organization ( $H''$ ). The succession of birds in a clearing differs from Margalef's (1968) theoretical model of succession, and passes through two phases. The ecotone exerts an effect on the bird community in the transition between these phases. In the succession in the clearing the climax community exhibits a rather slight decrease in  $H'$  and greater annual fluctuation in value  $D$  than is the case in the preclimax community. This is due to the spatial development of the habitat. The change in the organization of bird communities takes place abruptly in transition from a habitat with a single layer of vegetation into 2- and 3-layer vegetation.

### C o n t e n t s

1. Introduction
2. Methods
3. Primary succession
  - 3.1. Genetic connections of habitats, successional stages
  - 3.2. Results
  - 3.3. Discussion
4. Secondary succession of birds in an oak-hornbeam habitat
  - 4.1. Development stages of the forest
  - 4.2. Results
  - 4.3. Discussion
5. Final remarks
6. Appendix— list of full scientific names of the bird species examined
7. Summary
8. Polish summary (Streszczenie)
9. References

## 1. INTRODUCTION

Ecological succession, as a basic biocenotic problem, is a real and generally accepted concept, but one which is also a very controversial from many aspects (K a š k a r o v 1938, A l l e e et al. 1949, O d u m 1959, R a j s k i 1965, Z a r z y c k i 1966). Regardless of the way in which it is defined, it expresses the order in which certain plant associations and animal communities follow upon others – in a normal sere<sup>1</sup> from the pioneer (initial) stage to the so-called climax, that is, the state of complete maturity and relative stabilization of the ecosystem. O d u m (1963) accepts that ecological succession (1) is an ordered process of directional and thus of foreseeable changes in the biocenose, (2) that it takes place as a consequence of the physical habitat being modified by the biocenose, (3) that it attains a peak with the formation of an ecosystem as stable as is biologically possible under the given conditions.

Succession is usually considered on the plane of organization of biocenoses and energy flow through them, that is, the so-called metabolism of biocenoses. During its course it is possible to observe a large number of regularities, but their description and interpretation is based to a great extent on theoretical speculations. O d u m (1963) emphasises the four most evident phenomena accompanying succession:

1. continual exchange of taxa, leading to taxa which, although of considerable importance in the initial stages, become unimportant in the climax stage;
2. increase in species diversity as the succession progresses, at least in its initial stages;
3. increase over the course of succession of the amount of total biomass in the ecosystem;
4. decrease in net production and corresponding increase in the respiration of the biocenose, also expressed in the ratio of gross production ( $P$ ) to total respiration ( $R$ ) of the biocenose ( $P/R$ ) approaching 1 as succession progresses.

Further important trends can be mentioned here, after M a r g a l e f (1968):

5. increase in the stratification of the ecosystem as succession progresses;
6. increase in stability of the ecosystem (communities) from the early stages to the climax, where populations would be subject to relatively the least fluctuations.

It is necessary to emphasise here the formation during the course of succession of species diversity of communities (biocenoses). M a r g a l e f (1968) accepts that species diversity is to a certain degree a measure of the biocenose organization. Increase in the diversity index in a successional sere therefore suggests increase in organization of communities as succession proceeds. According to that author the ecosystem – as development proceeds – accumulates an increasing amount of information, although its capacity for cumulating new information decreases considerably in the later stages of succession. This gradual complication of the ecosystem is connected with the stratification taking place in it, with increase in ecological niches, extension of the food chain and stricter specialization of species. According to O d u m (1963) this means that during succession the number of possible relations increases between species, individuals and substances.

The question of biocenose stability is closely connected with species diversity. It is most often accepted (L o u c k s 1970) that those biocenotic units which exhibit greater diversity should be characterized by greater stability. This follows from the assumption that the greater the gene pool of the community (biocenose), the greater its adaptation potential (O d u m 1963).

Ecological succession may be of a primary or secondary character. The former applies if this

<sup>1</sup>The whole series of communities is called the sere after O d u m (1959).

process takes place in areas previously unoccupied and, in a certain sense, not prepared by another biocenose, e.g., on sand dunes exposed by a retreating lake (Shelford 1913; after Odum 1959), on the forelands of glaciers (Janetschek 1949), volcanic areas (Dammerman 1948; after Rajs ki 1965), fresh landslides, etc. Primary succession usually takes place very slowly, so that it can be more easily envisaged as taking place than be traced. We have to do with secondary succession when it occurs on an area previously occupied by another developed biocenose, e.g., on deserted cultivated field (Johnson 1945, Johnston and Odum 1956), in clear-cut or burnt woodland (for inst. Morley 1940, Pospelov 1957, Grodziński 1959, Neronov 1962, Haapanen 1965, Kratochvil and Gaisler 1967, Giller 1969, Ferry and Frochot 1970, Gashwiler 1970), meadows (Turček 1957), etc. Secondary succession takes place far more rapidly than primary succession, this being particularly evident in its initial phase.

Birds are a fairly passive element in the succession of ecosystems, but their participation in formation of biocenose cannot be regarded as entirely unimportant. They are, in general, animals distinguished by wide ecological tolerance, but during the breeding season their attachment to given habitats is often strongly marked (Lack and VENABLES 1939, Wasiłowski 1961). Birds — most dependent on vegetation — form as a result seres differing in formation, accompanying plant successions. In the case of forest succession these variations in the avifauna in successive stages are particularly easy to grasp. With age the forest is subject to gradual development in a vertical direction, new forest layers are created with new habitat variants which birds can make use of over an exceptionally wide range. It is to be expected that among vertebrates birds form the best test for evaluating forest succession.

As from the pioneer studies by H. C. Cowles, V. E. Shelford and F. E. Clements (after Allee et al. 1949, Rajs ki 1965) the question of succession has very frequently been considered, most often in botanical studies, but even today many of the opinions held on this phenomenon continue to be hypothetical in character. A large number of publications (inter alia, Morley 1940, Dierschke 1951, Lack and Lack 1951, Strautman 1954, Rabeler 1955, Yapp 1955, Johnston and Odum 1956, Kerzina 1956, Pospelov 1957, Turček 1957, Martin 1960, Haapanen 1965, Pikula 1967, Salo 1967, Karr 1968, Giller 1969, Ferry and Frochot 1970, Dyrce et al. 1972, Jones 1972) has appeared on the subject of bird succession, but the majority of such studies are very limited in scope on account of certain shortcomings, for instance a frequent deficiency is that their authors, in describing a succession in clear-cut or burnt tree stands, chose too small a number (3, more rarely 4) of transitional stages, and in addition these stages come within too wide a framework of habitat variation. Objection can also be made to arranging stages examined in different regions and not in the same season in successional seres.

The studies made up to the present deal with a succession from the point of view of the number of species and number of individuals. A study has been encountered (Karr 1968) in which species diversity has been taken as a criterion of succession. Some authors (Haapanen 1965, Ferry and Frochot 1970, Frochot 1971) traced the participation over the course of succession of bird species from the aspects of phenology, biomass, feeding and nesting ecology. An important and as yet unsolved problem is the formation during succession of the stability of communities.

Research on succession supplies a large number of data for theoretical consideration. It is possible to foresee, on the basis of the course taken by succession, certain practical consequences, particularly with regard to nature conservation. It is also possible to forecast and control bird communities in given types of habitat. Using the course of succession as a basis, it

is easy to indicate the places in which the avifauna attains maxima of information, species or biomass. A schema of succession gives a good guide as to where and which ecological groups disappear and where their greatest participation occurs, and also provides an excellent indication of the habitat preferences of species.

The purpose of this study is (1) to describe and interpret the formations of the basic structural characters of bird communities during the course of successions leading from the old river bed and freshly clear-cut woodland to climax forests, (2) definition in the successional seres examined of the positions of climax communities, in particular of their organization, (3) definition of the ecological groups of birds accompanying the succession of ecosystems.

## 2. METHODS

The succession was elaborated by the "comparative" method, consisting in analysis and comparison of simultaneously occurring different stages allocated to one successional sere. Examination of this phenomenon was preceded by establishment of the geobotanical substratum for all the more important successional seres characteristic of the Niepołomice Forest.

Description of the succession was based on the following criteria: number of species ( $N$ ), density of individuals ( $D$ ), species diversity ( $H'$ ) and domination structure of the bird species in a community ( $J'$ ). Only those birds occurring as nesting species in spring and early summer were taken into consideration, as the avifauna is most stabilized during the breeding season, and the various species exhibit maximum habitat preference at that time.

Bird communities were defined both on homogeneous and diverse study areas as the successional stage was transitional in character (e.g., old river bed becoming overgrown). The study areas were located in the central parts of habitats to eliminate, as far as possible, the effect exerted by the ecotone. In the case of certain stages (e.g., old river bed at the stage of formation of alderwood) it was impossible to adhere to this principle on account of the small size and scattered character of distribution of these habitats in the peripheral parts of the forest area. It is for this reason that species more proper to the margins of forests, such as *Pica pica*<sup>2</sup>, *Carduelis chloris* and *Motacilla alba* occur in some of the bird communities. It was decided that each study area should comply with 3 further conditions: (1) it could not omit more than 10% of any species of a given habitat the density of which was at least 0.1 pairs/10 ha, (2) should provide material suitable for statistical analysis, (3) one person should be able to inspect it within a period of 3 or at most 4 hours. An exception was made for the very poor bird community of the recently clear-cut forest area, which was exempted from condition 2. The dimensions of the study areas varied within limits of 5–25 ha. The smaller areas are most often those of habitats difficult to examine and split up into small units.

An important condition for arranging bird communities in successional series is the collection of material in the same breeding season, but for technical reasons this was not always possible. The oldest oak-hornbeam stand was examined during the period 1967–1970, the next oldest, about 95 years, from 1967 to 1969 (the average values for several years were taken for comparisons), and the remaining habitats – except for coniferous forest – were examined in 1971. Coniferous forests were examined on the basis of material collected in 1966 by W. Kania, and have been published from a different aspect (K a n i a 1968). It would, however, seem that it is permissible to compare the bird community of a pine forest with communities described in

<sup>2</sup>Full names of species, together with authors, are given in section 6 – Appendix.

other years, as some of the data (H a a p a n e n 1965, 1966, K a n i a 1968) point to the great stability of the avifauna of coniferous forests.

The density of birds was defined by means of the mapping method based on E n e m a r ' s (1959) premises. These calculations are in conformity with the recommendations of the I n - t e r n a t i o n a l B i r d C e n s u s C o m m i t t e e (1969). Sporadic species have been omitted from this material, that is, species of which density was lower than 0.1 pair/10 ha. Details of the field methods used and detailed documentation of the bird communities described have been given in another paper (G ł o w a c i ń s k i 1975).

Species diversity was defined by means of the Shannon-Wiener function (L l o y d, Z a r and K a r r 1968, K r e b s 1972):

$$H' = \sum_{i=1}^S p_i \log_2 p_i \approx C/N \left\{ N \log_{10} N - \sum n_i \log_{10} n_i \right\}$$

where:  $H'$  is the amount of information expressed in bits per individual in the group of species studied,  $S$  – number of species in a community  $n_i$  – number of individuals of each of the species in a community,  $N$  – total number of individuals of all species in a community,  $p_i \approx n_i/N$ ,  $C$  – constant value (3.321928). This formula of diversity, taken from the theory of information, is conditioned by two factors – number and dominance structure of species in the community.

The dominance structure of species ( $J'$ ) has been described by means of the equation given by T r a m e r (1969):

$$J' = H'/H'_{max}$$

where:  $H'_{max} = \log_2 S$ , while  $S$  – as in the preceding equation.

Difference between bird communities from the aspect of species diversity was calculated by means of C o d y ' s (1970) index:

$$CI = H_{1+2} - \frac{H_1 + H_2}{2}$$

where:  $H_1$  and  $H_2$  are values obtained by means of Shannon-Wiener's equation for habitats 1 and 2,  $H_{1+2}$  – species diversity calculated according to this same formula for the sum total of birds of the two habitats. The smaller value  $CI$ , the greater the similarity of the bird communities compared.

Values of C o d y ' s (1970) index were arranged in the form of a dendrite by means of the "Wrocław taxonomy" method (P e r k a l 1958).

### 3. PRIMARY SUCCESSION

#### 3.1. Genetic connections of habitats, successional stages

The Niepołomice Forest (50°04' N, 20°21' E) as a whole forms a mosaic of different plant associations and communities of a transitional character. These units stand in a defined hierarchy of sequence in relation to each other. The diagram of the natural succession of plant

associations described for the valley of the upper Vistula (P a w ł o w s k i 1959) in a main line running from the old river bed, in turn takes in: water plants most often belonging to the association *Myriophyllo-Nupharetum* → the marsh association *Scirpo-Phragmitetum* → associations of high sedge, particularly of *Caricetum gracilis* (in which sallow scrub appears, e.g., *Salix cinerea*<sup>3</sup> and *Alnus glutinosa*) → wet alderwood *Alnetum glutinosae* → oak-hornbeam forest *Quercus-Carpinetum* → oak-pine forest *Pino-Quercetum*. In the case of the Niepołomice Forest this sere can be supplemented by, inter alia, alder-carr *Circaeo-Alnetum*, coming between alder wood and oak-hornbeam forest (F e r c h m i n and M e d w e c k a - K o r n a ś — in press). The transition of oak-hornbeam to mixed and pine forest is, however, somewhat problematical here. The northern part of the Niepołomice Forest is situated on the low terrace of the Vistula, with traces of numerous old river beds formed at different ages. This terrace, covered by very diverse and fertile holocene matter, is overgrown by deciduous forests, chiefly lime-oak-hornbeam. One of the basic characters of forests in the northern part of the Niepołomice Forest is the lack of sharply defined boundaries between their diverse forms.

In the southern part of the forest, however, there is an extensive plain of old pleistocene sand terrace, situated at a slightly higher level, and the alluvial cone of the Raba river (B z o w s k i 1973). This area with a drier and less fertile substratum, is occupied almost entirely by coniferous forests, chiefly pine mixed forest. There are no such distinct transitional forms between the oak-hornbeam and coniferous woods in the Niepołomice Forest as can be observed in the earlier plant stages. There are, however, tree stands which suggest that such transitions are possible in the study area, namely *Pinus silvestris* and *Vaccinium myrtillus* occur in certain parts of the oak-hornbeam wood, which can be considered as the precursor of succession, which — due to continued draining of the area and introduction of coniferous trees — might lead to the formation of oak-pine forest. According to some concepts this forest would form a hypothetical climax of the area in question (F e r c h m i n and M e d w e c k a - K o r n a ś — in press). It would nevertheless seem that succession leading to formation of pine woods (usually through pine mixed forest) and oak-hornbeam woods proceed along courses independent of each other here.

Short successional seres, ending in mature and most established woods occur in the Niepołomice Forest to no lesser degree, probably even more frequently. Pioneer forest stages do not necessarily have to be sallow scrub and wet alderwood. In places which were not originally occupied by old river beds and fens depending on the type of geological substratum, soil and water relations, alder carrs, oak-hornbeam forests or simply pine woods, may develop straight away from non-forest associations (M e d w e c k a - K o r n a ś 1959).

In order even partially to reconstruct the natural succession of birds in the Niepołomice Forest two, possibly coinciding, successional plant seres were taken as a basis: the main sere (series A) — from the old river bed becoming covered by vegetation to the old oak-hornbeam forest and possibly mixed pine forest, and a shorter sere (series B) leading through bog pinewood to oak-pine forest. Both the described seres of the hypothetical primary succession are incomplete, since there are no pioneer stages in them.

Sere I (series A) has been distinguished on the basis of a habitat situated in the "Grobla" complex on the banks of the Vistula between the hamlets of Chobot and Ispina, while the pine mixed forest stages (series B) were distinguished in the "Gawłówek" pine complex near Baczków.

<sup>3</sup>Scientific names of species are given after S z a f e r, K u l c z y ń s k i and P a w ł o w s k i (1953).

I. Old Vistula bed (nature reserve called "Wiślisko Kobyle"). Study area 5.0 ha. Zonal distribution of vegetation can be observed over a considerable part of the old river bed, about 50% of which is becoming overgrown (Fig. 1). In the riverbank zone swamp plant communities of the order *Phragmitetalia* predominate. The centre is occupied by aquatic vegetation, in which *Potamogeton lucens* (Dubiel 1973) is the species occurring most abundantly. The old river bed is shaped like a loop and reaches a width of 30–40 m. It is situated within wooded land; about 85% of it is bordered with a pole-timber alder-poplar forest and a mature oak-hornbeam wood, and over a short section adjoins a fresh meadow (*Arrhenatheretum elatioris*). The water is highly eutrophized, and the bottom covered by a very thick layer of mud. Maximum depth about 3.0 m.

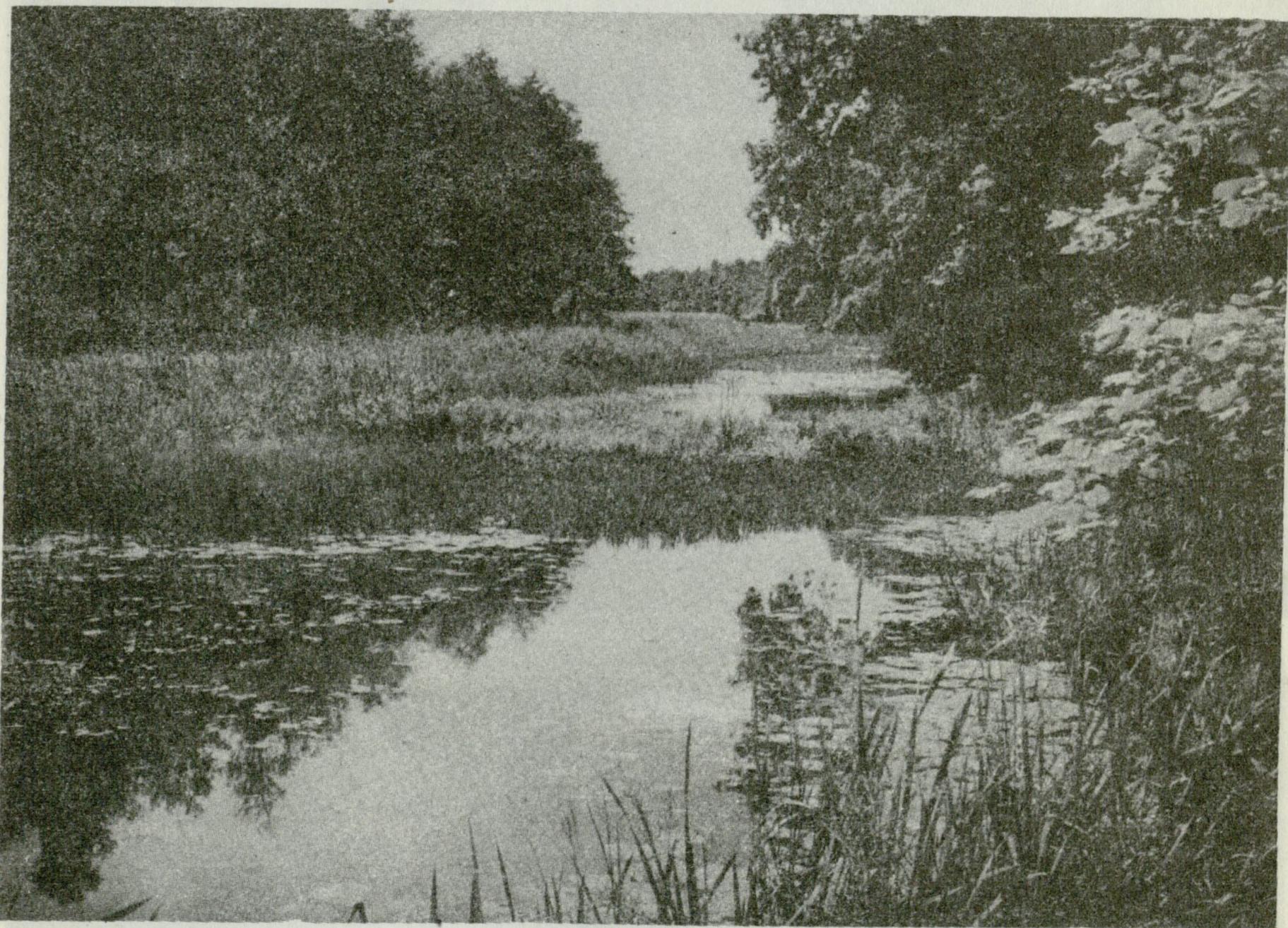


Fig. 1. Old river bed of the Vistula in process of becoming overgrown ("Wiślisko Kobyle" nature reserve)

II. Completely overgrown old river bed in the stage of formation of an alder wood (Fig. 2) in the interior of the "Grobla" complex (2.5 ha) and at Ispina (5.5 ha). Taken all together about 90% of the 8.0 ha study area is covered by the swamp vegetation communities (plant layer C), chiefly the *Scirpo-Phragmitetum* and *Caricetum Hudsoni* (Z. Denisiuk, A. Medwecka-Kornaś – personal communication). *Salix* sp. and *Alnus glutinosa* occur in thickets (layer B) representing the initial stage of wet alderwood. It is only in places that there are tall *Alnus glutinosa* trees (beginnings of layer A). The greater part of the ground is under water and very swampy. Small pools of water appear here and there among the vegetation. The part of the old river bed in the forest is almost completely surrounded by mature oak-hornbeam wood, but in the village of Ispina is bordered by cultivated fields and a meadow and in smaller sections by a young alder forest, a road and village smallholdings.

III. An alder carr *Circaeo-Alnetum* about 50 years old (Fig. 3). Study area 8.0 ha. Stands of *Carici elongatae-Alnetum* also occur in places in the study area (about 8% of the area) and in the drier parts small patches (about 10% of the area) of alluvial forest passing into the wet *Tilio-Carpinetum stachyetosum* association. In the very luxuriant herb layer (layer C) the dominant species are *Urtica dioica*, *Impatiens noli-tangere*, *Rumex* sp. and *Carex brizoides*. The understory trees and shrubs (layer B) consist chiefly of



Fig. 2. Overgrown old river bed of the Vistula with small patches of alder wood

*Frangula alnus* and *Crataegus* sp. div., and the overstory trees (layer A) chiefly *Alnus glutinosa*, with *Tilia cordata*, *Carpinus betulus* and *Quercus robur* in smaller numbers. The majority of the study area is surrounded by mature oak-hornbeam forest, only a small part being bordered by meadow.

IV. An oak-hornbeam forest about 95 years old, the wet variant of *Tilio-Carpinetum*<sup>4</sup>, without *Pinus silvestris* (Fig. 4). Study area 25.0 ha (for small and common birds – 11.5 ha). The forest is characterized by fairly evenly formed stratification. The herb layer (layer C) is generally luxuriant, particularly in wet places. It consists most often of *Ficaria verna*, *Impatiens noli-tangere*, *Aegopodium podagraria*. In the understory trees and shrubs (layer B) *Carpinus betulus* predominate, with slightly lesser participation of *Crataegus* sp. div. and *Tilia cordata*. The overstory trees (and layer A) consists chiefly of *Quercus robur*, with *Tilia cordata* and *Carpinus betulus* occurring less often. Oak-hornbeam forest also occurs in the surroundings of the study area.

<sup>4</sup> Until recently oak-hornbeam forests in Poland were allocated to one association – *Quercus-Carpinetum*. This name also corresponds to the typological characteristics of the forest in which oak and hornbeam predominate. This is in fact the case in the Niepołomice Forest. In accordance with new phytosociological classification the oak-hornbeam forests occurring there have been considered as belonging to *Tilio-Carpinetum* (Ferchmin and Medwecka-Kornaś – in press), but for zoological purposes their old name of *Quercus-Carpinetum* is more self-explanatory and useful.



Fig. 3. Alder carr about 50 years old



Fig. 4. Oak-hornbeam forest about 95 years old

V. Oak-hornbeam forest, about 150 years old, the dry variant of *Tilio-Carpinetum*, with the addition of *Pinus silvestris* ("Lipówka" nature reserve) (Fig. 5). Study area 25.0 ha (for small and common species of birds – 12.0 ha). The herb layer (C) and understory (B) are somewhat poor and only a small number of seedlings are observed there. This is due to the very strong development of the overstory tree layer (layer A), which greatly limits access of light to the lower parts of the forest. The density of shrubs and small trees is greater only in certain places. Layer B and C are also varied by fallen old trees and the hollows they leave behind them. The composition and dominance of the species forming the different plant layers are similar to those in the previous stage, except that there is greater participation of *Tilia cordata* and *Pinus silvestris* in the forest stand. The old trees examined have a very large number of natural holes in the trunks. About 80% of the old tree stand is bordered by older pole timber (in parts of which *Picea excelsa* occurs), and the remaining part adjoins a partial clearing.



Fig. 5. Oak-hornbeam forest about 150 years old ("Lipówka" nature reserve)

VI/IVb. A mixed pine wood about 100 years old, *Pino-Quercetum*, with a tendency to fresh oak-pine forest – *Vaccinio myrtilli-Pinetum* (Fig. 6). Study area – 36.0 ha. The substratum varies from degraded peat soil to sand of higher levels. *Pteridium aquilinum*, *Vaccinium myrtillus* and *Rubus* sp. occur most numerous in the herb layer (layer C). The chief components of the understory layer (layer B) are *Quercus robur* and *Frangula alnus*. The tree layer (A) consists of sub-layers: A1 – formed by the tree tops of *Pinus silvestris* and A2 – composed chiefly of *Quercus robur*, younger individuals of *Pinus silvestris* and *Betula verrucosa*, occurring singly. A similar pine mixed forest, young pine forest and partly dried bog pine wood border the area.

IIIb. Bog pinewood *Vaccinium uliginosi-Pinetum* (Fig. 7), about 50 years old, considerably dried. Study area – 7.5 ha. Peat soil predominates in this habitat, small sandy sites covered by fern occurring only here and there. Mosses, particularly *Sphagnum* and *Polytrichum*, predominate in the herb layer (layer C), and *Vaccinium myrtillus* and *V. uliginosum* also occur numerously. *Ledum palustris* grows in places. The very



Fig. 6. Oak-pine forest about 100 years old with tendency to fresh pine forest



Fig. 7. Bog pinewood about 50 years old

luxuriant understory is formed by *Frangula alnus*. *Pinus silvestris*, with a considerable amount of *Betula verrucosa* and *B. pubescens*, predominates in the fairly uniform layer A. Similarly degraded bog pinewood and mixed coniferous forest occur in the vicinity of the study area.

### 3.2. Results

A comparative group of bird communities, in accordance with a simplified successional sequence of the main habitats of the Niepołomice Forest, is given in Figure 8.

The bird communities of the old river bed in process of becoming overgrown (stage I) consists of 7 water and sedge species. The species most meriting the name of indicator species here (Allee et al. 1949) are *Acrocephalus scirpaceus* and also *A. arundinaceus*, which although occurring in the next stage as well, does so far more rarely. The most numerous species: *Gallinula chloropus* and *Anas platyrhynchos* represent the younger and the older river bed in approximately the same numbers. The bird community in the old river bed on which alder is growing (stage II) is clearly transitional. In addition to water birds (e.g., *Anas platyrhynchos*) and inhabitants of sedge associations (e.g., *Acrocephalus arundinaceus*), brush layer species (e.g., *Sylvia communis*) and even forest species (e.g., *Oriolus oriolus*) appeared in it. This stage is differentiated the best by *Sylvia communis*, *Emberiza schoeniclus* and *Acrocephalus schoenobaenus*. The alder carr (stage III) is occupied by avifauna characteristic of forests only, and from this stage onwards hollow-nesters also appear. *Fringilla coelebs* and *Emberiza citrinella* occur in the largest numbers. This latter species, and also *Carduelis carduelis* and *Hippolais icterina*, can be considered as indicator species. Under the conditions of the mature oak-hornbeam forest (stage IV) the bird community was enlarged by a further 11 species, while *Carduelis carduelis* disappeared, not to return again, and *Hippolais icterina* had nearly disappeared. *Sylvia borin* was also absent from time to time, due to the great density of the forest. In this stage in the successional sequence 10 new species enter, one of which — *Muscicapa striata* — attains maximum density here. The fact that *Crex crex* and *Phasianus colchicus* are observed in this stage only may be a fortuitous phenomenon. There is no distinct indicator species here. The bird community of the oldest oak-hornbeam wood (stage V) is the largest in the group examined. As many as 16 species reach maximum density here, this being seen most clearly in the case of *Ficedula albicollis*, *Erithacus rubecula*, *Sturnus vulgaris* and *Sitta europaea*. Among the five newcomer species the large hollow-dwellers are remarkable — *Strix aluco*, *Dryocopus martius* and *Columba oenas*. The mature oak-hornbeam forest and mixed coniferous forest in the Niepołomice Forest, which varies widely from the edaphic aspect, form the polyclimax phase. The stage of mixed coniferous forest enters the composition of successional coniferous series (series B), but under certain conditions — as previously mentioned — it may also prolong the oak-hornbeam sere (series A). The bird community of the mixed coniferous forest replaces the lost 17 species proper to oak-hornbeam forests by 8 new taxa for the first successional series. Characteristic species are: *Parus ater*, *P. cristatus*, *Garrulus glandarius* and in some degree *Certhia brachydactyla*. The stage of bog pinewood (IIIb) is subject only to the series which leads to pine forest (series B). In the bog pinewood a community was formed half the size of that in the mixed coniferous forest. The indicator species is *Ficedula hypoleuca* and, to a certain extent, *Phylloscopus trochilus*.

When arranging the spectrum of species in accordance with the principle of splitting up the columns of each succeeding community to the smallest possible extent, we obtain more or less differentiating ecological groups (Fig. 8). There is a distinct group of water and sedge species (G-1), limited by the range of species from positions 1-8. Further two groups of brush layer

and ecotone species can be distinguished, as follows: a group with a narrow range ( $G-2$ ), defined by species from positions (8) 9–11 (12) and a slightly smaller group with a wide range ( $G-3$ ), formed by species from positions 12–14. Species from positions 19–29 form a large group of typically forest birds with a wide range of occurrence ( $G-4$ ). *Fringilla coelebs*, *Anthus trivialis* and *Dendrocopos major* occupy an axial position in it. A relatively compact group can be distinguished for oak-hornbeam species ( $G-5$ ) from positions 12–45. Seven species from the final positions ( $G-6$ ), exhibiting a close connection with the coniferous woods of the Niepołomice Forest, have been placed within the most arbitrary framework.

Figure 9 presents the values of four basic indexes defining succession: number of species ( $N$ ), density ( $D$ ), species diversity ( $H'$ ) and domination structure of species in the community ( $J'$ ).

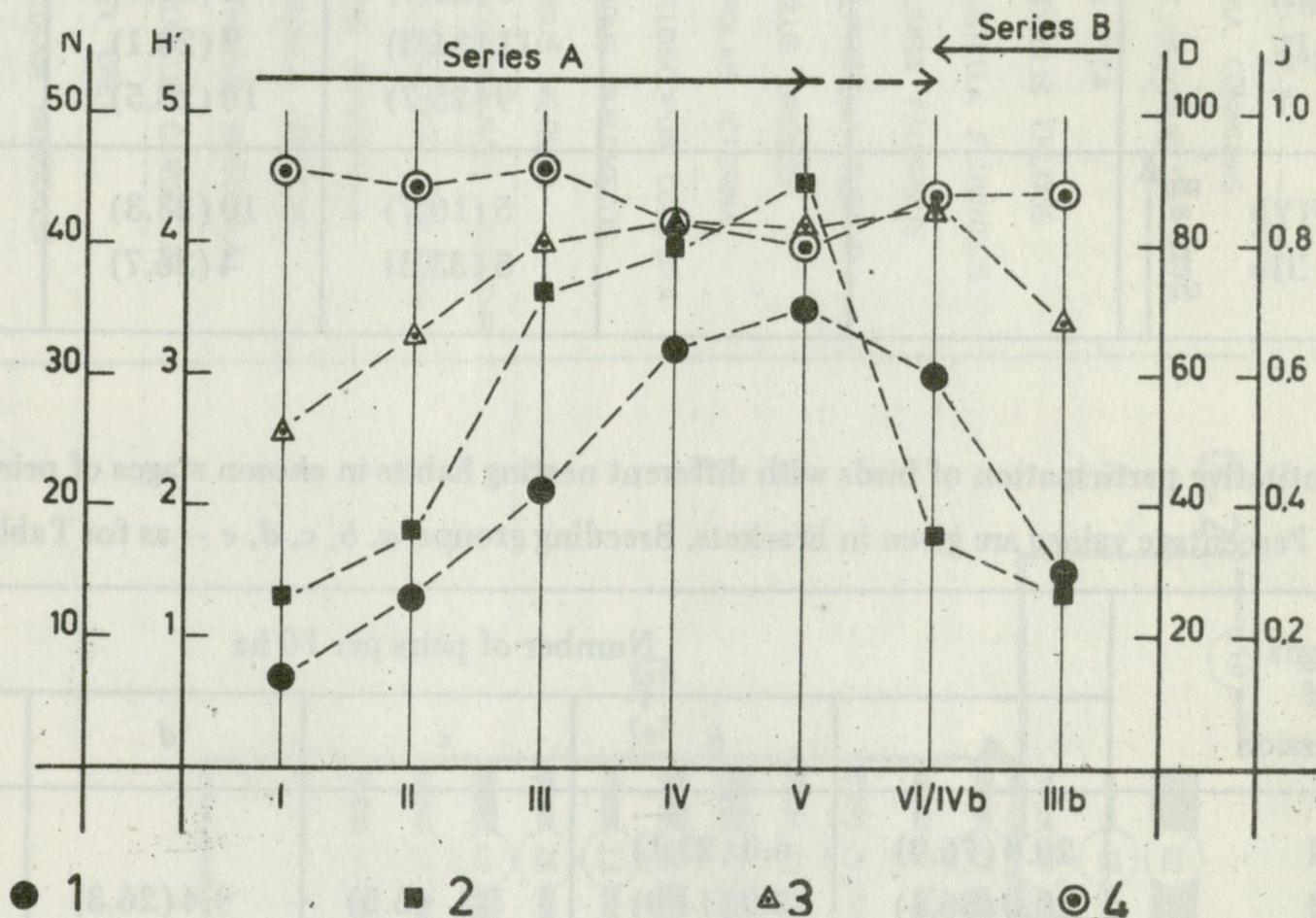


Fig. 9. Measurements defining the primary succession of birds in the Niepołomice Forest.

1 – number of species ( $N$ ), 2 – number of pairs per 10 ha ( $D$ ), 3 – species diversity ( $H'$ ), 4 – dominance structure of species in the community ( $J'$ )

It is clear from the list that the number of species in the consecutive communities changes relatively gradually and progressively. The oldest oak-hornbeam forest links the largest number of bird species. The density index of birds is characterized by the most abrupt transitions, and it attains its culminating value also in the oldest oak-hornbeam forest. It can also be seen from the list that there is a significant difference in density between the avifauna of deciduous (series A) and coniferous forests (series B); in coniferous forests the value of this character is almost 3 times smaller than in the oak-hornbeam forest. The index of species diversity  $H'$  is distinguished by more gradual transitions, and attains its maximum value in the stage of oak-pine forest, exceeding in this respect the oak-hornbeam forest communities, which have a greater number of species. The index of species domination  $J'$  reaches greater values in the small communities there. The least uniform distribution of number of species is found for the largest community formed in the oldest oak-hornbeam forest.

Table I presents the qualitative participation of birds in successive communities representing 5 chief types of nesting, while Table II presents the participation of birds of the same breeding groups, taking density into consideration. None of the breeding groups accompanies all the communities found. In the two first stages, both in respect of number of species and numbers

Tab. I. Qualitative participation of birds with different nesting habits in chosen stages of primary succession. Percentage values are given in brackets. Breeding groups: *a* — species building nests on water, in aquatic plants and wet meadows, *b* — building nests above water in sedge, *c* — building nests on the ground or immediately above it, *d* — building open nests in shrub and tree layer, *e* — nesting in hollows in trees

Stages of succession		Number of species				
		<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>
Series A	I	5 (71.4)	2 (28.6)			
	II	5 (38.5)	2 (15.4)	1 (7.6)	5 (38.5)	
	III			5 (23.8)	8 (38.1)	8 (38.1)
	IV			11 (34.3)	9 (28.1)	12 (37.6)
	V			9 (25.7)	10 (28.5)	16 (45.8)
	VI/IVb			5 (16.7)	10 (33.3)	15 (50.0)
	IIIb			5 (33.3)	4 (26.7)	6 (40.0)

Tab. II. Quantitative participation of birds with different nesting habits in chosen stages of primary succession. Percentage values are given in brackets. Breeding groups: *a*, *b*, *c*, *d*, *e* — as for Table I

Stages of succession		Number of pairs per 10 ha				
		<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>
Series A	I	20.0 (76.9)	6.0 (23.1)			
	II	20.0 (56.1)	5.0 (14.0)	1.3 (3.5)	9.4 (26.3)	
	III			28.7 (39.4)	19.7 (27.0)	24.6 (33.6)
	IV			19.4 (24.5)	23.3 (29.5)	36.5 (46.0)
	V			17.7 (19.7)	24.2 (27.0)	47.8 (53.3)
	VI/IVb			10.2 (29.1)	13.7 (39.1)	11.1 (31.8)
	IIIb			10.9 (40.8)	8.8 (32.8)	7.1 (26.4)

of individuals, species building nests on water or in the lower parts of aquatic plants (group "a") and species suspending nests above the water among sedge (group "b") occur in approximately similar proportions. The species on the water ("a") predominate by more than twice as much, however, in respect of number of species, and in respect of density by about 4 times as much. In the stage of the old river bed in processes of being overgrown (II) birds building nests on the ground, or immediately above it (group "c") also appear, as do birds nesting in open nests in the layer of shrubs and trees (group "d"). In the stage II of community the participation of representatives of group "c" is limited to one species only (*Luscinia luscinia*), whereas group "d" is represented there by the same number of species as group "a". In respect of numbers of individuals the participation of species of groups "c" and "d" is slight. From the stage of alder carr to oak-pine forest only 3 typically forest groups participate: "c", "d" and the group of hollow-nester species ("e"). In stage II the participation of species belonging to

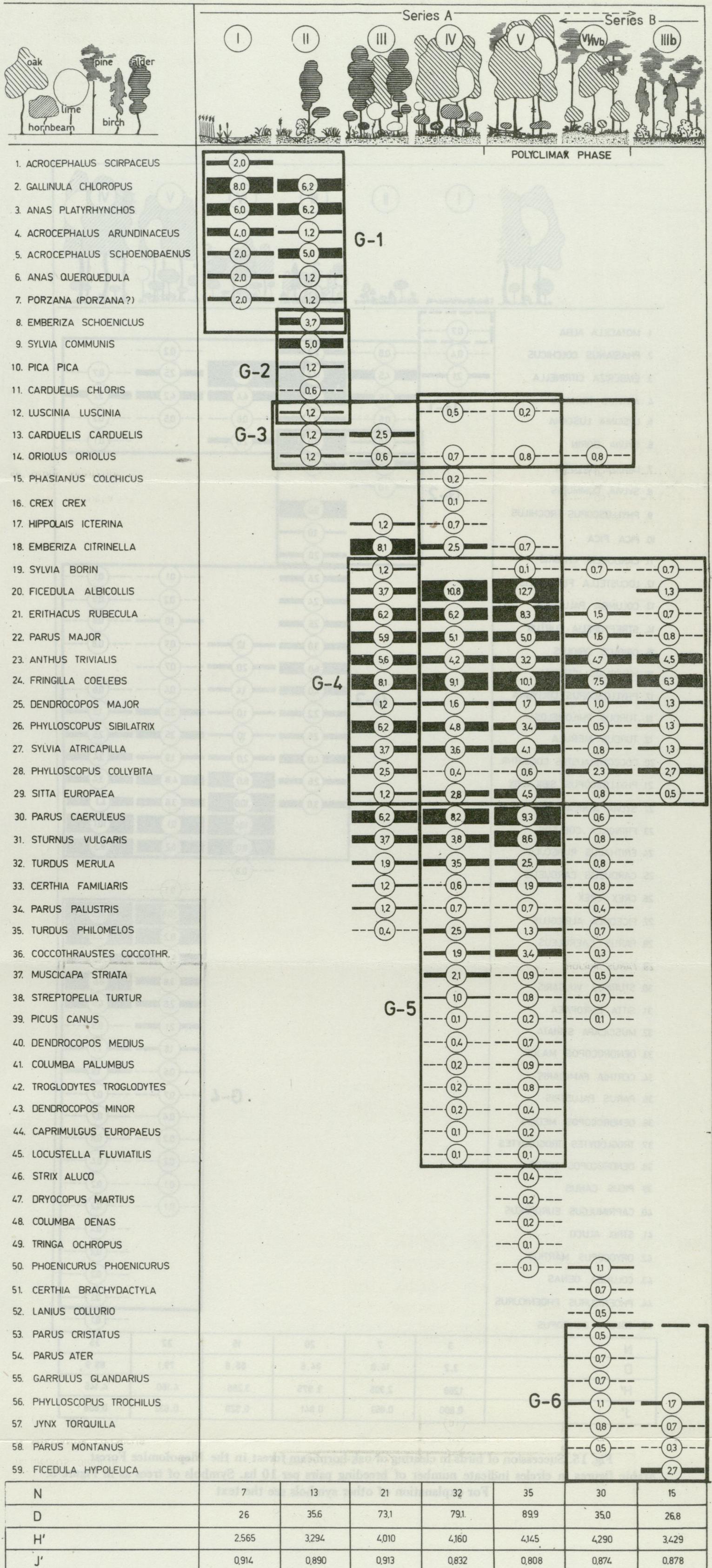


Fig. 8. Succession of birds in a line from the old river bed to mixed pinewood (series A) and from bog pinewood to mixed pine forest (series B) in the Niepołomice Forest  
 Arabic figures in circles indicate the number of breeding pairs of birds per 10 ha. For explanations of symbols see the text

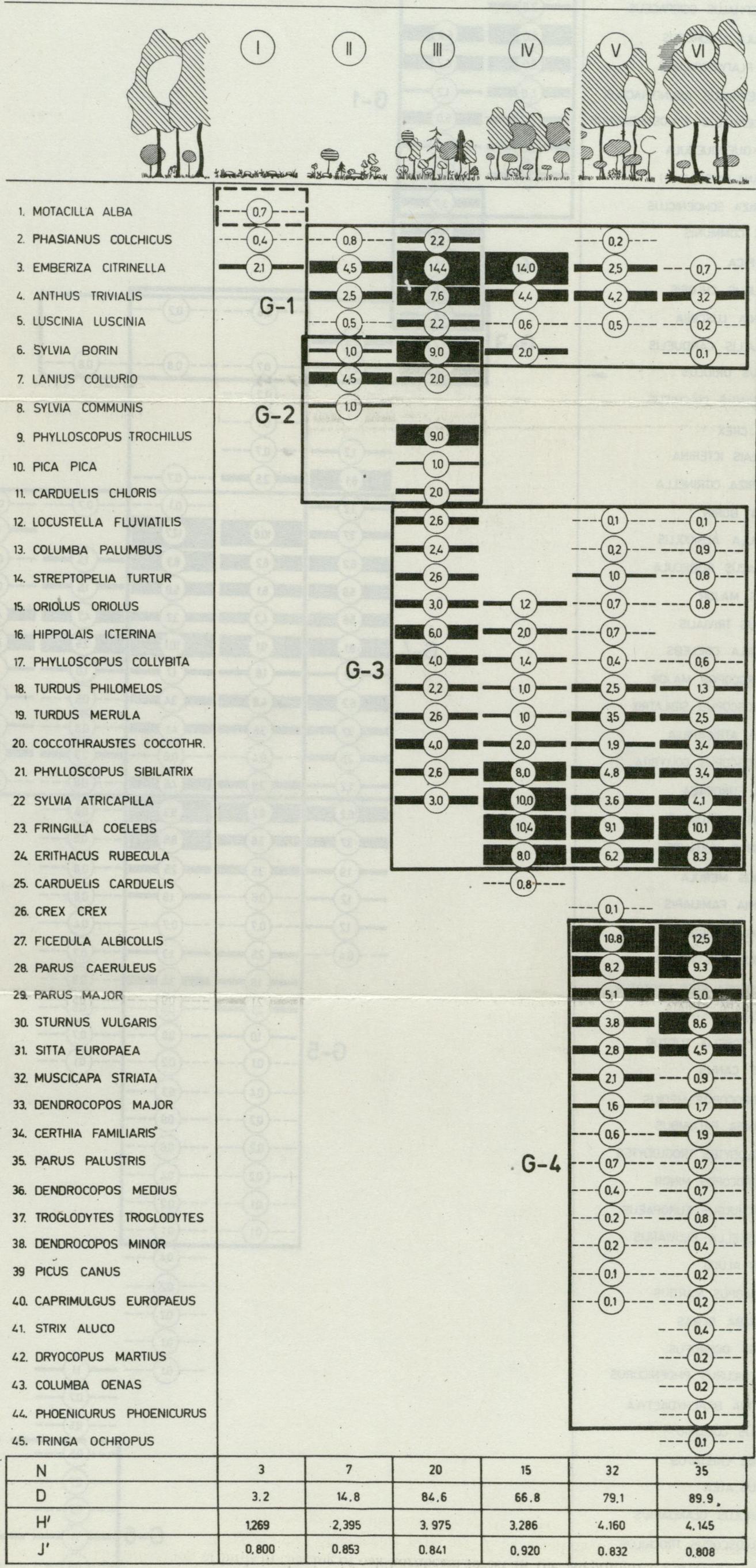


Fig. 15. Succession of birds in clearing of oak-hornbeam forest in the Niepołomice Forest  
 Arabic figures in circles indicate number of breeding pairs per 10 ha. Symbols of trees as in Figure 8.  
 For explanation of other symbols see the text

groups "c", "d", "e" both in respect of number of species and numbers of individuals – is fairly balanced, but as from the next stage hollow-nesters predominate. This is particularly marked in the stage of the old oak-hornbeam forest. The reciprocal distribution of values defining groups "c" and "d" in all the forest habitats studied takes varying forms. The distribution of the units distinguished in the oak-pine forest community is remarkable; in respect of the number of species groups "c", "d", "e" are most differentiated here, whereas when density is taken as a basis – their differentiation is minimum. The most balanced participation of groups "c", "d" and "e" is observed in the bog pinewood community. In forest bird communities, together with the transitional community of stage II, the fairly balanced percentages of breeding group "d" are remarkable (Fig. 10). Groups "c" and "e" are the ones replacing each other (in stage II also "a" and "b"). In addition a distinct tendency to increase in relative number of hollow-nesters (group "e") can be observed in the direction of older forests, at the expense, so to speak, of species of group "d".

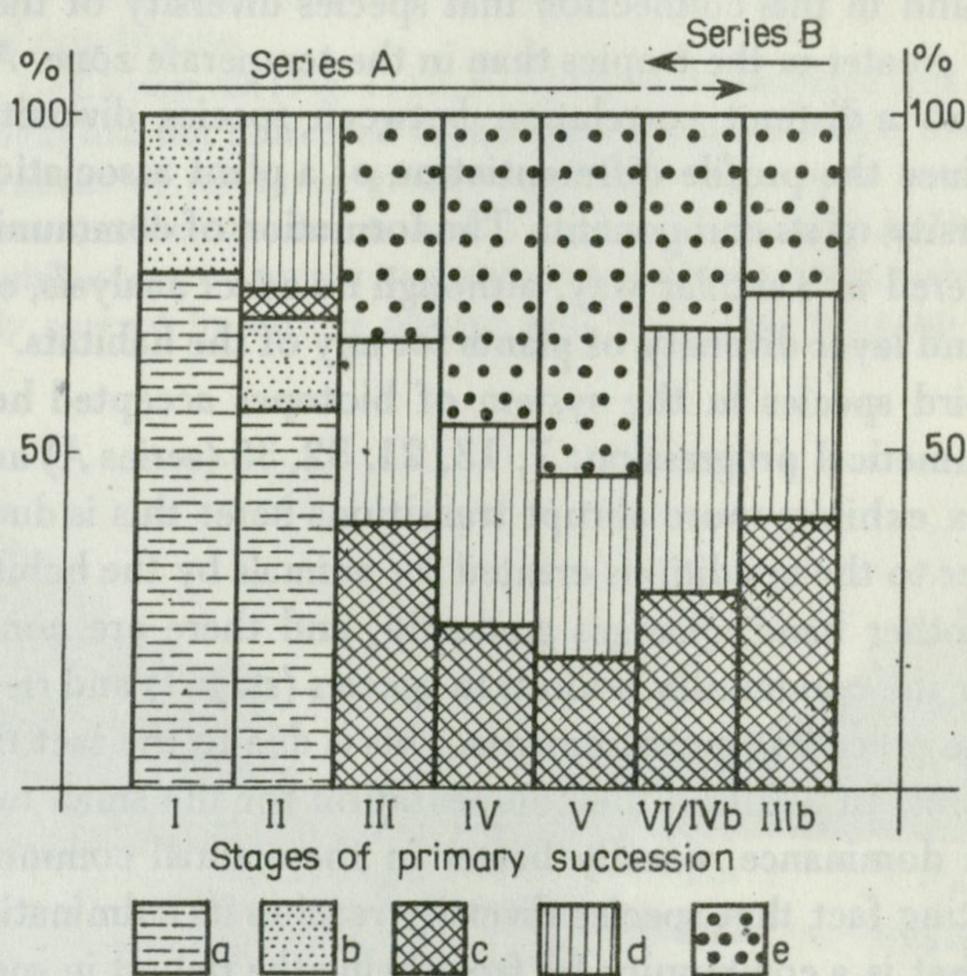


Fig. 10. Participation in percentages of breeding pairs of birds with different nesting habits in chosen stages of primary succession

Breeding groups: a – species laying eggs on water, among aquatic plants and in wet meadows, b – species building nests above water surface in sedge, c – building nests on the ground or immediately above it, d – building nests in the shrub and tree layer, e – hollow-nesters

### 3.3. Discussion

Each succession consists in the qualitative and quantitative transformation of ecosystems and communities (O d u m 1963). This is clearly illustrated for the case in question by Figure 8.

Plant succession is accompanied by increase in vertical stratification of the habitat, for instance stage I has 1 incomplete plant layer (layer C), stage II – 1 complete layer (C) and 2 layers in course of development (B, A), stage III and IIIb – 3 (C, B, A), stage V – 3 (C, B and a very strongly developed layer A), VI/IVb – 3 (C, B and A differentiated into sublayers A1

and A2). This is followed by increase in the capacity of the habitats and development of the bird communities proper to them. The character of a bird community is directly connected with the quality and quantity of ecological niches, accessibility of food, facilities for nesting, and also with the constancy and regime of the habitat. It is a well known fact that, e.g., more species occupy forests than meadows, and tropical habitats usually support more species than do their corresponding habitats in the temperate zone (Orians 1969). Similar factors determine the species diversity of birds. It is clear from Tramer's (1969) list that species diversity of the avifauna of marshes and meadows (1 plant layer) brush layer areas (2) forests of the temperate zone (3) and tropical forests (4) differ fundamentally from each other. The difference in value  $H'$  between bird communities of extreme habitats (marshes  $\leftrightarrow$  tropical forests) is as much as 4 bits per individual. R. H. MacArthur and J. W. MacArthur (1961) and later Karr (1968) showed a significant correlation between increase in species diversity of birds and the number and structural differentiation of plant layers (foliage height diversity). It was found in this connection that species diversity of the birds in habitats with similar profiles is far greater in the tropics than in the temperate zone. According to these same authors, there is also a distinct correlation between species diversity of birds and species diversity of plants, since the profile differentiation of a plant association is causally connected with the species diversity of its components. The formation of communities in the Niepołomice Forest can be considered in a similar way, although no exact analysis, expressed in figures, was made of the species and layer diversity of plants for any of the habitats.

The number of bird species in the system of biotopes accepted here (Fig. 8) increases in a similar way to arithmetical progression: 7, 13, 21, 32, 35 (series A) and 15, 30 species (series B). The density index exhibits more abrupt transitions here: this is due to the greater "sensitivity" of this character to the conditions created for animals by the habitat. The index of species diversity  $H'$  on the other hand, changes gradually, and there are none of the disproportions between values  $H'$  for the community poorest in species (stage I) and richest in species (stage V) as is the case with the preceding measurements. This is due to the fact that index  $H'$  is based on logarithmic calculations. In addition the compensation for the small number of species by the composition of taxa dominance, usually better in these small communities, also plays a part here. It is an interesting fact that species diversity reaches its culminating value in the oak-pine forest community, that is a community far from being the richest in species. As compared with larger communities, that is, those possessing more species of birds (stage IV and V), the index of dominance  $J'$ , relatively high in this stage, was of importance here. This is indirectly due to the evenly formed stratification and the even stronger physiological differentiation of oak-pine forest than in the oldest oak-hornbeam forest (cf. description of habitats — section 3.1.). In the northern part of the Forest the older oak-hornbeam stand forms an enclave of the tallest trees: the treetop zone is best developed there, but does not exhibit distinct differentiation into sublayers. In addition the compactness of the treetops and the cover formed by them is unfavourable, as it were, to the less well developed shrub layer here (layer B), and the herb layer (layer C). This system of habitat conditions favours the formation among birds of a larger number of dominants and subdominants ( $J'$  decreases), which has an unfavourable effect on value  $H'$ . It is to be anticipated that the natural renewal of this old tree stand, which recently is markedly inhibited, will involve, inter alia, thinning of the prevailing generation of old tall trees and the formation of gaps in the treetop zone. These changes should improve the dominance system so far prevailing among birds, which with maintenance of the same large number of species in the community would cause the value of index  $H'$  to rise.

It can therefore be seen that there is no decidedly most highly organized (with maximum  $H'$ ) and simultaneously richest (with maximum  $N$  and  $D$ ) bird community in the Niepołomice Forest. Two communities formed in stage V (maximum  $N$  and  $D$ ) and VI/IVb (maximum  $H'$ ) that is, exactly occurring in the phase of edaphic polyclimax, qualify for this rank.

#### 4. SECONDARY SUCCESSION OF BIRDS IN AN OAK-HORNBEAM HABITAT

##### 4.1. Development stages of the forest

Study areas were selected in habitats representing 6 development stages of the *Tilio-Carpinetum* forest within the "Grobla" complex. As far as possible homogeneous habitats which had developed under the influence of very similar physical conditions, were taken into consideration. Although the forest is affected by the activities of forestry workers, its development is close to that under natural conditions.

I. Recently clear-cut area, 1–2.5 year old (Fig. 11) in two parts with combined area of 7.0 ha (2.5 and 4.5 ha). Development of the habitat had not proceeded in this stage beyond the layer of herbaceous vegetation (C), in which numerous elements of the forest ground vegetation (e.g., *Carex brizoides*, *Impatiens noli-tangere*, *Aegopodium podagraria*) still oust associations of a meadow character (e.g., *Deschampsia caespitosa*, *Juncus efusus*) and the nitrophilous species proper to clearings (e.g., *Urtica dioica*, *Galeopsis* sp.). About 75% of the clear-cut area, densely covered by turf, is planted with very young trees (up to about 70 cm high)



Fig. 11. 1–2.5 year old clearing in oak-hornbeam forest

chiefly *Quercus robur*, *Pinus silvestris* and *Fraxinus excelsior*. There is no vegetation in this area forming a transition to thicket. Mature oak-hornbeam or pole timber occurs round the clearing, which is bordered over a short sector by forest glade and meadow.

II. Clear-cut area with 4–9 year old plantation of deciduous trees (Fig. 12), in two parts with combined study area of 10.0 ha (5.0 and 5.0 ha). Forest ground vegetation species occur far less frequently there than in the preceding clearing, only *Carex brizoides* growing abundantly in the form of large patches. Luxuriant grass associations prevail among the vegetation of layer C, particularly those covering cleared spaces with turf, i.e., *Deschampsia caespitosa* and *Juncus efusus*. Of the forest clearing species, species of the genus *Rubus* occurred in large patches in addition to *Urtica dioica*. The surface vegetation is enriched by the dense regrowth forming round lime stumps. *Quercus robur* predominates in the young tree plantation (layer B), while *Fraxinus excelsior* and *Alnus glutinosa* occur in groups and *Picea excelsa* and *Larix* sp. singly. The latter, in addition to *Alnus glutinosa*, represents the best grown generation of young trees (up to about 3 m high) in the clearing. Mature oak-hornbeam forest occurs in about 80% of the area surrounding the clearing, with a young oak-hornbeam stand in the remaining part.



Fig. 12. Clearing in oak-hornbeam forest, about 7 years old, with well-formed brushwood layer

III. Thicket and trees about 15 years old (Fig. 13) – study area 5.0 ha. The development of herbaceous vegetation of layer C was very luxuriant there, and the following species dominate among it: *Solidago* sp., *Dactylis glomerata*, *Tanacetum vulgare*, *Urtica dioica* and *Galium aparinae*. In thinned places the meadow element – *Deschampsia caespitosa* continues to occur fairly abundantly. The more or less compact layer of brush and small trees (layer B) is formed chiefly by *Quercus robur*, *Fraxinus excelsior*, *Frangula alnus*, *Evonymus europaea*, *Crataegus* sp. div., *Carpinus betulus* and *Prunus spinosa*. In places young trees of up to 12 m in height stand up above their surroundings, in particular *Betula verrucosa*, *Larix* sp. and *Populus nigra*, forming the start of the treecrown layer (layer A). About 75% of the study area is neighboured by a similar plantation of young trees and in smaller sectors by oak pole timber, alder carr and meadow.



Fig. 13. Thicket and trees about 15 years old



Fig. 14. Oak-hornbeam forest about 30 years old

IV. An oak-hornbeam forest from 25 to 35 years old (Fig. 14), in three parts, with combined study area of 5.0 ha. Three well-formed forest layers occur here: the layer of ground vegetation (C), of fairly thin brush and understory trees (B) and the layer of compact treetops of the developing trees (A), considerably limiting light access into the interior of the forest. The ground vegetation is typical in character of oak-hornbeam forests, with species such as *Anemone nemorosa*, *Galium vernum*, *Carex brizoides*, *Milium efusum* and *Asperula odorata*, dominating in it. The understory trees consist chiefly of *Carpinus betulus* and *Crataegus* sp. div., and the tree stand of *Quercus robur*, *Carpinus betulus* and *Tilia cordata*. There are as yet no hollows in this tree stand. The study areas are surrounded by mature oak-hornbeam forest, with pole timber, deciduous thicket and meadow in over smaller sectors adjoining it.

V. Oak-hornbeam forest about 95 years old, previously described as stage IV of primary succession (Section 3.1.):

VI. Oak-hornbeam forest about 150 years old, previously described as stage V of primary succession (Section 3.1.). Under the conditions of the northern part of the Niepołomice Forest near the Vistula this forest can be considered as the climax form.

#### 4.2. Results

The formation of bird communities over the whole successional sere is presented in Figure 15. The initial community of the almost completely clear-cut area (stage I) consists of only 3 species nesting in the ground zone. A species which is to a certain degree an indicator species is *Motacilla alba*. It is the bird species characterising this clearing to the greatest degree, but may also be a species entering the area from open treeless areas. The community corresponding to the older clearing (stage II) is almost twice as large and is formed chiefly of species occupying brush. The indicator species here are *Lanius collurio* and *Sylvia communis*. A typically forest species — *Anthus trivialis* — appears here for the first time. The next community (stage III) is one outstandingly typical of brush and thicket and includes 20 species. The best indicators here are: *Phylloscopus trochilus*, *Sylvia borin*, *Hippolais icterina* and *Phylloscopus collybita*. It was found that the first of these species also acts as an excellent indicator of young tree stands of European coniferous forests (Lack 1939, D. Lack and E. Lack 1951, Pospelov 1957, Hapane 1965). Further typically forest elements appear in the stage of thicket and young trees, e.g., *Phylloscopus sibilatrix*, *Streptopelia turtur*. Optimum occurrence reaches as many as 13 species, among which *Emberiza citrinella* attained record density. In the first decidedly forest habitat (stage IV) the bird community decreased by 5 species in relation to the previous one. It was chiefly the thicket-brush and ecotone elements which disappeared, e.g., *Lanius collurio*, *Phylloscopus trochilus*, *Carduelis chloris*. *Sylvia atricapilla* and *Phylloscopus sibilatrix* reached optimum occurrence here; these species can be considered as indicator species of young forests. There are not as yet any hollow-nesters in this forest. In the bird community of the mature oak-hornbeam forest (stage V) elements dominate connected in different ways with the treestands; a large percentage is formed here by hollow-nesters, such as *Ficedula albicollis* and *Parus caeruleus*. There is no distinct indicator species. The bird community of the approx. 150 years old oak-hornbeam forest (stage VI) is the largest in the whole successional sere; but differs only slightly from the preceding one. Maximum density is clearly attained by 5 species here (including *Sturnus vulgaris*, *Sitta europaea*, *Certhia familiaris*), and, less distinctly, 7 species. A specific character of this stage is the occurrence in it of rare and large hollow-nesters — *Strix aluco*, *Dryocopus martius* and *Columba oenas*.

On the basis of spectra of the different bird species it is possible to distinguish 4 groups of birds in this sere (Fig. 15). There is no such group for the clear-cut area. The group of "eury" species (G-1) occupying positions 2-6, is clearly distinguished here. Species of thin thicket and brush (G-2) form a fairly highly specialized group, the horizontal range of which is

determined by the species from position 7. A more compact group (G-3) is formed by species of brushwood and trees which are not hollow-nesters. The core of this unit is formed by species from positions 15-22. A compact and relatively numerous group (G-4) is also formed by hollow-nesters. Its range is determined by species from positions 27-44, only species from positions 37 and 40 not being hollow-nesters.

The distribution of values of the ecological criteria accepted is illustrated in Figure 16, from which it can be seen that the number of species ( $N$ ), density of breeding pairs ( $D$ ) and index of species diversity ( $H'$ ) are not formed in a progressively continuous way during the course of succession, but that distinct peaks in stage III can be observed in their progress. A particularly great jump in value is observed in the case of the density index which, at the stage of brush and thicket, is higher than at the stage of mature oak-hornbeam forest (V). Index  $H'$  is formed very similarly, but it exhibits a scarcely marked decrease in the stage of the oldest forest stand (VI). The curve of the number of species is observed to take the simplest course. There is also a decided peak in stage II for the curve of dominance structure index ( $J'$ ). The value of this character attains even a peak state here. Increase in the values of the parameters examined in the community of stage III is the more remarkable in that it occurs without the participation of birds nesting in hollows in trees, which appear in the old forest.

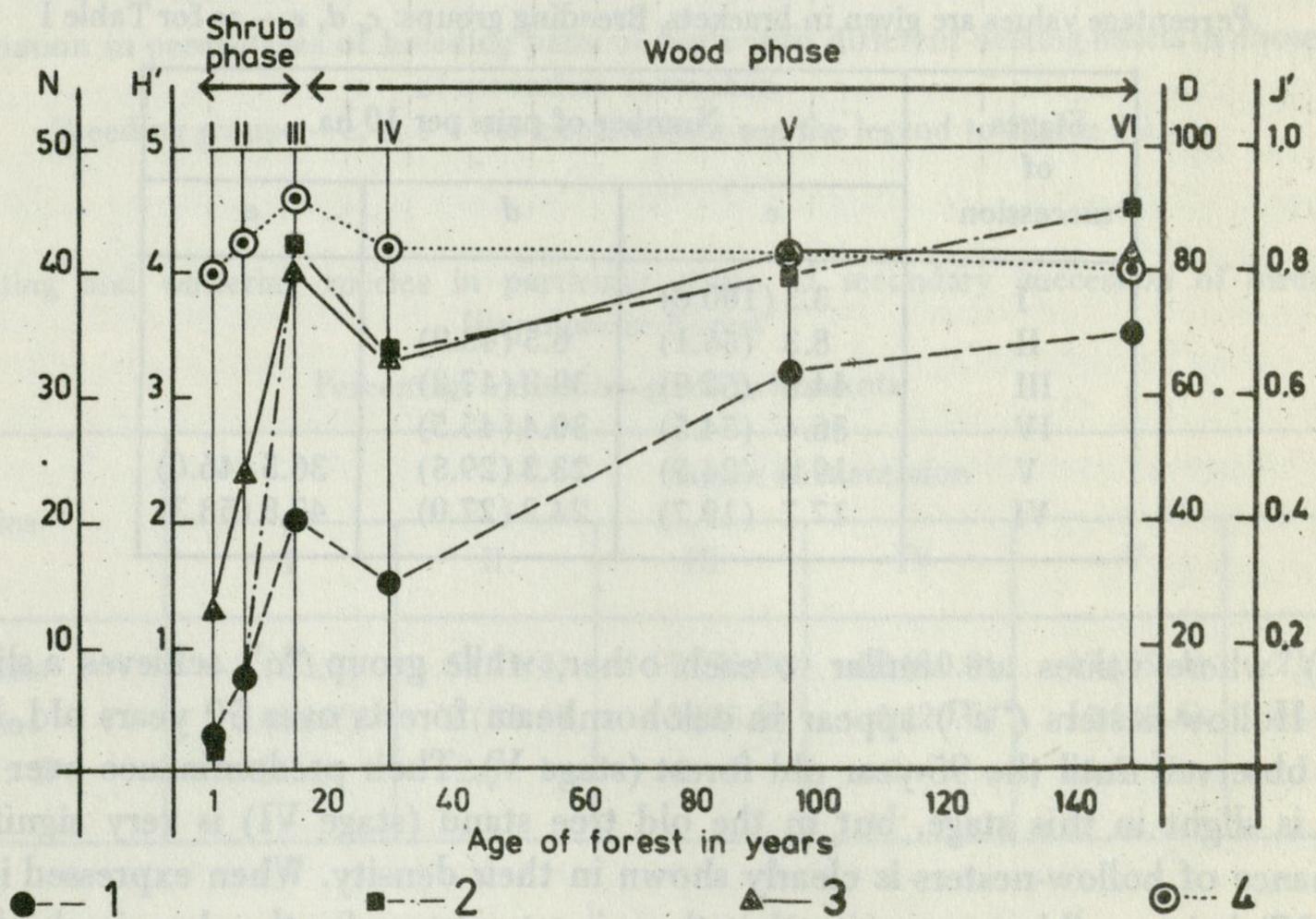


Fig. 16. Measurements defining secondary succession of birds in oak-hornbeam habitat  
 1 - number of species ( $N$ ), 2 - number of pairs per 10 ha ( $D$ ), 3 - species diversity ( $H'$ ), 4 - dominance structure of species ( $J'$ )

The formation during succession of breeding groups "c", "d" and "e" is illustrated in Table III and IV. Only those species which nest on the ground in the bottom of the forest ("c") are present in all stages (Tab. III), but birds nesting in trees and shrubs ("d") occur in the stage of the older clearing (stage II). Their participation, in relation to the preceding group of birds is different in form but generally speaking is fairly similar. The greatest differences between these groups can be observed at the stage of brush and young tree stand (stage III) where the number of species in group "d" is far greater. The situation changes here in respect of density of pairs

Tab. III. Qualitative participation of birds with different nesting habits in different stages of secondary succession

Percentage values are given in brackets. Breeding groups: *c*, *d*, *e* — as for Table I

Stages of succession	Number of species		
	<i>c</i>	<i>d</i>	<i>e</i>
I	3 (100.0)		
II	4 (57.1)	3 (42.9)	
III	8 (40.0)	12 (60.0)	
IV	6 (40.0)	9 (60.0)	
V	11 (34.4)	9 (28.1)	12 (37.5)
VI	9 (25.7)	10 (28.6)	16 (45.7)

Tab. IV. Quantitative participation of birds with different nesting habits in different stages of secondary succession

Percentage values are given in brackets. Breeding groups: *c*, *d*, *e* — as for Table I

Stages of succession	Number of pairs per 10 ha		
	<i>c</i>	<i>d</i>	<i>e</i>
I	3.3 (100.0)		
II	8.3 (56.1)	6.5 (43.9)	
III	44.6 (52.8)	39.8 (47.2)	
IV	36.4 (54.5)	30.4 (45.5)	
V	19.4 (24.5)	23.3 (29.5)	36.5 (46.0)
VI	17.7 (19.7)	24.2 (27.0)	47.8 (53.3)

(Tab. IV), where values are similar to each other, while group “*c*” achieves a slight predominance. Hollow-nesters (“*e*”) appear in oak-hornbeam forests over 50 years old, hence they were not observed until the 95-year old forest (stage V). Their predominance over groups “*c*” and “*d*” is slight in this stage, but in the old tree stand (stage VI) is very significant. The predominance of hollow-nesters is clearly shown in their density. When expressed in percentages (Fig. 17) it is possible to perceive that there is a tendency for the changing bird communities to increase their complexity, manifested in the appearance of new nesting groups. In stage I, the most primitive from the successional aspect, there is only 1 such group (“*c*”), whereas in stage VI there are 3 such groups (“*c*”, “*d*”, “*e*”). There is also a tendency for dominance of hollow-nesters to increase during succession.

In the succession progressing towards tall trees (e.g., Fig. 15) on account of the time the birds stay there it is possible to distinguish two basic categories of bird species: “shrub-loving” species, dominating in stages II and III, and “tree-living” species, represented in their greatest number in the mature forest. There are about 12 species in the first category, and as many as approximately 30 species of birds in the second.

Table V gives the absolute and percentage participation in occurrence of migrating and wintering species of birds during the course of development of the oak-hornbeam forest. The results obtained do not reveal any unequivocal tendencies.

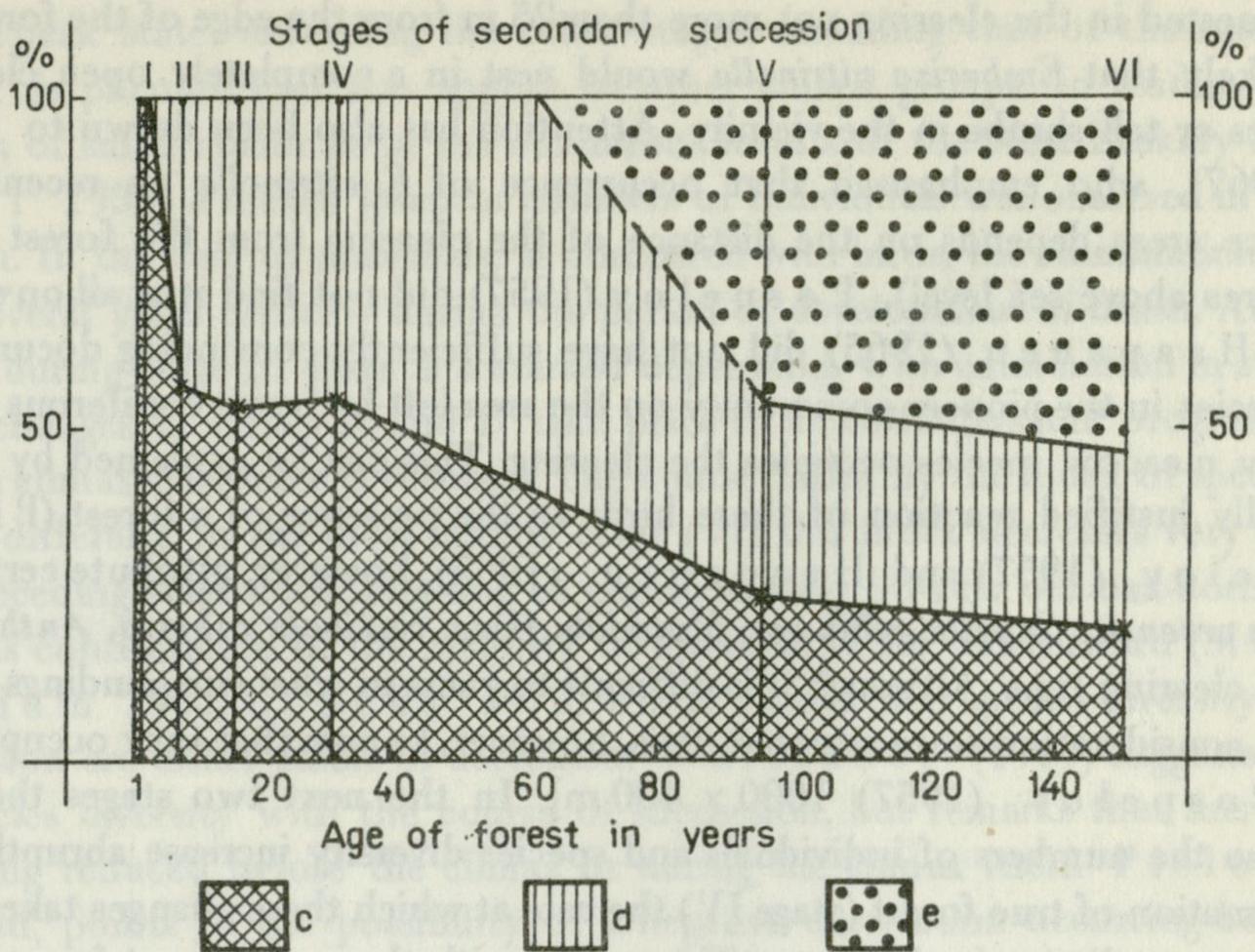


Fig. 17. Participation in percentages of breeding pairs of birds with different nesting habits in chosen stages of secondary succession  
Breeding groups – c, d, e – for explanations see the legend to Figure 10

Tab. V. Migrating and wintering species in particular stages of secondary succession of birds in the Niepołomice Forest

Percentage values are given in brackets

Species	Stages of succession					
	I	II	III	IV	V	VI
Migratory species	1 (33.3)	5 (71.4)	15 (75.0)	12 (80.0)	19 (59.4)	21 (60.0)
Wintering species	2 (66.7)	2 (28.6)	5 (25.0)	3 (20.0)	13 (40.6)	14 (40.0)
Proportion <i>M</i> : <i>W</i>	1 : 2	2.5 : 1	3 : 1	4 : 1	1.5 : 1	1.5 : 1

### 4.3. Discussion

Succession on clear-cut areas in a forest provides the opportunity of relatively accurately tracing development of biocenoses. The development of vegetation and stratification of the habitat takes place at a rapid rate: in stage I there is only one plant layer (C), in stage II – 2 (C, B), in stage III – 2 complete layers (C, B) and 1 partly formed layer (A), in stage IV and V – 3 (C, B, A) and in stage VI – 3 (C, B and very markedly developed layer A). Generally speaking this is followed by an increase in the organization of the avifauna (increase in  $H'$ ) but this process is not continuous (Fig. 16), as assumed in Margalef's (1968) and Odum's (1963) simplified models of succession.

Succession in the clear-cut area is initiated by the bird community containing only 3 species (Fig. 15). In addition the presence in it of an ubiquitous element, *Emberiza citrinella*, is clearly

conditional; it nested in the clearing not more than 25 m from the edge of the forest. It would seem very unlikely that *Emberiza citrinella* would nest in a completely open clearing unless there were trees or tall shrubs in the vicinity. Attention has also been drawn to this fact by P i k u l a (1967), who emphasised that occurrence of *E. citrinella* on recently clear-cut mountain spruce areas depends on the distance of the clearing from the forest (and on the height of the area above sea level). P o s p e l o v (1957) did not find it at all on spruce forest clearings, and H a a p a n e n (1965) did not have sufficiently convincing documentation to include this species in the pioneer community on the area left by burnt coniferous forest. None of the typically meadow species occupies the clearing. This can be explained by the negative and evolutionally justified reaction of these birds to the presence of a forest (P i n o w s k i 1954). P o s p e l o v (1957) and H a a p a n e n (1965), however, attribute certain meadow species (*Alauda arvensis*, *Capella gallinago*, *Motacilla flava*, *Saxicola rubetra*, *Anthus pratensis*) to areas of the clearing type. Although it is difficult to guess in what surroundings the clearings they took into consideration were situated, it is, however, known that they occupied large and intact areas [P o s p e l o v (1957) 1000 × 400 m]. In the next two stages the number of species, and also the numbers of individuals and species diversity increase abruptly. From the moment of formation of true forest (stage IV) the rate at which these changes take place, as the forest stand matures, distinctly decreases. This agrees with the opinion put forward by M a r g a l e f (1957) and O d u m (1963) that the early stages of succession are distinguished by greater dynamism. Bird communities in stages II and III are the type characteristic of shrub and young tree stands. They are best distinguished by the group of indicator species G-2. The bird community of stage III also forms a decided transition to typically forest avifauna, the group of species G-3 forming the most important link here. There are no specific species in stage IV and it undoubtedly passes into the forest phase. The occurrence in this stage only of *Carduelis carduelis* may be fortuitous, and the same applies to the occurrence in the other communities of such birds as: *Crex crex*, *Tringa ochropus* and *Caprimulgus europaeus* [e.g., P i k u l a (1967) observed this last species only in the recently clear-cut area]. The communities of mature forests (stages V and VI) are most differentiated by the group of species nesting in tree-hollows (G-4).

The course taken by curves *N*, *D* and *H'* (and even *J'*) points to the existence in the secondary successional sere of two phases of development of the avifauna: a shorter, but expressed by more abrupt increase in the values of the characters examined, brush phase and a longer phase of true forest following a more even course (Fig. 16). Interchange of these phases takes place approximately from stage III, when the abundant development of birds characteristic of thin brush and young tree stands still continues, and simultaneously species closely connected with tree stands appear. This break in succession of birds is justified in the structural changes of vegetation tending successionally in the direction of mature forest. In stage III brush arrives at peak development, and young trees appear among it. In this stage the influence of the ecotone effect is still strong, hence the values for the bird community formed here are relatively very high. It would not appear that this pattern of succession was due to some random errors. Data given by other authors also support the foregoing, for instance, density values for breeding pairs (individuals) obtained in studies on succession of birds in northern and east European coniferous forests (P o s p e l o v 1957, H a a p a n e n 1965), in oak forests of Burgundy (F e r r y and F r o c h o t 1970), or in habitats leading in course of development to oak-hickory forests in the United States of America (J o h n s t o n and O d u m 1956) are very similarly formed, with appearance of a decided peak in the 12–20 year old stage. In studies by P o s p e l o v (1957) and R a b e l e r (1955) density of birds at this stage of succession even

reached a peak state, exceeding the other stages, including that of the mature forest in this respect. This phenomenon also applies to other animal groups. In studies on the secondary succession of small mammals in the coniferous forests of the West Beskidy Mountains (Grodziński 1959) a similar jump in numbers of individuals was observed in the early phase of succession. In the case of mammals, as compared with birds, the culmination of this progress is evident several years earlier — during the period of development of brush. After intensification occurring during stage III there is a marked depression, with culmination in stage IV. From this time on changes in values  $N$  and  $D$  take place in a continuous and progressive way until the stage of a climax character is reached. The course taken by the index of species diversity  $H'$  is, however, different. In the most mature stage (VI) this index decreases very slightly in relation to the preceding stage corresponding to approximately 95-year old oak-hornbeam forest. This fact forms confirmation of the majority of opinions so far put forward (Margalef 1957, 1968, Odum 1963, Loucks 1970) which assume that species diversity in the final stages of succession are either stable or decreased. Whittaker (1969) suggests a constant increase in species diversity with the course of succession, but remarks that there are cases of this index being reduced before the climax or during the climax itself. Pielou (1966), on the other hand, points to the possibility of a negative correlation occurring between progress of succession and species diversity. This latter possibility has not, however, found really reliable confirmation. In the case in question attainment of maximum species diversity by the subclimax community (stage V) can be connected with the complete and most balanced stratification in secondary succession of the habitat corresponding to it. The oldest oak-hornbeam forest, on the other hand (stage VI), accepted under the local conditions as the climax or almost the climax, although exhibiting stronger vertical development than the preceding stages, but the uneven development in it of the various layers of plants results in a relatively worse dominance structure of bird species (lower  $J'$ ). This factor thus determined the value  $H'$ , not the highest in this stage, although the community of the oldest forest stand contains the largest number of bird species qualifying for consideration. The difference between the highest value  $H'$  in the successional sere of the preclimax community (stage V) and value  $H'$  of the climax community (stage VI) is, however, very small (only 0.015 bit). It may therefore be concluded that this index had reached a state of relative stability by these stages of development which, under natural conditions, is manifested in the form of slight oscillation in relation to a certain average value. It is probable that the bird community of the oldest oak-hornbeam forest was exactly in the lower position of these periodic fluctuations in value  $H'$ . This is due — as already mentioned during discussion of primary succession — to the temporary structure of the forest stand in this stage.

The question of stability is closely connected with succession and diversity. There are hypotheses assuming that stability increases with an increase in species diversity (linear increase may also reach only to a certain point) and there are also certain grounds for concluding that there is no correlation between these indexes (Loucks 1970). In the present case it is impossible to establish stability in successive bird communities since, except for the last two stages, they were examined in one season only. When, however, analysis is made of communities V and VI (Głowaciński — 1975) it is possible to discern a distinct yearly fluctuation, chronologically agreeing in both stages, in the density of birds, somewhat similar to the cyclic changes in numbers found in the case of small rodents. It was further found that the values of these changes, taken jointly, are almost 3 times greater in the bird community of the old forest stand (coefficient of variation  $V = 12.10$ ) than in the 95-year old forest stand ( $V = 4.76$ ). This is thus evidence of the greater fluctuations of the ornithocenoses of the old

oak-hornbeam forest (VI) than in the younger stand (V). At the same time this provides support for the hypothesis that the greater the species diversity distinguishing the community, the greater the community's stability.

If both wintering and migrating birds are taken into consideration it is possible to put forward the hypothesis, that in habitats developing later, that is, more complicated ones, the importance of wintering species becomes greater. It may be assumed that natural selection favours the settled way of life in birds in increasingly later stages of succession, particularly when hollow-nesters appear. This assumption is confirmed by Ferry and Frochot (1970). The material obtained in the Niepołomice Forest does not lead to this unequivocal conclusion. Up to the stage of the young forest stand (IV) the relative participation of species migrating for the winter increases, but in mature forests (stages V and VI) proportions between the two categories of avifauna are far more balanced (Tab. V). Probably, under the climatic conditions of the Niepołomice Forest, the wintering or migratory tendencies of birds are significantly affected by their appurtenance to one of the two ecological groups of avifauna – hollow-nesters ("e") and non-hollow-nesters ("c", "d"). It must be assumed that non-hollow-nesters have slightly worse chances of surviving severe winter conditions, hence natural selection favours migratory tendencies in them (in group "c" and "d" of the bird communities examined as much as 76% is formed by migrating species). In successional stages V and VI hollow-nesters appear (group "e") in which wintering is a clearly more frequent phenomenon than migration (only 31% of migrating species). Since hollow-nesters in old tree stands form a large part of the avifauna (Tab. III), the participation of wintering species markedly increased in these stages (Tab. V). Differences in results obtained in the oak-hornbeam forest on the river Saon (Ferry and Frochot 1970) and in a similar forest on the river Vistula are probably due to the different climatic conditions affecting the avifauna of these regions of Europe, which lie at a considerable distance from each other.

## 5. FINAL REMARKS

The successional seres examined become increasingly similar to each other in the older stages and finally reach almost the same formations. The bird communities described were compared by means of the system of each with each, using Cody's (1970) index (*CI*). This index takes into consideration the number and dominance of the species in the community; it is particularly sensitive to changes in the dominance structure of species. The communities compared were arranged in the form of a dendrite (Fig. 18).

The group of forest communities, the most highly organized (*BW*, *Q1*, *Q2*, *Q3*, *CA*, *PQ*, *VP*) were decidedly differentiated. The central position in this group is occupied by bird communities of habitats of a climax (*Q3*, *PQ*) and subclimax (*Q2*, *CA*) character. A further group is formed by the communities of the old river bed *V1* and *V2*. Bird communities of the regrowing clearing *C2* and recently clear-cut *C1* form separate units.

It is clear from the dendrite comparison that the beginnings of primary succession of series A (the stages preceding the forest phase were not described in series B) and secondary succession are fundamentally different. The bird communities of the two successional sequences, however, become very similar at the stage of appearance of three vegetation layers (layers C, B and A) in habitats, that is, in the forest group. The distance of the bird community of the recently clear-cut area *C1* (single-layer habitat) from the community of the brushwood clearing *C2* (2-layer habitat) is as great as that between community *C2* and the group of forest communities

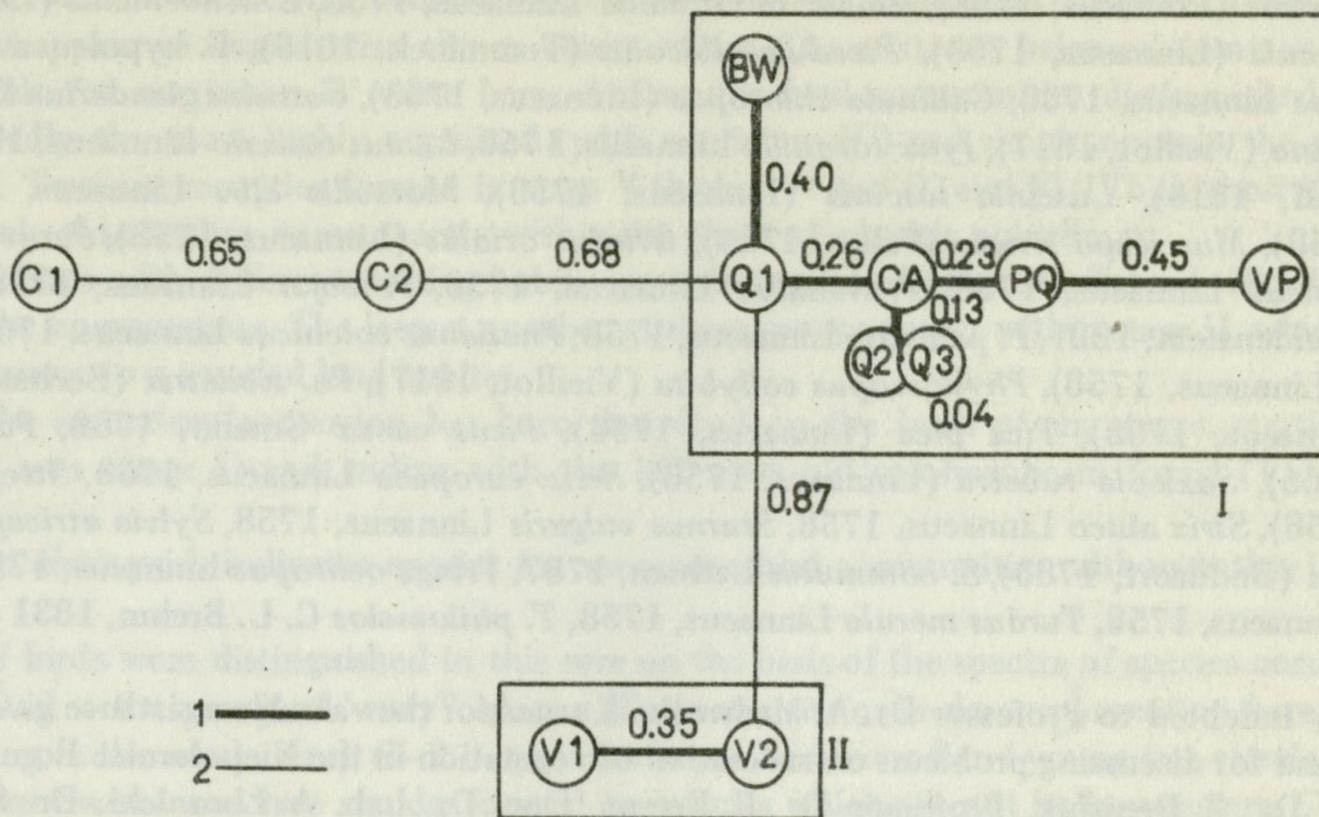


Fig. 18. Bird communities examined and arranged in a dendrite, on the basis of Cody's (1970) index 1 – differentiation to 0.50, 2 – differentiation  $> 0.50$ , I – group of bird communities of forest habitats, II – of brushwood habitats. Symbols for bird communities: V1 – bird community of the old river bed of the Vistula, V2 – of the overgrown old river bed of the Vistula, CA – *Circaeo-Alnetum* forest, C1 – recently clear-cut area, C2 – older clearing, BW – oak-hornbeam stand of thicket and young trees, Q1 – *Quercus-Carpinetum* forest about 30 years old, Q2 – *Quercus-Carpinetum* forest about 95 years old, Q3 – the oldest *Quercus-Carpinetum* forest, PQ – mixed pine forest *Pino-Quercetum*, VP – coniferous forest *Vaccinium uliginosi-Pinetum*

(3-layer habitats). An even greater distance separates the forest group from the old river bed community V2 (a habitat which in parts has two, and in others even three layers) which – like the clearing community C2 – ought to be considered as belonging to the brushwood category. The relatively close position to each other of the communities of the old river bed are due to the fact that tall sedge occurred here and there in the younger part of the old river bed, that is, a kind of counterpart of brushwood, which to a great degree rendered it similar to the completely overgrown old river bed. The organization of bird communities is thus a faithful reflection of the structure and quality of their habitats. Increase in this organization at the transition from a habitat with one layer of vegetation to a 2-layer habitat, and then 3-layer, is abrupt – almost a jump.

#### 6. APPENDIX – LIST OF FULL SCIENTIFIC NAMES OF THE BIRD SPECIES EXAMINED<sup>5</sup>

*Acrocephalus arundinaceus* (Linnaeus, 1758), *A. schoenobaenus* (Linnaeus, 1758), *A. scirpaceus* (Hermann, 1804), *Alauda arvensis* Linnaeus, 1758, *Anas platyrhynchos* Linnaeus, 1758, *A. querquedula* Linnaeus, 1758, *Anthus pratensis* (Linnaeus, 1758), *A. trivialis* (Linnaeus, 1758), *Capella gallinago* (Linnaeus, 1758), *Caprimulgus europaeus* Linnaeus, 1758, *Carduelis carduelis* (Linnaeus, 1758), *C. chloris* (Linnaeus, 1758), *Certhia brachydactyla* C. L. Brehm, 1820, *C. familiaris* Linnaeus, 1758, *Coccothraustes coccothraustes* (Linnaeus, 1758), *Columba oenas* Linnaeus, 1758, *C. palumbus* Linnaeus, 1758, *Crex crex* (Linnaeus, 1758), *Dendrocopos major* (Linnaeus, 1758), *D. medius* (Linnaeus, 1758), *D. minor* (Linnaeus, 1758),

<sup>5</sup>Nomenclature of species is accepted after F e r e n s (1967, 1971).

*Dryocopus martius* (Linnaeus, 1758), *Emberiza citrineilla* Linnaeus, 1758, *E. schoeniclus* (Linnaeus, 1758), *Erithacus rubecula* (Linnaeus, 1758), *Ficedula albicollis* (Temminck, 1815), *F. hypoleuca* (Pallas, 1764), *Fringilla coelebs* Linnaeus, 1758, *Gallinula chloropus* (Linnaeus, 1753), *Garrulus glandarius* Linnaeus, 1758, *Hippolais icterina* (Vieillot, 1817), *Jynx torquilla* Linnaeus, 1758, *Lanius collurio* Linnaeus, 1758, *Locustella fluviatilis* (Wolf, 1810), *Luscinia luscinia* (Linnaeus, 1758), *Motacilla alba* Linnaeus, 1758, *M. flava* (Linnaeus, 1758), *Muscicapa striata* (Pallas, 1764), *Oriolus oriolus* (Linnaeus, 1758), *Parus ater* Linnaeus, 1758, *P. caeruleus* Linnaeus, 1758, *P. cristatus* Linnaeus, 1758, *P. major* Linnaeus, 1758, *P. montanus* F. Conrad v. Baldenstein, 1827, *P. palustris* Linnaeus, 1758, *Phasianus colchicus* Linnaeus, 1758, *Phoenicurus phoenicurus* (Linnaeus, 1758), *Phylloscopus collybita* (Vieillot, 1817), *Ph. sibilatrix* (Bechstein, 1793), *Ph. trochilus* (Linnaeus, 1758), *Pica pica* (Linnaeus, 1758), *Picus canus* Gmelin, 1788, *Porzana porzana* (Linnaeus, 1766), *Saxicola rubetra* (Linnaeus, 1758), *Sitta europaea* Linnaeus, 1758, *Streptopelia turtur* (Linnaeus, 1758), *Strix aluco* Linnaeus, 1758, *Sturnus vulgaris* Linnaeus, 1758, *Sylvia atricapilla* (Linnaeus, 1758), *S. borin* (Boddaert, 1783), *S. communis* Latham, 1787, *Tringa ochropus* Linnaeus, 1758, *Troglodytes troglodytes* Linnaeus, 1758, *Turdus merula* Linnaeus, 1758, *T. philomelos* C. L. Brehm, 1831.

I am greatly indebted to Professor Dr. A. Medwecka-Kornaś for the valuable assistance given in organizing these studies and for discussing problems on succession of vegetation in the Niepołomice Forest. I should also like to thank Dr. Z. Denisiuk, Professor Dr. B. Ferens, Doc. Dr. hab. A. Łomnicki, Dr. S. Michalik, Dr. Z. Witkowski and Professor Dr. hab. K. Zarzycki for their critical appraisal of this paper, and to express my gratitude to all in charge of the Nature Conservation Research Centre of the Polish Academy of Sciences in Cracow for creating such favourable conditions for carrying out these studies.

## 7. SUMMARY

Using the method of comparisons and indirect drawing of conclusions, two types of succession of birds were described in the Niepołomice Forest: (1) primary succession, leading from old river bed (series A) and bog pinewood (series B) to forests forming local polyclimax and (2) secondary succession on a clearing in an oak-hornbeam forest. The sequence of bird communities (community understood in the sense of a group of species nesting in a given habitat) was related to the natural changes in the ground and plant cover. Examination was made of the avifauna during the period of its maximum stabilization.

The following were taken as criteria for evaluating the succession of bird communities: number of species ( $N$ ), density of pairs or individuals ( $D$ ), species diversity ( $H'$ ) and dominance structure of species in the community ( $J'$ ).

The density of the birds was defined by means of the mapping method, omitting sporadic species ( $D < 0.1$  pair/10 ha) from the analyses. Species diversity was established on the basis of the Shannon-Wiener function (Lloyd, Zar and Karr 1968). Differentiation of bird communities was calculated by means of Cody's (1970) index. In order to make the comparisons, the values of this index were arranged in the form of a dendrite by means of the "Wrocław taxonomy" (Perkal 1958). Dominance structure of species was defined by means of the equation given by Tramer (1969).

Two probably coinciding successional series A and B were taken for the simplified reconstruction of primary succession of birds. The main series (A) is formed by: old bed of the Vistula (stage I) → old bed of the Vistula in the stage of formation of wet alderwood (II) → alder carr (III) → humid oak-hornbeam forest about 95 years old without the addition of pine (IV) → slightly drier oak-hornbeam forest about 150 years old, with the addition of pine (V) → oak-pine forest with tendency to fresh pinewood (VI/IVb). The shorter series (B) which can be derived from peat bog, is formed by bog pine-wood (IIIb) and oak-pine forest (VI/IVb) (Figs. 1–7).

Succession is accompanied by increase in the stratification of habitats. This is followed by increase in the capacity of habitats and the development of different and increasingly complex bird communities (Fig. 8). Certain species can be considered as indicators [in the sense of Alleé et al. (1949)] in the different communities.

The spectra of species permit of distinguishing 6 more or less distinct ecological groups of birds (Fig. 8). These are: the group of water and sedge species ( $G-1$ ), the group of brushwood and ecotone species of narrow ( $G-2$ ) and wide range ( $G-3$ ), the group of forest species with a wide scale of occurrence ( $G-4$ ), the group of oak-hornbeam forest species ( $G-5$ ) and coniferous forest species ( $G-6$ ).

Changes in indexes  $N$ ,  $D$ ,  $H'$  and  $J'$  in successional series A and B form in the way shown in Figure 9. The

stage of oak-pine forest – which may connect both seres – has the most highly organized bird community ( $H'$ ), which would appear to characterize climax communities. The relatively balanced dominance of species ( $J'$ ) was responsible for maximum  $H'$  value here. Among the bird communities distinguished there is no community decidedly the most highly organized (with maximum  $H'$ ) and simultaneously the richest (with highest  $N$  and  $D$ ). Two communities formed in stage V (highest  $N$  and  $D$ ) and VI/IVb (highest  $H'$ ), however, qualify for this rank, that is, they come exactly within the phase of edaphic polyclimax.

Five groups of birds with different nesting habits were distinguished (Fig. 10, Tabs. I, II). None of them accompanies all the communities. The largest number of these groups comes within stage II, which forms the transition from a water to a wooded land habitat.

The sere of the secondary succession has been described on the basis of six stages, starting with the recently clear-cut area (stage I) and ending with the 150 year old oak-hornbeam forest (VI) (Figs. 4, 5, 11–15).

It is possible to distinguish indicator species for successive bird communities, although this is difficult in stage V.

Four groups of birds were distinguished in this sere on the basis of the spectra of species occurrence (Fig. 15). These are: G-1 – the group of ‘eury’ species (*Emberiza citrinella* deserves mention here as the only species participating in the whole sere), G-2 – species of open brushwood and young tree stands, G-3 – the group of forest brushwood and tree stands, formed by species which are not hollow-nesters, G-4 – forest group formed chiefly by hollow-nesters.

The course taken by curves  $N$ ,  $D$  and  $H'$  (Fig. 16) shows that succession of birds on the clearing is a two-phase process, since it is possible to distinguish a short brushwood phase and a longer phase of forest proper in it. The transition between these phases can be traced at the stage of the 15-year old young tree stand. The ecotone effect influences the bird community formed here. Indexes  $N$ ,  $H'$  and  $D$  reach their highest values in the avifauna of high forests. There is a slight decrease in index  $H'$  in the stage of the oldest forest stand (4.145 bits) in relation to the mature but younger oak-hornbeam forest (4.160 bits). This fact confirms the assumption (e.g., Loucks 1970) of stabilization or even decrease in species diversity in climax communities.

Seasonal variations in numbers of birds are almost three times greater in the community of the older forest (coefficient of variation  $V - 12.10$ ) than in the community of the 95-year old oak-hornbeam stand ( $V - 4.76$ ). This forms support for the opinion that the greater the species diversity distinguishing the community, the greater the stability of the community.

Participation in the course of secondary succession of species with different nesting habits is shown in Figure 17 and Tables III, IV.

The hypothesis may be put forward that in later stages of succession settled (wintering) species are of greater importance than migrating species. It is to be expected that the settled way of life of birds would be favoured by natural selection, particularly in the stages in which hollow-nesters appear. This hypothesis is confirmed by studies made in the forests of Burgundy (Ferry and Frochet 1970), but material from the Niepołomice Forest does not lead to any such unequivocal conclusion (Tab. V).

Comparison of the bird communities studied (Fig. 18) reveals the differentiation of the group of most highly organized forest communities ( $BW$ ,  $Q1$ ,  $Q2$ ,  $Q3$ ,  $CA$ ,  $PQ$ ,  $VP$ ), and then of communities typical of brushwood ( $C2$ ,  $V2$  and to some degree  $V1$ ) and the community of the recently clear-cut area ( $C1$ ). In the forest group the central positions are occupied by communities of the climax habitats and those similar to them. The distance between the forest group (three layers of vegetation in the habitat) and brushwood communities (two layers) is similar to that between the communities of the regrowing clear-cut area and the recently clear-cut area (single layer). This suggests that the change in the organization of bird communities at the transition from the habitat with single-layer vegetation to two- and three-layer vegetation takes place abruptly, in the form of a jump.

## 8. POLISH SUMMARY (STRESZCZENIE)

W oparciu o metodę porównań i pośredniego wnioskowania opisano w Puszczy Niepołomickiej dwa typy sukcesji ptaków: 1) sukcesję pierwotną, prowadzącą od starorzecza (seria A) i boru bagiennego (seria B) do lasów tworzących lokalny poliklimaks oraz 2) sukcesję wtórną na zrębie lasu grądowego. Nastęstwo zespołów ptaków (zespół w sensie: zbiór gatunków gnieźdzących się w konkretnym siedlisku) odniesiono do naturalnych przemian podłoża i szaty roślinnej. Uwzględniono awifaunę w okresie jej największej stabilizacji.

Za kryteria oceny sukcesji zespołów ptaków przyjęto: liczbę gatunków ( $N$ ), zagęszczenie par lub osobników ( $D$ ), różnorodność gatunkową ( $H'$ ) i strukturę dominacji gatunków w zespole ( $J'$ ).

Zagęszczenie ptaków określano za pomocą metody kartowania. W analizach pominięto gatunki sporadyczne ( $D < 0,1$  pary/10 ha). Różnorodność gatunkową ustalono na podstawie funkcji Shannona-Wienera (Lloyd, Zar i Karr 1968). Zróżnicowanie zespołów ptaków obliczono stosując wskaźnik Cody'ego (1970). Wartości tego wskaźnika uporządkowano dla porównań w formie dendrytowej, metodą „taksonomii wrocławskiej” (Perkal 1958). Strukturę dominacji gatunków określano za pomocą wzoru podanego przez Tramera (1969).

Dla uproszczonego zrekonstruowania pierwotnej sukcesji ptaków przyjęto dwa, prawdopodobnie zbiegające się, szeregi sukcesyjne A i B. Szereg główny (A) tworzą: zarastające starorzecze Wisły (stadium I) → starorzecze na etapie tworzenia się olesu (II) → łęg olszowy (III) → wilgotny, około 95-letni grąd bez domieszki sosny (IV) → nieco suchszy, około 150-letni grąd z udziałem sosny (V) → bór mieszany z tendencją do boru sosnowego świeżego (VI/IVb). Szereg krótszy (B), który można wyprowadzić od torfowisk, tworzą sosnowy bór bagienny (IIIb) i bór mieszany (VI/IVb) (fig. 1–7).

Sukcesji towarzyszy wzrost stratyfikacji siedlisk. Za tym postępuje wzrost chłonności siedlisk i rozwój odmiennych, coraz bardziej złożonych zespołów ptaków (fig. 8). W poszczególnych zespołach pewne gatunki można uznać za wskaźnikowe [w sensie Allee et al. (1949)].

Spektra gatunków pozwalają wydzielić sześć mniej lub bardziej wyraźnych grup ekologicznych ptaków (fig. 8). Są to: grupa gatunków wodnych i szuwarowych (G-1), grupa gatunków zaroślowych i ekotonalnych wąskiego zasięgu (G-2) i szerokiego (G-3), grupa gatunków leśnych o szerokiej skali występowania (G-4); grupa gatunków grądowych (G-5) i borowych (G-6).

Zmiany wskaźników  $N$ ,  $D$ ,  $H'$  i  $J'$  w szeregach sukcesyjnych A i B kształtują się tak, jak przedstawia figura 9. W stadium boru mieszanego – które może łączyć oba szeregi – występuje zespół ptaków o najwyższej organizacji ( $H'$ ), co wydaje się cechować zespoły klimaksowe. O najwyższej wartości  $H'$  w tym stadium zaważyła stosunkowo wyrównana dominacja gatunków ( $J'$ ). Wśród wyróżnionych zespołów ptaków brak jest zespołu zdecydowanie najwyżej zorganizowanego (z najwyższym  $H'$ ) i zarazem najbogatszego (z najwyższymi  $N$  i  $D$ ). Do rangi tej kwalifikują się natomiast dwa zespoły ukształtowane w stadium V (najwyższe  $N$  i  $D$ ) i VI/IVb (najwyższe  $H'$ ), czyli mieszczące się akurat w fazie edaficznego poliklimaksu.

Wydzielono pięć grup ptaków o różnym typie gnieźdzenia się (fig. 10, tab. I, II). Żadna z nich nie towarzyszy wszystkim zespołom. Najwięcej tych grup zawiera stadium II, stanowiące przejście od środowiska wodnego do środowiska lądowego leśnego.

Szereg sukcesji wtórnej opisano w oparciu o sześć stadiów, poczynając od świeżego zrębu (stadium I) i kończąc na 150-letnim grądzie (VI) (fig. 4, 5, 11–15).

Dla kolejnych zespołów ptaków można wydzielić gatunki wskaźnikowe; trudno je jednak wyróżnić w stadium V.

Na podstawie spektrów występowania gatunków wydzielono w tym szeregu cztery grupy ptaków (fig. 15). Są to: G-1 – grupa gatunków eurytopowych (zwraca tu uwagę *Emberiza citrinella* jako jedyny gatunek uszczestniczący w całym szeregu), G-2 – otwartych zarośli i młodnika, G-3 – zarośli leśnych i drzewostanów, obejmująca gatunki nie będące dziuplakami, G-4 – grupa leśna, obejmująca głównie dziuplaki.

Przebieg krzywych  $N$ ,  $D$  i  $H'$  (fig. 16) wskazuje, że sukcesja ptaków na zrębie jest procesem dwufazowym. Zaznacza się w niej krótka faza zaroślowa i dłuższa faza właściwego lasu. Przejście między tymi fazami zaznacza się na etapie 15-letniego młodnika. Na wykształcony tu zespół ptaków oddziałuje efekt ekotonu. Wskaźniki  $N$ ,  $H'$  i  $D$  osiągają najwyższe wartości u awifauny wysokopiennych lasów. Zaznacza się pewien spadek wskaźnika  $H'$  w stadium starodrzewia (4,145 bita) w stosunku do grądu dojrzałego, lecz młodszego (4,160). Fakt ten potwierdza tezę (np. Loucks 1970), zakładającą stabilizację lub nawet obniżanie się różnorodności gatunkowej w zespołach klimaksowych.

Sezonowa zmienność liczebności ptaków jest prawie trzykrotnie większa w zespole starodrzewia (współczynnik zmienności  $V = 12,10$ ) aniżeli w zespole grądu 95-letniego ( $V = 4,76$ ). Przemawia to za poglądem, że im zespół odznacza się większą różnorodnością gatunkową, tym jest bardziej stabilny.

Udział w trakcie sukcesji wtórnej gatunków o różnym typie gnieźdzenia się przedstawia figura 17 i tabele III, IV.

M można postawić hipotezę, że w późniejszych stadiach sukcesji większe znaczenie mają gatunki osiadłe (zimujące) niż migrujące. Wsparcia osiadłości przez dobór naturalny należałoby oczekiwać zwłaszcza w stadiach, w których pojawiają się dziuplaki. Hipotezę tę potwierdzają badania w lasach Burgundii (Ferry i Frochot 1970). Materiały z Puszczy Niepołomickiej nie prowadzą do tak jednoznacznego wniosku (tab. V).

Porównanie badanych zespołów ptaków (fig. 18) prowadzi do wyróżnienia grupy zespołów leśnych, najwyżej zorganizowanych (*BW, Q1, Q2, Q3, CA, PQ, VP*), a następnie zespołów o charakterze zaroślowym (*C2, V2*, do pewnego stopnia *V1*) oraz zespołu świeżego zrębu (*C1*). W grupie leśnej centralne pozycje zajmują zespoły siedlisk klimaksowych i do nich zbliżonych. Dystans między grupą leśną (trzy warstwy roślinne w siedlisku) i zespołami zaroślowymi (dwie warstwy) jest podobnie duży, jak między zespołem zrębu zarastającego i zrębu świeżego (jedna warstwa). Sugeruje to, że zmiana organizacji zespołów ptaków na przejściu z siedliska o jednej warstwie roślinności w dwu i trójwarstwowe następuje gwałtownie, jakby skokowo.

## 9. REFERENCES

1. Allee W.C., Emerson A.E., Park T., Schmidt K.P. 1949 – Principles of animal ecology – W. B. Saunders, Philadelphia, London, 837 pp.
2. Bzowski M. 1973 – Rzeźba i stosunki wodne dna doliny Wisły w rejonie północnej części Puszczy Niepołomickiej – *Studia Naturae A*, 7: 7–37.
3. Cody M.L. 1970 – Chilean bird distribution – *Ecology*, 51:453–464.
4. Dierschke F. 1951 – Die Vogelbestände einiger Erlenbruchnalder Ostpreussens und Niedersachsens – *Orn. Abh. H*, 10: 1–32.
5. Dubiel E. 1973 – Zespoły roślinne starorzeczy Wisły w Puszczy Niepołomickiej i jej otoczeniu – *Studia Naturae A*, 7: 67–124.
6. Dyrz A., Okulewicz J., Tomiałojć L., Witkowski J. 1972 – Ornitofauna łęgowa Bagien Biebrzańskich i terenów przyległych – *Acta orn.*, Warsz. 13: 343–422.
7. Enemar A. 1959 – On the determination of the size and composition of a passerine bird population during the breeding season. A methodological study – *Var Fagelvarld*, Suppl. 2: 1–114.
8. Ferchmin M., Medwecka-Kornaś A. (in press) – Lasy dębowe, głównie *Tilio-Carpinetum*, w północnej części Puszczy Niepołomickiej – *Studia Naturae*.
9. Ferens B. (Ed.) 1967 – Klucze do oznaczania kręgowców Polski. Part IV A, Ptaki, *Non-Passeriformes* – PWN, Warszawa, Kraków, 414 pp.
10. Ferens B. (Ed.) 1971 – Klucze do oznaczania kręgowców Polski. Part IV B, Ptaki, *Passeriformes* – PWN, Warszawa, Kraków, 249 pp.
11. Ferry C., Frochot B. 1970 – L'avifaune nidificatrice d'une forêt de chênes pedunculés en Bourgogne: étude de deux successions écologiques – *Terre Vie*, No. 2: 153–250.
12. Frochot B. 1971 – L'évolution saisonnière de l'avifaune dans une futaie de chênes en Bourgogne – *Terre Vie*, No. 2: 145–182.
13. Gashwiler J. S. 1970 – Plant and mammal changes on a clearcut in West-Central Oregon – *Ecology*, 51: 1018–1026.
14. Giller F. 1969 – Der Sukzessionsverlauf nach einen grossen Fichtenkalschlag in Hochsauerland – *Natur Heimat*, 29: 16–19.
15. Głowaciński Z. 1975 – Ptaki Puszczy Niepołomickiej (studium faunistyczno-ekologiczne) – *Acta zool. cracov.* 20: 1–88.
16. Grodzinski W., 1959 – Sukcesja zespołów drobnych ssaków na zarastającym zrębie izsuwie górskim w Beskidzie Średnim (Karpaty Zachodnie) – *Ekol. pol.* A, 7: 83–144.
17. Haapanen A. 1965 – Bird fauna of the Finnish forests in relation to forest succession. I – *Ann. Zool. fenn.* 2: 153–196.
18. Haapanen A. 1966 – Bird fauna of the Finnish forests in relation to forest succession. II – *Ann. Zool. fenn.* 3: 176–200.
19. International Bird Census Committee 1969 – Recommendations for an international standard for a mapping method in bird census work – *Bird Study* 16: 248–255.
20. Janetschek H. 1949 – Tierische Sukzessionen auf hochalpinen Neuland – *Ber. naturw.-med. Ver. Innsbruck*, 48/49: 215 pp.
21. Johnson W. M. 1945 – Natural revegetation of abandoned crop land in the Ponderosa Pine Zone of the Pike's Peak Region in Colorado – *Ecology*, 26: 363–374.
22. Johnston D. W., Odum E. P. 1956 – Breeding bird population in relation to plant succession on the Piedmont of Georgia – *Ecology*, 37: 50–62.
23. Jones P. H. 1972 – Succession in breeding bird population of sample Welsh oakwoods – *Br. Birds*, 65: 291–299.

24. K a n i a W. 1968 – Ptaki południowo-wschodniej części Puszczy Niepołomickiej – Acta orn., Warsz .11: 61–86 .
25. K a r r J. R. 1968 – Habitat and avian diversity on strip-mined land in East-Central Illinois – Condor, 70: 348–357.
26. K a š k a r o v D. N. 1938 – Osnovy ékologii životnych – Gosudarstvennoe Izdatel'stvo Sovetskaja Nauka, Moskva, Leningrad, 601 pp .
27. K e r z i n a M. N. 1956 – Vlijanie vyrubok i garej na formirovanie lesnoj fauny (In: Rol životnych w žizni lesa. Ed. A. A. Nasimovič) – Izdatel'stvo Moskovskogo Universiteta, Moskva, 217–303 .
28. K r a t o c h v i l J, G a i s l e r J. 1967 – Die Sukzession der kleinen Erdsäugetiere in einem Bergwald *Sorbeto-Piceetum* – Zool. Listy, 16: 301–324.
29. K r e b s C. J. 1972 – Ecology, the experimental analysis of distribution and abundance – Harper and Row Publishers Inc., New York, 694 pp.
30. L a c k D. 1939 – Further changes in the Brechland avifauna caused by afforestation – J. Anim. Ecol. 8: 277–299.
31. L a c k D., L a c k E. 1951 – Further changes in bird-life caused by afforestation – J. Anim. Ecol. 20: 173–179.
32. L a c k D., V e n a b l e s L. S. V. 1939 – The habitat distribution of British woodland birds – J. Anim. Ecol. 8: 39–71.
33. L l o y d M., Z a r J. H., K a r r J. R. 1968 – On the calculation of information-theoretical measures of diversity – Am. Midl. Nat. 79: 257–272.
34. L o u c k s O. L. 1970 – Evolution of diversity, efficiency, and community stability – Am. Zool. 10: 17–25.
35. M a c A r t h u r R. H., M a c A r t h u r J. W. 1961 – On bird species diversity – Ecology, 42: 594–598.
36. M a r g a l e f R. 1957 – La teoria de la informacion en ecologia – Memos R. Acad. Cienc. Artes Barce-lona, 32: 373–449.
37. M a r g a l e f R. 1968 – Perspectives in ecological theory – University of Chicago Press, Chicago, London, 111 pp.
38. M a r t i n N. D. 1960 – An analysis of bird populations in relation to forest succession in Algonquin Provincial Park, Ontario – Ecology, 41: 127–140.
39. M e d w e c k a - K o r n a ś A. 1959 – Zespoły leśne i zaroślowe (In: Szata roślinna Polski. I. Ed. W. Szafer) – PWN, Warszawa, 368–427.
40. M o r l e y A. 1940 – Recolonization by bird species on burnt woodland – J. Anim. Ecol. 9: 84–88.
41. N e r o n o v V. M. 1962 – O vlijanii chozjajstvennoj dejatel'nosti čeloveka na nasielenie myševidnych gryzunov v predgorjach Altaja – Zool. Ž. 41: 922–926.
42. O d u m E. P. 1959 – Fundamentals of ecology – W. B. Saunders Company, Philadelphia, 546 pp.
43. O d u m E. P. 1963 – Ecology – Holt, Rinehart and Winston, New York, 107 pp.
44. O r i a n s G. H. 1969 – The number of bird species in some tropical forest – Ecology, 50: 783–801.
45. P a w ł o w s k i B. 1959 – Dynamika zbiorowisk roślinnych (In: Szata roślinna Polski. I. Ed. W. Szafer) – PWN, Warszawa, 463–482.
46. P e r k a l J. 1958 – Matematyka dla rolników – PWN, Warszawa, 254 pp.
47. P i e l o u E. C. 1966 – Species-diversity and pattern-diversity in the study of ecological succession – J. theor. Biol. 10: 370–383.
48. P i k u l a J. 1967 – Die Artenzusammensetzung der Vogelpopulationen in den Entwicklungsphasen sekundärer und natürlicher Fichtenwald-Gesellschaften – Zool. Listy, 16: 279–292.
49. P i n o w s k i J. 1954 – Wpływ obszarów zadrzewionych na awifaunę terenów otwartych i związane z tym zagadnienia adaptacji populacyjnych – Ekol. pol. 2: 379–446.
50. P o s p e l o v S. M. 1957 – Pticy i mlekopitajusčie elnika-černičnika različnych vozrastov – Zool. Ž. 36: 603–607.
51. R a b e l e r W. 1955 – Die Artenfolge in den Vogelbeständen der Oberharzer Fichten-Forsten – Mitt. flor.-soz. ArbGemein. 5: 193–197.
52. R a j s k i A. 1965 – Sukcesja ekologiczna (wprowadzenie) – Ekol. pol. B, 11: 23–49.
53. S a l o L. J. 1967 – The changes in the nesting bird-fauna of lake Nurmijärvi during the period 1896–1965 with special reference to the present bird populations – Ornis fenn, 44: 57–65.
54. S t r a u t m a n F. J. 1954 – Pticy sovetskich Karpat – Izdatel'stvo Akad. Nauk Ukraïnskoj SSR, Inst. Agrob. Kiev, 331 pp.

55. Szafer W., Kulczyński S., Pawłowski B. 1953 – Rośliny polskie – PWN, Warszawa, 1020 pp.
56. Tramer E. J. 1969 – Bird species diversity: components of Shannon's formula – Ecology, 50: 927–929.
57. Turček F. J. 1957 – The bird succession in the conifer plantations on mat-grass land in Slovakia (ČSR) – Ibis, 99: 587–593.
58. Wasilewski A. 1961 – Certain aspects of the habitat selection of birds – Ekol. pol. A, 9: 109–137.
59. Whittaker R. H. 1969 – Evolution of diversity in plant communities (In: Diversity and stability in ecological systems. Ed. by Brookhaven National Laboratory) – Brookhaven Symp. Biol. 22: 178–196.
60. Yapp W. B. 1955 – The succession of birds in developing *Quercetum-petraeae* – NWest. Nat. 26: 58–67.
61. Zarzycki K. 1966 – Kilka uwag o sukcesjach roślinnych – Ekol. pol. B, 12: 231–236.

Paper prepared by H. Dominas

AUTHOR'S ADDRESS:

Dr Zbigniew Głowaciński  
Zakład Ochrony Przyrody PAN  
ul. Lubicz 46  
31–512 Kraków  
Poland.