

<p style="text-align: center;">EKOLOGIA POLSKA (Ekol. pol.)</p>	<p style="text-align: center;">28</p>	<p style="text-align: center;">1</p>	<p style="text-align: center;">71-94</p>	<p style="text-align: center;">1980</p>
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ENERGETICS OF BIRD FAUNA IN CONSECUTIVE STAGES OF SEMI-NATURAL PINE FOREST

ABSTRACT: In five consecutive developmental stages of cultivated pine forest the main structural and energetic characteristics in breeding bird communities were determined. Energy parameters were estimated with the help of dynamic computer simulation model. As the forest matures the following parameters of bird communities increase: number of species (S), density (N), species diversity calculated for individuals (H'_N) and energy (H'_A, H'_P, H'_{SC}), standing crop (SC), assimilation (A), and production (P). However, the changes of these characters are not entirely a continuous process. The ecological efficiency ($P : A$) and correlation of this coefficient with species diversity suggests that the series of communities described does not fully answer the patterns usually attributed to succession.

KEY WORDS: Birds communities, coniferous forest (Niepołomice Forest), southern Poland, succession, energy flow, simulation model.

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1. INTRODUCTION

In one of our earlier papers (Głowaciński and Weiner 1977) we have presented in detail the secondary succession of birds from the viewpoint of productivity and bioenergetics. As it seems it is an only work of this type, apart from some researches (Karr 1968, Ferry and Frochot 1970, Väisänen and Järvinen 1977), where — apart from a description of the structure of bird community — some functional energetic parameters are given ("consuming biomass", "existence energy requirements", "total energy consumed"). The present paper contains an estimation of energy flow through bird communities nesting in several development stages of coniferous forest, which, as opposed to the previously described series (Głowaciński and Weiner 1977), is carefully cultivated. It is also an attempt to explain how the changes of characteristics described correspond to some general concepts of succession.

2. AREA AND HABITATS

Investigations were carried out in the Niepołomice Forest about 30 km east of Cracow in the western part of the Sandomierz Basin. The forest complex in which the successional series was described (latitude 50°03' N, longitude 20°21' E, altitude 180–200 m a.s.l.) is situated in the Vistula valley on the plain of old Pleistocene sand terrace and the alluvial cone of the Raba river. This higher terrace of the Vistula is occupied almost entirely by acidophilous pine (*Pinus sylvestris* L.) and oak-pine forests.

Mean annual air temperature is 7.8°C, the highest occurs in July (+17.9°C), the lowest in January (−4.8°C). The vegetation period (with the mean 24-hour temperature higher than 5°C) lasts for 227 days, breeding season of birds — about 150 days.

The areas examined represent habitats of pine forest of a different age with an addition of oak, *Quercus robur* L., birch, *Betula verrucosa* Ehrh., and other trees. Five developmental stages of forest under special cultivation have been distinguished.

Stage I. Clear cut, 1 year old, overgrown with grass and sedge (mainly *Carex brizoides* L.) attaining 1 m in height. In places, there are still plant communities where *Vaccinium myrtillus* L. dominates and which are the component of herb layer of freshly cut forest. The examined area covered 0.8 ha.

Stage II. Forest cultures about 4 years old, consisting mainly of *Pinus sylvestris* (85% of the plantation area), and to a smaller extent of *Larix* sp., *Picea excelsa* Link. and *Alnus glutinosa* Gaertn. The young trees were up to 2.5 m high. There were also lush grass and sedge communities. Study area: 0.5 ha.

Stage III. Dense 10 years old thicket, which consisted of: *Pinus sylvestris* (85% of trees), *Larix* sp., *Quercus robur* and *Betula verrucosa*. The height of trees reaches up to 5 m. In herb layer there were low grasses (50% of surface area), *Vaccinium myrtillus* (10%) and *Calluna vulgaris* Salisb. (5%). Study area: 7.7 ha.

Stage IV. Dense pole wood about 35 years old. Prevalance of *Pinus sylvestris* (95% of trees), less frequently *Betula verrucosa* and *Quercus robur*. Typical forest layer of shrubs was absent. Herb vegetation poorly developed. Study area: 5.0 ha.

Stage V. Forest about 80 years old, natural characters. Tree layer composed of *Pinus sylvestris* (85% of trees), *Quercus robur* (10%) and *Betula verrucosa* (5%). The brushwood

consisted of: *Frangula alnus* Mill. (50% of shrubs), *Quercus robur* (25%), *Betula verrucosa* (20%) and other species. In herb layer occur mainly *Vaccinium myrtillus* (50% of the surface area), *Pteridium aquilinum* Kuhn., and *Carex brizoides*. Study area: 8.0 ha.

In this successional series there is no stage of climax, because old cultivated forest stands are being cut in this area.

3. METHODS

3.1. FIELD STUDIES AND STRUCTURAL INDICES

The putative successional series has been reconstructed on the basis of an appropriate soil-botanical expertise. Method of consecutive comparisons and simultaneously analysed development stages of the same type of forest under similar physical conditions, was used (cf., e.g., Głowaciński 1975).

Density (N) of birds (number of breeding territories per surface area unit) was determined by means of mapping method. Birds were counted in the breeding season of 1975.

Species diversity (H') was determined according to Shannon's (1948) formula:

$$H' = - \sum_{i=1}^S p_i \log_2 p_i$$

where: S – number of species in a community, p_i – fraction of individuals belonging to i th species.

Evenness (J') of bird communities was calculated according to formula given by Pielou (1966), and others:

$$J' = \frac{H'}{\log_2 S}$$

where: H' and S stand for the same as above.

H' and J' formulas were also used in relation to standing crop (H'_{SC} , J'_{SC}), assimilation (H'_A , J'_A) and production (H'_p , J'_p), substituting in p_i the number of pairs (or individuals) by proportion of total standing crop, assimilation and production belonging to i th species.

3.2. SIMULATION MODEL OF ENERGY FLOW IN BIRD COMMUNITY

Computer simulation becomes an important tool in studying the energy flow in bird communities (Wiens and Innis 1974, Weiner and Głowaciński 1975, Wiens and Nussbaum 1975, Głowaciński and Weiner 1977, Furness 1978). The model used in this study is identical to that used by the authors in a previous paper (Głowaciński and Weiner 1977).

The model makes it possible to simulate the energetic parameters of a single species popula-

tion as well as of the whole bird community (up to 70 species). The period of simulation lasts for 150 days, since March 15 till August 15, which represents the whole breeding season of every species considered, but does not include the process of intense dispersal of juveniles and emigration. It has been already proved that the breeding season comprises the major part of the annual population energy demand (Weiner and Głowaciński 1975).

The model of the energy flow in bird communities consists of the following main equations:

Species population variables

Numbers of birds

$$NGAT_{j,i} = N_j \cdot (1 - AMORT_j \cdot ID) \quad (1)$$

$$JUV_{j,i} = N_j \cdot EGCN_j \cdot SUCC_j \cdot BR_j \cdot (1 - JMORT_j \cdot IF) \quad (2)$$

Daily existence energy requirements

$$EMR_{j,i} = a_k W^{b_k} - c_k W^{d_k} \cdot T_i \quad (3)$$

$$EX_{j,i} = [EMR_{j,i} + 0.3 \cdot EMR_{j,i}(30^\circ\text{C})] \cdot (NGAT_{j,i} + JUV_{j,i}) \quad (4)$$

Daily cost of nest building

$$AN_{j,i} = 0.1 \cdot EMR_j(30^\circ\text{C}) \cdot FN_{j,i} \quad (5)$$

Daily cost of egg laying

$$AE_{j,i} = [(EGCN_j \cdot EGGW_j \cdot ECAL_k : 0.73) : (NEST_j + LEGG_j)] \cdot FE_{j,i} \quad (6)$$

Daily cost of incubation

$$AI_{j,i} = EX_j(30^\circ\text{C}) \cdot 0.3 \cdot FI_{j,i} \quad (7)$$

Energy requirements for growth

$$AGT_j = P_j : 0.2 = (EGCN_j \cdot SUCC_j \cdot VCAL_k \cdot W_j - EGGW_j \cdot ECAL_k) : 0.2 \quad (8)$$

$$AC_{j,i} = \varphi(AGT_{j,i}, NURS_j) \cdot FG_{j,i} \quad (9)$$

Community variables

$$SC_i = \sum_{j=1}^n [(NGAT_{j,i} + JUV_{j,i}) \cdot W_j \cdot VCAL_j] \quad (10)$$

$$R_i = \sum_{j=1}^n (EX_{j,i} + AN_{j,i} + AE_{j,i} + AI_{j,i} + 0.8 AC_{j,i}) \quad (11)$$

$$P_i = \sum_{j=1}^n (0.2 \cdot AG_{j,i}) \quad (12)$$

$$A_i = R_i + P_i \quad (13)$$

$$C_i = \frac{A_i}{0.75} \quad (14)$$

The variables and parameters contained in the model are explained below.

Subscripts

i – day of simulation

j – species

k – systematic group of birds

Model variables and their units

<i>N</i>	– number of adult individuals	· ha ⁻¹
<i>JUV</i>	– number of juveniles	· ha ⁻¹
<i>ID</i>	– number of days after arrival	
<i>IF</i>	– number of days after leaving the nest	
<i>FN</i>	– fraction of population involved in nest building at the day <i>i</i>	percentage
<i>FE</i>	– fraction of population involved in egg laying at the day <i>i</i>	percentage
<i>FI</i>	– fraction of population incubating at the day <i>i</i>	percentage
<i>FG</i>	– fraction of population nursing young at the day <i>i</i>	percentage
<i>EMR</i>	– existence metabolic rate	kJ · bird ⁻¹ · day ⁻¹
<i>EX</i>	– population daily cost of maintenance	kJ · ha ⁻¹ · day ⁻¹
<i>AN</i>	– additional cost of nest building in population	kJ · ha ⁻¹ · day ⁻¹
<i>AE</i>	– daily cost of egg laying in population	kJ · ha ⁻¹ · day ⁻¹
<i>AI</i>	– daily cost of incubation in population	kJ · ha ⁻¹ · day ⁻¹
<i>ACT</i>	– total energy demand of a brood during nestling period	kJ · brood ⁻¹
<i>AG</i>	– daily energy demand of nestlings in population	kJ · ha ⁻¹ · day ⁻¹
<i>SC</i>	– community standing crop	kJ · ha ⁻¹
<i>R</i>	– community respiration	kJ · ha ⁻¹ · day ⁻¹
<i>P</i>	– community production	kJ · ha ⁻¹ · day ⁻¹
<i>A</i>	– community assimilation	kJ · ha ⁻¹ · day ⁻¹
<i>C</i>	– community consumption of energy	kJ · ha ⁻¹ · day ⁻¹

Parameters

Local population specific parameters

<i>NGAT</i>	– maximum breeding density as determined in field	· ha ⁻¹
<i>T</i>	– ambient temperature	°C
<i>A</i>	– date of arrival of the 1st pair	

Species-specific parameters		
<i>ECCN</i>	– clutch size	
<i>ECCW</i>	– egg weight	g
<i>SUCC</i>	– breeding success	percentage
<i>BR</i>	– proportion of the whole population taking part in the next brood	percentage
<i>W</i>	– body weight	g
<i>NEST</i>	– duration of nest building	days
<i>LEGG</i>	– duration of egg-laying	days
<i>INC</i>	– duration of incubation	days
<i>NURS</i>	– duration of nestling period	days
<i>ISB</i>	– time break between 1st and 2nd brood	days
Model parameters		
<i>AMORT</i>	– mortality of adult birds	% · day ⁻¹
<i>JMORT</i>	– mortality of fledglings	% · day ⁻¹
<i>ECAL</i>	– caloric value of eggs	kJ · g ⁻¹
<i>VCAL</i>	– caloric value of the body	kJ · g ⁻¹
<i>a, b, c, d</i>	– parameters of the <i>EMR</i> function	

The model includes 21 parameters: three local population-specific parameters, which have to be determined in field, 10 species-specific parameters and 8 model-specific parameters. The actual values of species-specific and model-specific parameters were established on the basis of literature, however, if only the original authors' own data concerning local bird populations were available, those were used in simulations.

Figure 1 illustrates the way of calculating dynamics of numbers of birds and the proportion of the whole population which is involved in the activities of consecutive phenophases. It is assumed that the number of adults (*NGAT*) increases linearly from the day of occurrence of the first pair till the arrival is completed. The peak density is equal to those determined in field (*N*). The number of juveniles (*JUV*) increases also linearly starting from the date of leaving the nest by the first brood until the last nest is empty (Fig. 1). According to P a e v s k i j (1974) the average daily mortality ratio in passerines reaches 0.15%. This is, however, an over-year average, which includes periods of increased mortality during migrations, wintering, etc. For this reason, the coefficient of mortality of adults (*AMORT*) was arbitrarily diminished to 0.07%, while for the juveniles during their first month of life the mortality ratio (*JMORT*) of 0.15% was assumed for simulation.

The proportion of the whole population involved in any of the consecutive breeding activities was estimated according to the phenology of the species and also to the assumed time extension (*IPER*) in population (Fig. 1). The proportion of population taking part in the 1st, 2nd and eventually in the 3rd brood (*BR*) are specified (Fig. 1).

The energy budget of the population for each day of simulation is estimated according to various breeding activities and environmental conditions. Energetic calculations are based mainly on the functions and data elaborated by K e n d e i g h, D o l n i k and G a v r i l o v (1977). The parameters *a, b, c, d* of the function (3) relating existence metabolism (*EMR*) to body weight and ambient temperature (Table 1) for passerines, were recalculated using K e n d e i g h, D o l n i k and G a v r i l o v's (1977) data, but excluding the tropical and sub-arctic species (76 species of temperate climatic zone were considered). For all other

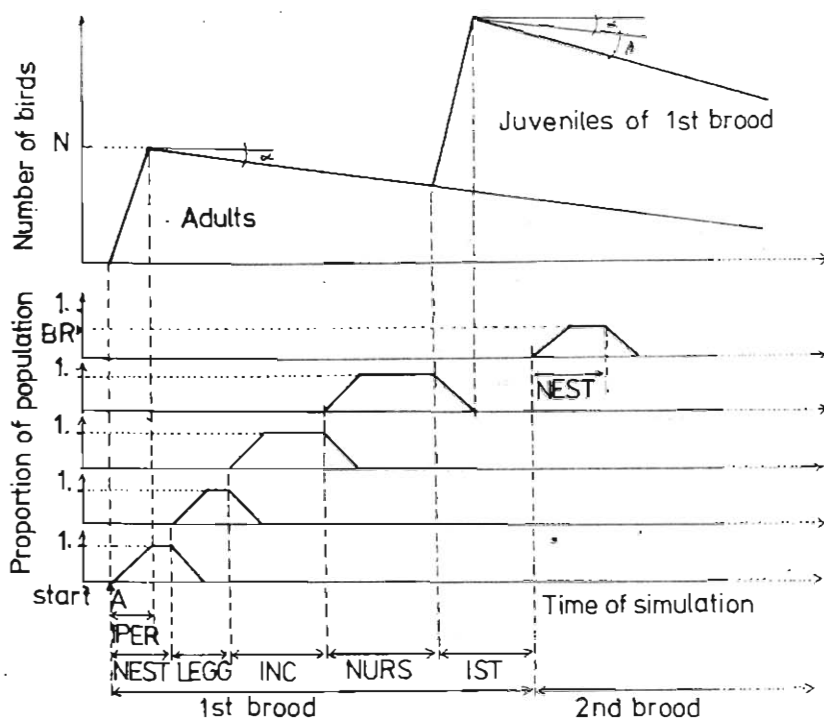


Fig. 1. Simulation of population dynamics and time table of a species

Species-specific parameters: A – date of the arrival of first pair, $IPER$ – time delay in arrival of the last pair, N – maximum breeding bird density as determined in field, $NEST$ – duration of the period of nest building, $LEGG$ – duration of the period of egg laying, INC – duration of incubation period, $NURS$ – duration of nestling care period, IST – time lag before 2nd brood is started, BR – fraction of population taking part in the 2nd brood. Model parameters: $JMORT = 1g\beta$ = juveniles' mortality ratio, $AMORT = 1g\alpha$ = adults' mortality ratio

taxonomic groups of birds Kendeigh, Dolnik and Gavrilov's (1977) original parameters were applied. The activity correction of 30% of thermoneutral existence metabolism ($0.3 \cdot EMR (30^{\circ}C)$, equation (4)) was added. Additional 10% of $EMR (30^{\circ}C)$ is added for the increased activity during nest building and young's care (equation (5)). The activity correction factors are temperature independent. A 30% increase of $EMR (30^{\circ}C)$ was assumed for the period of incubation (equation (7)). The cost of egg laying is estimated by calculation of the total energetic value of the clutch (equation (6)) and by assuming the 73% efficiency of egg production (El-Wailly 1966). The total energy demand for egg production is uniformly distributed over the period of nest building and egg laying.

The efficiency of the biomass production in nestlings ($P : A$) averages 20% (Pinowski 1968, Diehl 1971, Myrcha, Pinowski and Tomek 1973, Westerterp 1973, Blem 1974, Tomek 1975). For the sake of simplification the total production during the nestling period was assumed to be equal to the energy value of the biomass of fledglings leaving the nest (in the model the losses in brood are assumed to occur at the day of hatching). The total energy demand of the brood (AGT) may be easily computed (equation (8)). The amount,

Table 1. Standing crop and energy balance in the bird community of stage I
 N – density, A – assimilation, R – respiration, P – production, C – consumption, FU – excreta, SC – standing crop

No.	Species	N (pairs · 10 ha ⁻¹)	$\text{kJ} \cdot 10^3 \cdot \text{ha}^{-1} \cdot \text{season}^{-1}$					SC	
			A	R	P	C	FU	$\text{g} \cdot \text{ha}^{-1}$	$\text{kJ} \cdot \text{ha}^{-1}$
1	<i>Anthus trivialis</i>	1.0	8.34	8.13	0.21	11.15	2.81	6.0	47.8
2	<i>Saxicola rubetra</i>	1.3	3.06	3.02	0.04	4.07	1.01	4.0	31.8
	Total	2.3	11.40	11.15	0.25	15.22	3.82	10.0	79.6

of energy, however, is not uniformly distributed over the nestling period. To simulate the dynamics of this process a function φ (equation (9)) is arbitrarily fitted with the following constraints: the definite integral of the function φ during the nestling period is equal to AGT , the value of φ at the day of leaving the nest is equal to the sum of the existence metabolisms of all fledglings, the maximum value of φ falls at 2/3 of the nestling period. The shape of the function φ is similar to the pattern obtained in field studies (Diehl 1971, Myrcha, Pinowski and Tomek 1973, Tomek 1975). The efficiency of biomass production and the energetic value of the whole production seem to be the most certain estimates of nestlings' energetics. Therefore, the way of simulation (as described above) leads to relatively small errors, at least in computation of the entire energy demand for growth.

According to the definitions of energy flow (Petrusewicz and Macfadyen 1970) the energy balance of the whole community is calculated in terms of respiration (R), production (P), assimilation (A), and consumption (C) (equations (11–14)). Community standing crop (SC , equation (10)) was estimated assuming the energy equivalent of adults' biomass of $7.96 \text{ kJ} \cdot \text{g}^{-1}$. The efficiency of energy assimilation of 75% was assumed (equation (14)) because the food of birds during the breeding season consists almost entirely of invertebrates (Kendeigh, Dolnik and Gavrillov 1977). In further considerations mainly the seasonal sums of energy assimilation (= energy flow), respiration and production are used.

The simulations were performed by FORTRAN-programmes on CYBER-72 computer.

4. RESULTS

4.1. BIRD COMMUNITIES, CHARACTERISTIC AND DOMINANT SPECIES

Species composition, structure and detailed description of energetics of particular bird communities are given in Tables I–V.

On the clear cut (stage I, Table I) only 2 species nest, and of these two *Saxicola rubetra* (L.) the characteristic

Table II. Standing crop and energy balance in the bird community of stage II
For explanation of symbols see Table I

No	Species	N (pairs · 10 ha ⁻¹)	kJ · 10 ³ · ha ⁻¹ · season ⁻¹				SC	
			A	R	P	C	FU	g · ha ⁻¹
1	<i>Emberiza citrinella</i>	5.0	34.07	0.46	46.05	11.52	28.0	222.9
2	<i>Lanius collurio</i>	3.4	13.41	0.25	18.23	4.57	20.4	162.6
3	<i>Sylvia communis</i>	2.6	10.43	0.21	14.20	3.56	7.8	62.0
4	<i>Anthus trivialis</i>	1.0	6.29	0.17	8.60	2.14	4.6	36.5
5	<i>Sylvia curruca</i>	2.0	5.15	0.04	6.95	1.76	4.8	38.1
6	<i>Phylloscopus trochilus</i>	1.0	3.52	0.04	4.73	1.17	2.2	17.6
	Total	15.0	74.04	1.17	98.76	24.72	67.8	539.7

Table III. Standing crop and energy balance in the bird community of stage III
For explanation of symbols see Table I

No	Species	N (pairs · 10 ha ⁻¹)	kJ · 10 ³ · ha ⁻¹ · season ⁻¹				SC	
			A	R	P	C	FU	g · ha ⁻¹
1	<i>Phylloscopus trochilus</i>	14.4	50.62	0.50	68.13	17.01	31.7	252.2
2	<i>Turdus merula</i>	3.3	47.72	1.09	65.07	16.26	56.6	450.4
3	<i>T. philomelos</i>	2.9	41.90	0.96	57.15	14.29	42.9	341.9
4	<i>Erithacus rubecula</i>	3.9	22.33	0.38	30.25	7.54	13.3	106.0
5	<i>Garrulus glandarius</i>	1.3	19.78	0.59	27.15	6.79	44.2	352.0
6	<i>Emberiza citrinella</i>	1.7	11.61	0.17	15.68	3.90	9.5	75.8
7	<i>Sylvia curruca</i>	3.9	10.06	0.13	13.58	3.39	9.4	74.6
8	<i>S. borin</i>	1.9	6.79	0.08	9.13	2.26	7.8	62.0
9	<i>Anthus trivialis</i>	0.7	4.40	0.13	6.04	1.51	3.2	25.6
	Total	34.0	215.20	4.02	292.17	72.95	218.6	1740.5

Table IV. Standing crop and energy balance in the bird community of stage IV
For explanation of symbols see Table I

No	Species	N (pairs · 10 ha ⁻¹)	A	R	P	C	FU	SC	
								g · ha ⁻¹	kJ · ha ⁻¹
			kJ · 10 ³ · ha ⁻¹ · season ⁻¹						
1	<i>Eritacus rubecula</i>	7.0	40.69	40.06	0.63	54.27	13.58	23.9	190.6
2	<i>Phylloscopus trochilus</i>	10.4	36.92	36.54	0.38	49.24	12.32	22.9	186.5
3	<i>Anthus trivialis</i>	5.0	32.14	31.34	0.80	42.83	10.69	23.0	183.1
4	<i>Fringilla coelebs</i>	3.6	22.88	22.63	0.25	30.67	7.79	14.4	115.6
5	<i>Phylloscopus sibilatrix</i>	5.6	18.77	18.60	0.17	25.01	6.24	11.2	89.3
6	<i>Carrulus glandarius</i>	1.0	15.63	15.21	0.42	20.87	5.24	34.0	270.7
7	<i>Turdus philomelos</i>	1.0	14.80	14.46	0.34	19.74	4.94	14.8	117.7
8.	<i>Parrus ater</i>	3.0	11.27	11.02	0.25	15.04	3.77	6.0	47.8
9	<i>Sylvia atricapilla</i>	2.0	8.93	8.76	0.17	11.90	2.97	6.9	54.9
10	<i>Turdus merula</i>	0.6	8.88	8.67	0.21	11.86	2.98	10.3	81.7
11	<i>Sylvia curruca</i>	1.0	2.64	2.60	0.04	3.52	0.88	2.4	19.3
Total		40.2	213.55	209.89	3.66	284.95	71.40	169.8	1357.2

species of meadow sites is rather accidental here. At a similar density *Anthus trivialis* (L.) had almost three times higher contribution to the energetics of this initial community.

Indicatory species (in the sense of Allee et al. 1949) for the 4 years old pine cultivation (stage II, Table II) are *Lanius collurio* L., *Sylvia communis* Lath. and to some extent *Emberiza citrinella* L. which attains maximal numbers in this stage (43.3% of individuals in the community) of the whole series examined. For these species falls about 80% of energy flow through all birds of this stage.

Community of birds in the young growth (stage III, Table III) is represented first of all by *Sylvia borin* (Bodd.) and by the most numerous in this stage *Phylloscopus trochilus* L. (42.3% individuals). Three species there contribute mostly to the energy flow: *Phylloscopus trochilus* L., *Turdus merula* L. and *T. philomelos* Brehm, which together assimilate about 60% of energy.

Among the birds of pole wood (stage IV, Table IV) there are no indicatory species, but *Phylloscopus trochilus* (25.6%), *Erithacus rubecula* (L.) (19.9%) and *Phylloscopus sibilatrix* (Bechst.) (13.9%) dominate in numbers. These species together with *Anthus trivialis* and *Fringilla coelebs* L. make up almost 70% contribution to the energy flow through the whole community.

Most characteristic bird species of mature forest (stage V, Table V) are first of all hole-nesters (e.g., *Parus major* L., *P. caeruleus* L., *Sitta europaea* (L.), *Ficedula hypoleuca* (Pall.), *Dendrocopos major* (L.), *Dryocopus martius* (L.)) – a group of species not represented in other stages. However, most numerous are *Anthus trivialis* (13.0%), *Erithacus rubecula* (9.5%) and *Fringilla coelebs* (9.5%). The highest amount of energy (about 34%) in this community flows through three species: *Anthus trivialis*, *Dendrocopos major* and *Sitta europaea*, although only the first bird species is dominant in numbers (over 5% of individuals, acc. to Palmgren 1930).

4.2. MAIN STRUCTURAL INDICES AND STANDING CROP

The increase of the number of species (S) is not a continuous process in this series of communities. Progression of S index distinctly slows down between stages III (9 species) and IV (11 species). It attains the maximum value in stage V (30 species, Fig. 2). According to other papers on bird succession both in typical forest culturus (Lack 1939, Haapanen 1965, Dierschke 1973) and in forests renewed without intense interference of foresters (Pikula 1976, Głowaciński and Weiner 1977) the numbers of bird species in stages of pole wood and/or young growth show even some regression. In mature forests the abundance of avifauna is usually the greatest.

Density of breeding pairs (N) in the first 10 years of forest renewal increases very quickly (from 2.3 to 34.0 pairs per 10 ha), afterwards the process is slower till the maximum in the last stage is attained (62.9). Slower N progression is indicated first of all between stages III (34.0) and IV (40.2, Fig. 2). According to other papers (Johnston and Odum 1956, Haapanen 1965, Dierschke 1973, Głowaciński 1975, and others) more or less at this stage of overgrowing the cut area there is even a decrease of density of birds in relation to the stages of young growth and mature forest. Birds of young growth (10–15 years of age) displayed exceptionally high density.

Table V. Standing crop and energy balance in the bird community of stage V
For explanation of symbols see Table I

No	Species	N (pairs · 10 ha ⁻¹)	A	R	P	C	FU	SC	
								g · ha ⁻¹	kJ · ha ⁻¹
			kJ · 10 ³ · ha ⁻¹ · season ⁻¹						
1	<i>Anthus trivialis</i>	8.1	52.00	50.74	1.26	69.35	17.35	37.3	296.7
2	<i>Dendrocoptes major</i>	3.8	47.01	45.75	1.26	62.68	15.67	66.1	526.3
3	<i>Sitta europaea</i>	2.5	46.26	44.04	2.22	61.68	15.42	10.6	84.2
4	<i>Fringilla coelebs</i>	6.0	38.17	37.67	0.50	50.91	12.74	24.0	191.1
5	<i>Erithacus rubecula</i>	6.0	34.86	34.32	0.54	46.51	11.65	20.5	163.4
6	<i>Parus major</i>	5.0	34.86	34.02	0.84	46.47	11.61	18.9	150.4
7	<i>P. caeruleus</i>	5.0	30.38	29.71	0.67	40.52	10.14	12.5	99.7
8	<i>Phylloscopus sibilatrix</i>	3.8	12.74	12.61	0.13	16.97	4.25	7.6	60.3
9	<i>Carrulus glandarius</i>	0.3	12.40	12.07	0.33	16.51	4.11	19.2	152.9
10	<i>Turdus merula</i>	0.8	11.82	11.56	0.26	15.75	3.94	13.7	109.4
11	<i>Parus ater</i>	2.8	10.52	10.26	0.26	14.04	3.52	5.6	44.4
12	<i>Turdus philomelos</i>	0.7	10.35	10.10	0.25	13.79	3.44	10.4	82.5
13	<i>Ficedula albicollis</i>	2.5	9.60	9.47	0.13	12.78	3.18	7.3	57.8

14	<i>Dendrocopos medius</i>	1.0	8.88	8.71	0.17	11.86	2.98	11.6	92.2
15	<i>Streptopelia turtur</i>	0.7	7.33	7.12	0.21	9.76	2.43	20.5	163.8
16	<i>Dryocopus martius</i>	0.3	7.08	6.83	0.25	9.43	2.35	18.6	147.9
17	<i>Certhia familiaris</i>	2.5	6.87	6.79	0.08	9.18	2.31	4.7	37.3
18	<i>Oriolus oriolus</i>	0.9	6.46	6.33	0.13	8.60	2.14	13.1	104.8
19	<i>Sylvia atricapilla</i>	1.4	6.25	6.12	0.13	8.35	2.10	4.8	38.1
20	<i>Certhia brachydactyla</i>	1.5	6.20	6.12	0.08	8.25	2.05	3.0	23.9
21	<i>Phylloscopus trochilus</i>	1.5	5.32	5.28	0.04	7.08	1.76	3.0	26.4
22	<i>P. collybita</i>	1.0	4.52	4.44	0.08	6.03	1.51	1.8	14.3
23	<i>Ficedula hypoleuca</i>	1.5	4.36	4.20	0.08	5.83	1.47	4.4	34.8
24	<i>Parus cristatus</i>	0.9	3.72	3.64	0.08	4.94	1.22	2.1	16.3
25	<i>Sturnus vulgaris</i>	1.2	3.10	3.02	0.08	4.15	1.05	4.8	38.1
26	<i>Phoenicurus phoenicurus</i>	0.3	1.63	1.59	0.01	2.18	0.55	1.0	8.0
27	<i>Agriphalos caudatus</i>	0.3	1.26	1.22	0.01	0.68	0.42	0.6	4.6
28	<i>Parus palustris</i>	0.3	1.26	1.22	0.04	0.68	0.42	0.7	5.5
29	<i>Sylvia borin</i>	0.2	0.71	0.71	0.01	0.96	0.25	0.8	6.7
30	<i>Jynx torquilla</i>	0.1	0.54	0.50	0.04	0.71	0.17	0.7	5.9
Total		62.9	426.46	416.24	10.22	568.63	142.17	349.9	2787.7

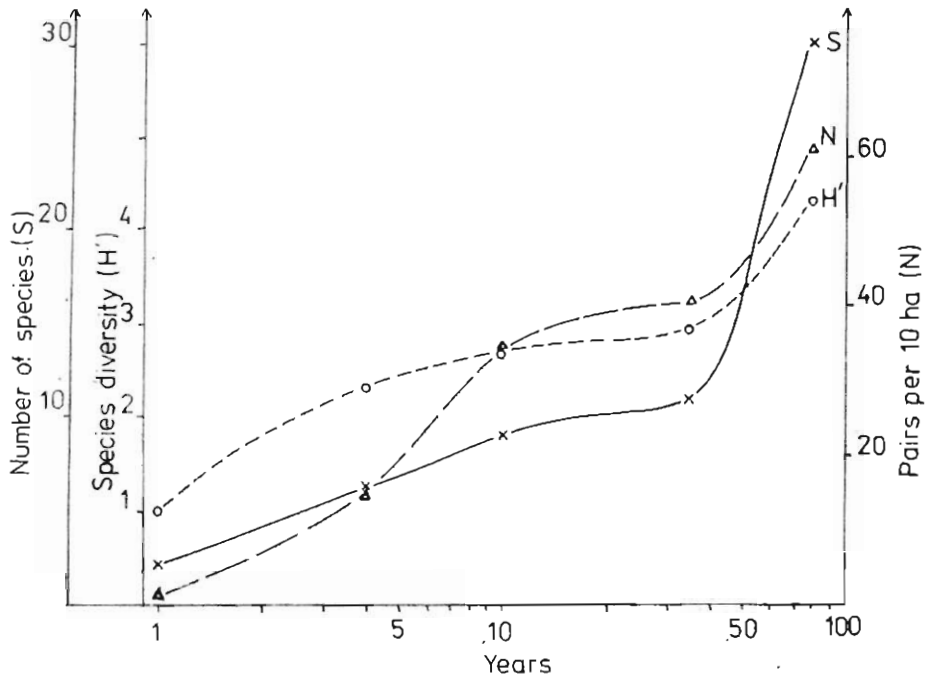


Fig. 2. Number of species (S), density (N) expressed by number of pairs per 10 ha of forest, and species diversity (H') calculated on the basis of the number of individuals in bird communities examined (logarithmic time scale)

Values of bird species diversity (H') change from 0.99 to 4.28 almost as progressively as in the case of indices S and N (Fig. 2). The pattern of H' changes confirms the general assumptions that the community (ecosystem) development is usually accompanied by an increase of its species diversity. Some papers have indicated that the changes of diversity show similar tendencies in all ecosystem components (Drury and Nisbet 1973). The strong relation between species diversity of avifauna and the structure of habitats and other biocenotic elements has been proved well on several examples (MacArthur, Recher and Cody 1966, Karr and Roth 1971).

Standing crop (SC) of adult birds increases rapidly to the stage of young growth (III; $1744.7 \text{ kJ} \cdot \text{ha}^{-1}$), slightly decreases in the pole wood stage (IV; $1360.4 \text{ kJ} \cdot \text{ha}^{-1}$), increases again to the stage of almost mature forest (V; $2794.3 \text{ kJ} \cdot \text{ha}^{-1}$) where it attains the maximum (Fig. 3). Similar results have been obtained by Ferry and Frochot (1970) when investigating bird communities on overgrowing clearings of deciduous forest in France. In some other papers of this type (e.g., Karr 1968) such tendencies have not been indicated.

Average biomass of an individual in a bird community ($SC:N$) quickly increases to the young-growth stage ($31.9 \text{ g} = 223.7 \text{ kJ}$; maximum state) to decrease considerably in the pole wood stage ($20.8 \text{ g} = 169.2 \text{ kJ}$; minimum state) and increases again in the oldest forest

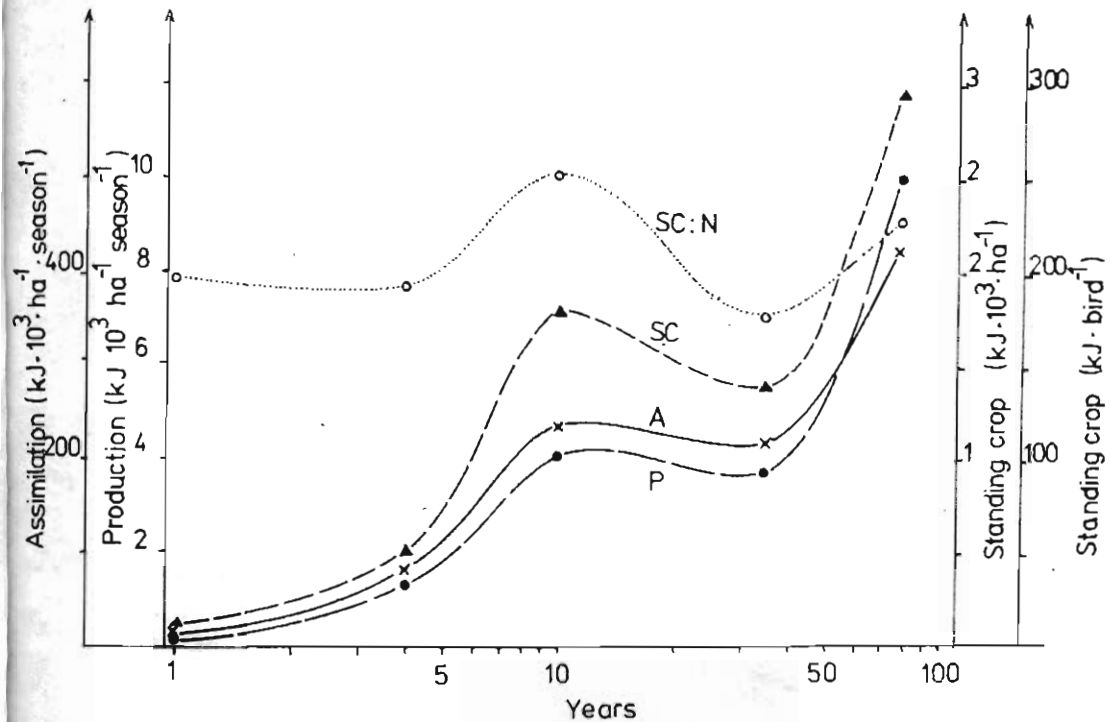


Fig. 3. Standing crop (SC), energy equal to average biomass of a bird (SC : N), assimilation (A) and production (P) in consecutive bird communities (logarithmic time scale)

(28.4 g = 222.1 kJ; Fig. 3). The sometimes described regularity that the average weight of birds increases along with the ageing of forest (Ferry and Frochot 1970) is not explicit on the example described here.

4.3. ASSIMILATION AND PRODUCTION

The rate of energy flow (assimilation) and production of birds in this semi-natural successional series (Table IV, Fig. 3) increase with time almost monotonically, and the rate of growth of these parameters intensifies in the stage of young growth ($A = 219.7 \text{ kJ} \cdot \text{ha}^{-1} \cdot \text{season}^{-1} \cdot 10^3$; $P = 4.02 \text{ kJ} \cdot \text{ha}^{-1} \cdot \text{season}^{-1} \cdot 10^3$) and mature forest ($A = 426.5 \text{ kJ} \cdot \text{ha}^{-1} \cdot \text{season}^{-1} \cdot 10^3$; $P = 10.2 \text{ kJ} \cdot \text{ha}^{-1} \cdot \text{season}^{-1} \cdot 10^3$). As compared with natural succession of birds in a deciduous forest (Głowaciński and Weiner 1977) there is no distinct double peak. It is very likely that in this successional series the maximum state of avifauna of the young growth phase as recorded for the series of deciduous forest has not been grasped, because the number of developmental stages distinguished and described was not sufficient. The rate of energy flow and net production of birds in semi-natural coniferous forest are 20–75% lower than in natural more fertile deciduous forest, in corresponding successional stages (cf. Głowaciński and Weiner 1977).

Table VI. Energy balance and ecological efficiency in bird communities studied
P : *SC* — biomass turnover, *P* : *A* — ecological efficiency; explanation of remaining symbols in Table I

Stage	Age (years)	$\text{kJ} \cdot 10^3 \cdot \text{ha}^{-1} \cdot \text{season}^{-1}$					<i>P</i> : <i>SC</i>	<i>P</i> : <i>A</i> (%)
		<i>A</i>	<i>R</i>	<i>P</i>	<i>C</i>	<i>FU</i>		
Cutting (I)	1	11.40	11.15	0.25	15.21	3.81	3.16	2.20
Saplings (II)	4	74.04	72.87	1.17	98.76	24.72	2.17	1.60
Thicket (III)	10	219.22	215.20	4.02	292.17	72.95	2.31	1.83
Poles (IV)	35	213.53	209.88	3.65	284.93	71.40	2.68	1.71
Mature forest (V)	80	426.46	416.24	10.22	568.59	142.13	3.62	2.35

Other components of energy budget of particular bird communities, such as consumption, respiration and excreta are given in Table VI.

4.4. TURNOVER AND ECOLOGICAL EFFICIENCY

Biomass turnover (*P* : *SC*) of birds ranges from 2.2 to 3.6 in the series of communities examined (Table VI). This coefficient is at a similar level in bird communities of almost naturally overgrowing clearing of a deciduous forest (cf. Głowaciński and Weiner 1977) and of many old forests (Z. Głowaciński and J. Weiner — unpublished data).

Ecological efficiency (*P* : *A*) of birds in this series of forest development is more or less at a constant level of 2% (Table VI). Such efficiency is characteristic of avifauna of mature and old forests on the area examined (Z. Głowaciński and J. Weiner — unpublished data). In young stages of more natural autogenic succession (Głowaciński and Weiner 1977) ecological efficiency of birds is few times higher than in the case described here and in old forests.

4.5. SEASONAL DYNAMICS OF ENERGY FLOW THROUGH BIRD COMMUNITIES

Because of great differences in the total energy flow through bird communities the seasonal dynamics also shows considerable differences in particular developmental stages of coniferous forest. In the initial stage (I) maximum daily energy flow does not exceed $209.5 \text{ kJ} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$, whereas in stage V maximum daily energy flow reaches $5447 \text{ kJ} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$ (Fig. 4). Dates of maximum concentration of energy flow are quite similar in all stages. They fall on the period between the last decade of June and first decade of August. In stage V there is a distinct peak at the end of July; in other stages the period of maximum energy flow lasts longer and is more even: in stages III and IV maximum intensity of energy flow lasts 30–40 days and falls in periods June 10–July 10 and July 5–August 10, re-

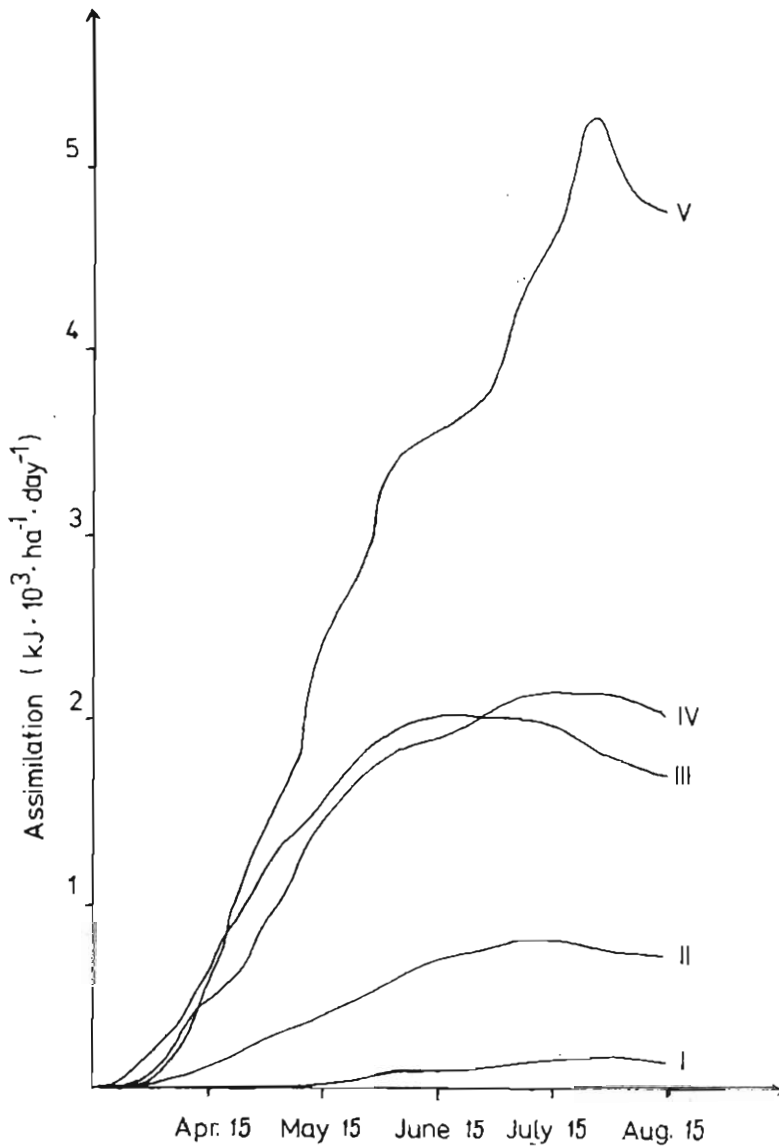


Fig. 4. Seasonal patterns of daily energy flow through breeding bird populations of examined developmental series of forest

I-V – consecutive development stages of forest and avifauna

spectively. Seasonal energetic peaks of older bird communities (stages IV and V) in relation to younger communities (stages II and III) are, however, some two weeks later towards the end of the breeding season (Fig. 4).

4.6. ENERGY FLOW AND SPECIES DIVERSITY

Energy flow (assimilation) through bird populations in this series correlates exponentially with species diversity of communities (Fig. 5). Identical correlation of these two characteristics has been shown also in the almost natural successional series of avifauna of oak-hornbeam forest (Głowaciński and Weiner 1977), but this relation is to some extent due to the fact that both parameters depend on the number of species (S) and numbers of birds (N) in the community.

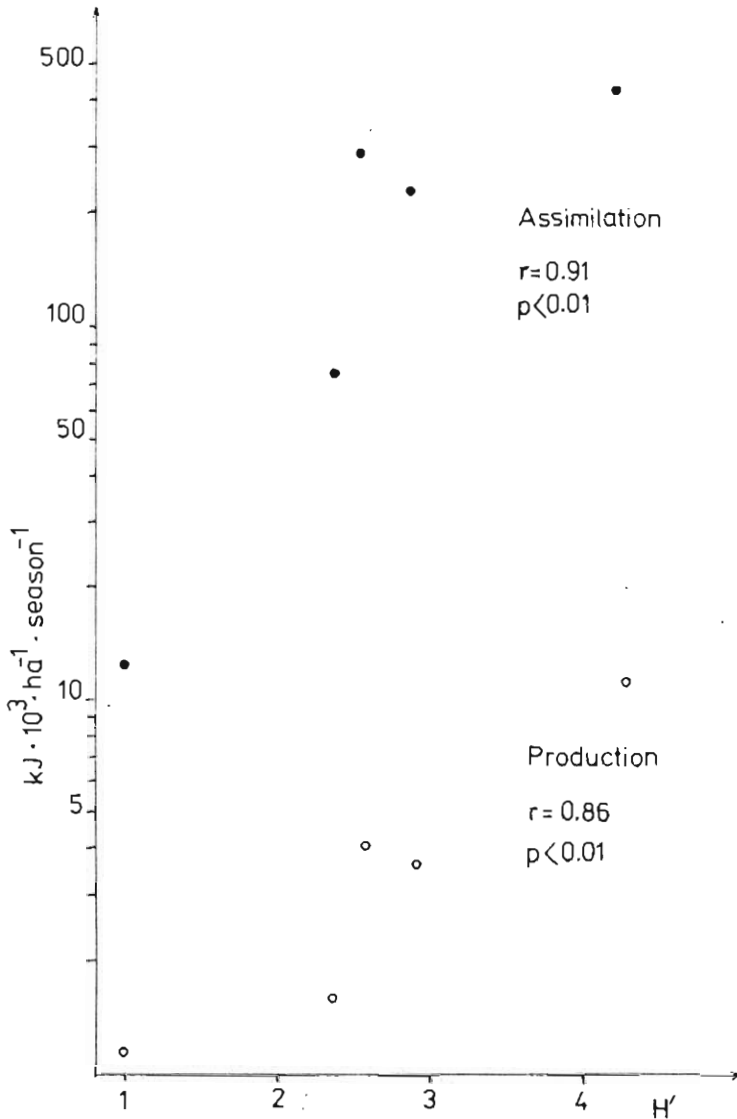


Fig. 5. Correlation between species diversity (H') and assimilation (dark circles) and between species diversity and production (white circles)

A similar correlation can be also observed between production and species diversity (Fig. 5), although such relation has not been proved in bird communities settling into the clearing of deciduous forest (cf. Głowaciński and Weiner 1977). This shows that production value in different bird communities is not a simple function of their numbers.

4.7. ECOLOGICAL EFFICIENCY AND SPECIES DIVERSITY

In this successional series production efficiency of birds participating in reproduction is low (about 2%) and almost constant at the increasing with the age of forest species diversity of avifauna. This is an entirely different result than the one obtained in the natural series (Głowaciński and Weiner 1977), where negative correlation of both indices has been distinctly proved. It is worth mentioning that these two different successional series finally lead to the same values of H' and $P : A$ as for the bird communities of mature forest ($P : A$ – about 2%, H' – about 4.5 bits) (Z. Głowaciński and J. Weiner – unpublished data).

4.8. DIVERSITY AND EVENNESS IN ENERGY DISTRIBUTION AMONG THE SPECIES

Diversity of bird communities calculated from the proportion of the distribution of energy of assimilation (H'_A), production (H'_P) and standing crop (H'_{SC}) trends similarly as the diversity estimated on the basis of population numbers (H'_N ; Fig. 6, cf. Section 4.2). These indices increase on the linear time scale according to logarithmic curve: first quickly, then slower, asymptotically. As compared with more natural succession on the oak-hornbeam clearing (Głowaciński and Weiner 1977) two separate developmental phases are missing: the earlier phase of rapid growth of diversity to the young growth about 20 years old, and the later phase of relative stability of this index.

Indices of evenness (J'_A, J'_P, J'_{SC}) in birds from pine cultures of different age do not display such distinct directional differentiation and remain on a constantly high level of 0.74–0.97 (Fig. 6). In other words, the evenness of energy distribution for particular species in different developmental stages of forest avifauna is almost the same. This makes it clear that in this successional series the increasing number of species (S) decides more about the increase of energetic diversity of bird communities than the component J' which is quite even in the distinguished stages. Similarly as in the case of diversity also the changes in the evenness in this series have a different course than in the renewing avifauna in the clearing of oak-hornbeam forest (Głowaciński and Weiner 1977), where young successional communities emerge with very low evenness of energy distribution and communities of older phase having a high evenness. Only J'_N has a more or less similar course in both successional series.

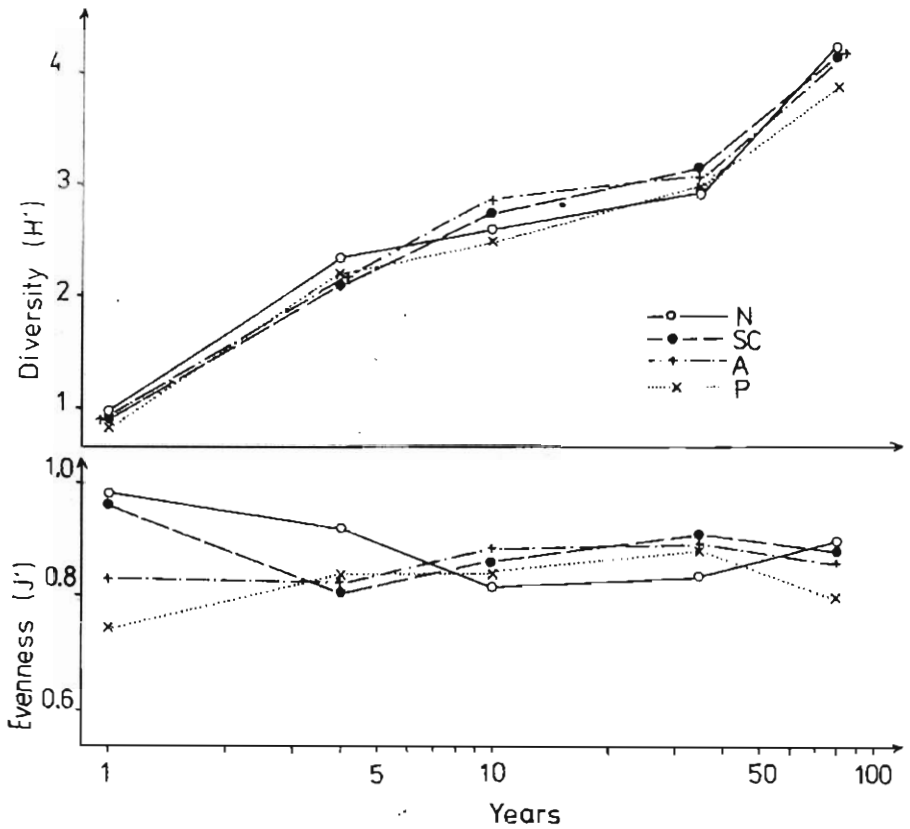


Fig. 6. Diversity (H') and evenness (J') of bird communities in forest stages examined: diversity and evenness of species abundance (H'_N, J'_N) and of energetic parameters ($H'_{SC}, H'_A, H'_P, J'_{SC}, J'_A, J'_P$)
Logarithmic time scale. N – density, SC – standing crop, A – assimilation, P – production

5. CHANGES OF BIRD COMMUNITIES AND THE PROBLEM OF SUCCESSION

The changes of bird communities presented here concern the cultivated habitats. Therefore, this whole development series of forest avifauna should be treated as a semi-natural system which can behave differently than the natural system. This is confirmed partly by relating this development series of avifauna to a more natural succession of birds in an oak-hornbeam clearing in the same geographic-forest area of southern Poland (Głowaciński and Weiner 1977). However, it is not certain whether the general assumptions of ecological succession can be referred to or estimated on the basis of only one group of organisms which belongs moreover to consumers. The theory of this ecological process is based mainly on complex studies of autotrophes (Margalef 1968, Odum 1969, 1977, Whittaker

1975). However, it seems that some rules and trends characterizing succession should be also reflected in heterotrophes and even in some narrower groups. Birds are so far a good material to study succession because they are animals strongly reacting to changes of habitats (e.g., Hildén 1965), they represent consumers of several orders, and also have a special ability to fill various new ecological niches.

Tendencies to changes of such ecological indices as number of species (S), diversity (H') and density (N) of birds in this series are generally consistent with theoretical assumptions of Margalef (1968) and others, where it is assumed during the succession process values of these characteristics increase either to unstable equilibrium or slight regress in the climax. Together with the age of forest the bird community standing crop (SC) also increases, but this increase has two distinct peaks here. Similarly, there is an increase of assimilation (A) and production (P).

These facts confirm that there is a bimodal pattern in the avifauna of renewing forest (Głowaciński 1975, Głowaciński and Weiner 1977) which goes beyond the classical general scheme of the phenomenon of succession (Odum 1969). Average biomass of a bird in community is quite variable, but these changes do not indicate a straight direction. Thus the results obtained do not confirm explicitly the prevalence of species of a higher biomass (dimension) in older stages, where K -selection should prevail over r -selection (Łomnicki 1976, and others). Still, they are in favour of the thesis (Pianka 1970, and others) that species considered as typical K -strategists have a greater body weight than conventionally eliminated r -strategists (Głowaciński 1979).

Some characteristics, such as, e.g., ecological efficiency ($P:A$), evenness (J') of energy distribution or relation of ecological efficiency to species diversity (H'_N) prove the existence of considerable differences between this series of bird communities as compared with an almost natural series, described on the basis of oak-hornbeam avifauna (Głowaciński and Weiner 1977). Constant level of ecological efficiency in this developmental series of avifauna differs considerably from the general conception of succession as given by Odum (1969, 1977) and others. Perhaps, the distinguished here in a determined order bird communities do not illustrate a typical successional sequence and are only a set of accidental bird aggregations representing various age gradients of the same type of forest. The decrease in ecological efficiency of birds has been shown in the more natural series (Głowaciński and Weiner 1977), thus it cannot be argued that in the present case the changes of this index have not been shown due to some methodical simplifications, since identical assumptions were applied in both series described. For example, it has been necessary to make a not checked assumption that particular species behave identically in various habitat stages.

The examined series of bird communities leads to the final community which, in regard to some ecological parameters (e.g., H' and correlation of this index to A , P and $P:A$) is similar to all mature ornithocenoses of the Niepołomice Forest (Z. Głowaciński and J. Weiner — unpublished data). Avifauna of pine forest is, however, less numerous than of an averagely abundant forest in southern Poland with an energy flow smaller by 20–75% than in a mesophilous deciduous forest.

6. SUMMARY

In five consecutive developmental stages (I-V) of cultivated pine forest in southern Poland (Niepołomice Forest) main structural and energetic characteristics of breeding avifauna were determined. All bird communities in field were described by the mapping method in 1975. In order to estimate energetic parameters the dynamics computer simulation model was used. Main assumptions, variables and equations to this model are given in Section 3 (Fig. 1).

Species composition, structure and detailed description [of energetics] of particular bird communities are given in Tables I-V. In the presented series of communities the number of bird species (S) is from 2 in initial stage to 30 in the final stage, density (N) 0.2–6.3 pairs per 1 ha of forest, species diversity (H'_N) 0.99–4.28 bits of information, diversity calculated from proportion of distribution of assimilation energy (H'_A) 0.84–4.19 (Figs. 2, 6), biomass (SC) 79.6–2787.6 kJ · ha⁻¹, energy flow (= assimilation, A) 11.40–426.46 kJ · 10³ · ha⁻¹ · breeding season⁻¹, production (P) 0.25–10.22 kJ · 10³ · ha⁻¹ · season⁻¹ (Table VI, Fig. 3). These parameters have the lowest values in initial stage (I) and the highest in the oldest stage, pre-climax one (V; Figs. 2, 3). Because of cyclic cutting of old forest stands this successional series does not have a climax stage.

The rate of energy flow and production of bird community in this semi-natural development series of forest have two peaks: (Fig. 3) the phase of young growth (III), and especially in the mature forest (V). In comparison with fertile deciduous forest (Głowaciński and Weiner 1977) energy flow of less numerous bird communities of coniferous forest is by 20–75% lower in respective stages. Considerable differences in particular stages are shown by seasonal dynamics of energy flow (209.5–5447.0 kJ · ha⁻¹ · day⁻¹). Distinct seasonal energy peaks in older stages, and especially in the last (V), as compared with birds of younger stages (II and III) are shifted towards the end of breeding season by about two weeks (Fig. 4). Assimilation and production of bird communities are strongly correlated to species diversity of birds (Fig. 5), because parameters A , P , H' depend on the size of communities.

Even if changes of some structural indices (e.g., S , N , H') are relatively consistent with opinions expressed nowadays on the development of biocenotic units (cf. Margalef 1968, Odum 1969, and others), still the increase of some functional indices (e.g., A , P) is not a continuous process and deviates from these general assumptions. The almost unchangeable in all stages ecological efficiency ($P:A$) of avifauna (Table VI) and correlative relation of this coefficient to species diversity suggest that the series of communities examined does not fully answer the rules generally attributed to succession.

7. POLISH SUMMARY

W pięciu kolejnych stadiach (I-V) rozwojowych uprawianego lasu sosnowego w południowej Polsce (Puszcza Niepołomska) określono podstawowe charakterystyki strukturalne i energetyczne awifauny lęgowej. Wszystkie zespoły ptaków opisano w terenie w roku 1975 za pomocą metody kartowania. Do oceny parametrów energetycznych użyto dynamicznego komputerowego modelu symulacyjnego. Główne założenia, zmienne i równania do tego modelu podano w rozdz. 3 (rys. 1).

Skład gatunkowy, strukturę i szczegółowy opis energetyki poszczególnych zespołów ptaków przedstawiają tabele I-V. W prezentowanej serii zespołów liczba gatunków (S) ptaków wynosi od 2 w stadium początkowym do 30 w stadium końcowym, zagęszczenie (N) – 0,2–6,3 pary na 1 ha lasu, różnorodność gatunkowa (H'_N) – 0,99–4,28 bita informacji, różnorodność obliczona z proporcji podziału energii asymilacji (H'_A) – 0,84–4,19 (rys. 2, 6), stan biomasy (SC) – 79,6–2787,6 kJ · ha⁻¹, przepływ energii (= asymilacja, A) – 11,40–426,46 kJ · 10³ · ha⁻¹ · sezon lęgowy⁻¹, produkcja (P) – 0,25–10,22 kJ · 10³ · ha⁻¹ · sezon⁻¹ (tab. VI, rys. 3). Wyszczególnione parametry mają najniższe wartości w stadium inicjalnym (I), najwyższe natomiast w stadium najstarszym, przedklimaksowym (V; rys. 2, 3). Z uwagi na cykliczny wyrąb starych drzewostanów brakuje w tej serii sukcesyjnej stadium o cechach klimaksu.

Tempo przepływu energii i produkcja ptaków w tej półnaturalnej serii rozwojowej lasu wzrastają dwuszczytowo (rys. 3), z nasileniem w fazie młodnika (III), a zwłaszcza w lesie dojrzałym (V). W porównaniu z żyznym lasem liściastym (Głowaciński i Weiner 1977) przepływ energii licznie uboższych zespołów ptasich lasu szpilkowego jest w odpowiednich stadiach o 20–75% mniejszy. Znaczne różnice w

poszczególnych stadiach wykazuje sezonowa dynamika przepływu energii ($209,5-5447,0 \text{ kJ} \cdot \text{ha}^{-1} \cdot \text{dzień}^{-1}$). Wyraźniej zaznaczające się sezonowe szczyty energetyczne w stadiach starszych, zwłaszcza ostatnim z badanych (V), w porównaniu z ptakami stadiów młodszych (II i III) są tu przesunięte ku końcowi okresu lęgowego o około 2 tygodnie (rys. 4). Asymilacja i produkcja zespołów ptaków są dość silnie skorelowane z różnorodnością gatunkową ptaków (rys. 5), co wynika z tego, że parametry A , P , H' są uzależnione od wielkości zespołów.

O ile zmiany niektórych wskaźników strukturalnych (np. S , N , H') przebiegają dość zgodnie z panującymi dziś poglądami na rozwój jednostek biocenotycznych (por. M a r g a l e f 1968, O d u m 1969 i inni), o tyle wzrost niektórych wskaźników funkcjonalnych (np. A , P) nie jest procesem ciągłym i odbiega od tych ogólnych założeń. Prawie niezmienna we wszystkich stadiach wydajność ekologiczna ($P : A$) awifauny (tab. VI) i korelacyjna zależność tego współczynnika z różnorodnością gatunkową wskazują, że badana seria zespołów nie podlega w pełni prawidłowościom przypisywanym na ogół sukcesji.

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