

# ENERGY FLOW THROUGH A BIRD COMMUNITY IN A DECIDUOUS FOREST IN SOUTHERN POLAND

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The bioenergetic approach to ecosystem function requires the investigation of energy flow through the various components. In many terrestrial ecosystems birds are an important link in the trophic chain, being consumers of the first, second, and/or higher orders.

Investigations of energy flow through these homeothermic animals entail many specific methodological difficulties. Bird communities in terrestrial ecosystems usually comprise many species with different population dynamics and phenology. Most bird species of the temperate zone migrate seasonally. To determine the energy requirements of birds under natural conditions, one must take into account the costs of thermoregulation and intensive locomotor activity as well as the cost of reproduction. Therefore, such investigations are laborious. Existing published works include a number of studies concerning energy flow through single species populations (Odum et al. 1962, Kale 1965, Pinowski 1968) or through communities composed of several bird species (Uramoto 1961, Wiens 1973, West and DeWolfe 1974). However, these papers give results covering periods of several months only. Up to now only one complete energy flow study presenting a yearly cycle has been conducted for complete multi-species bird communities (Holmes and Sturges 1973).

The purpose of this work was to estimate the yearly energy flow through a multi-species bird community in a deciduous forest in the temperate zone. We did not attempt a complete population and bioenergetical investigation. Energy flow was estimated using field data on the dynamics of bird numbers in the area in 1968 and 1971 and bioclimatic data. Numerous parameters of the biology and physiology (bioenergetics) of birds used were taken from the literature.

## STUDY AREA AND METHOD

The investigations were completed in the Niepołomice Forest (50°04' N, 20°21' E), one of the largest lowland forest complexes in southern Poland. The forest is situated on the Vistula River, about 20 km E of Cracow. The Niepołomice Forest (11,000 ha = 27,180 acres) is dominated by stands of oak-pine of the *Pino-Quercetum* association. About 30% of the area is covered by stands of oak-hornbeam (*Quercus-Carpinetum*) or moist alder (*Circaeo-Alnetum*). A number of habitats have retained their natural or semi-natural character up to the present. The investigations were conducted in a 100-year-old deciduous forest of the *Quercus-Carpinetum* association (fig. 1).

The study area is situated in a zone of overlapping continental and oceanic climates. During the years 1966-70, the mean annual air temperature was 7.8°C, the mean of July, 17.9°C, and that of January, 4.8°C. The growing season (between the first and last days with mean 24 hr air temperatures > 5°C) is relatively long, lasting more than 220 days. Thermal winter (between the first and last days with 24 hr mean air temperatures < 0°C) lasts an average of 88 days. The annual precipitation varies from 600-700 mm (Klein and Langer, unpubl.). The mean monthly temperatures during 1968 and 1971 are given in table 1.

Quantitative information about the birds in this habitat was obtained in two ways. To determine the stationary breeding avifauna, a mapping method based on assumptions of the "Scandinavian Ornithological School" (mainly of Enemar 1959) with certain improvements described by Tomiałojć (1968) was used. This method conforms with the guidelines of the International Bird Census Committee (1969). The sample plots were set up deep in the forest in order to minimize ecotone effects, "island effects," and influences of other habitats (e.g., fields and meadows). The sample plots were divided into subplots of different sizes for birds with different territory features and frequency. The smallest area (350 × 300 m, 10.5 ha) was used to analyze abundance of common small passerine birds (e.g., Collared Flycatcher, *Ficedula albicollis*; Chaffinch, *Fringilla coelebs*; Blue Tit, *Parus caeruleus*; Yellowhammer, *Emberiza citrinella*). For bigger, rarer birds (e.g., Blackbird, *Turdus merula*; Lesser Spotted Woodpecker, *Dendrocopos minor*; Grey-headed Woodpecker, *Picus canus*) areas of 25 and 100 ha were selected. The mapping method



FIGURE 1. Oak-hornbeam forest stand in the Niepołomice Forest.

does not account for nomadic individuals that do not take part in reproduction. Therefore, the results obtained by this method probably underestimate slightly the actual avian biomass.

Strip censuses were used to evaluate the avifauna outside the breeding season. Such procedures involve a single census of a strip (belt-like zone not overgrown by trees) while passing through it at an average speed of 1 km/hr. Strip lengths were 1.5 to 2.0 km. Bird counts were carried out usually once a month in the years 1968 and 1971. From late autumn to spring observations were made in a strip 50 m wide; during the other seasons, this was narrowed to 40 m because the vegetation is thicker at that time (foliage development) and is more densely inhabited by birds. The results were corrected for detection failure during a single census, Tomiałoć (1968) having found that in a deciduous forest in southern Poland during the spring-summer season, only about two-thirds of the actual bird population is detected. For the autumn-winter period, we arbitrarily assumed it to be three-fourths. The population was estimated during the middle of each month.

The results obtained using the aforementioned methods were converted to a standard figure for units of 10 ha. The methods jointly provide the data necessary for the determination of bird abundance for

the one-year period. The population value was determined for the years 1968 and 1971. Because an appraisal of breeding populations was performed in 1971 using the census method, the results obtained for that year were added to the mean values of breeding populations of 1967-70.

#### CALCULATIONS OF ENERGY

To determine the energy balance of a complete multi-species bird community, several bioenergetic parameters of individual species populations, such as respiration (R), assimilation (A), consumption (C), and production (P), were calculated. These parameters were defined according to the guidelines of the International Biology Program (Petrusewicz 1967). According to Odum (1959), assimilation (A) is synonymous with energy flow. A simple computer model for evaluation of energy flow in the bird community was developed.

The following items were calculated separately: (1) the energy expended for main-

TABLE 1. Mean monthly air temperatures in °C in the Niepołomice Forest in 1968 and 1971.

Year	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1968	-4.1	0.7	3.4	8.4	12.6	17.7	17.1	16.7	13.1	9.0	4.8	-4.6
1971	0.4	-1.0	-2.0	6.0	13.5	14.7	17.8	19.7	10.1	8.0	3.0	2.8

tenance by individuals, (2) the energy budget of young from hatching until the moment of leaving the nest, and (3) the energetic cost of reproduction to the parents. The yearly energy balances for whole populations of individual species, and then for the entire bird community, were calculated on the basis of these data.

*Consumption, assimilation, and respiration of adults.* We assumed that adult body weight does not change significantly during the year. Seasonal changes in body weight depend mainly on the deposition and secondary metabolism of surplus fat and usually do not exceed 10% of the body weight (Dolnik and Blyumental 1964, Pinowski 1967). Thus, assimilation equals respiration ( $P = O$ , therefore  $A = R$ ) and expresses the maintenance cost of individuals.

As a basis for calculation, we used the existence energy ( $EMR =$  existence metabolism rate) measured in relatively large cages according to the feeding method of Kendeigh (1949, 1968). These measurements show the average maintenance cost in conditions approaching natural ones in a better way than do other measurements of metabolism used for birds (e.g., the standard metabolic rate— $SMR$ , Lasiewski and Dawson 1967, and others), since the latter exclude the cost of existence activities and thermoregulation. However, whether this method measures all the energy expenditures of a free-living bird is questionable, as is the significance of technical disturbances. Nevertheless, the use of existence energy values for further calculations without any arbitrary correction factors appears to be the most reliable procedure. Kendeigh (1970) listed data on existence energy of various avian species and calculated from these the dependence of the  $EMR$  on body weight in both passerines and nonpasserines. This dependence can be expressed as an exponential function, but it varies according to the ambient temperature. As a basis for our calculations, we used an equation that Kendeigh (1970) introduced for passerine birds at an air temperature of  $30^{\circ}\text{C}$ ,

$$EMR = 1.572 W^{0.6210} \quad (1)$$

where  $EMR =$  existence energy in kcal/bird-day and  $W =$  body weight in g. This equation was selected because the great majority of birds in the study forest are either small passerines or nonpasserines (e.g., woodpeckers, doves) that are similar to passerines. The nonpasserines used by Kendeigh (1970) were

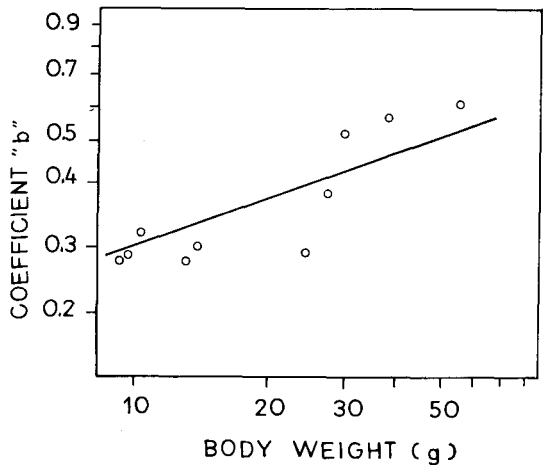


FIGURE 2. Correlation between body weight ( $W$ ) and coefficient " $b$ " of the regression of thermoregulation in passerines.

members of the Anseriformes, Galliformes, or Falconiformes.

The existence energy of individual species is significantly dependent on ambient temperature and usually is described using a rectilinear regression equation of the type,

$$EMR = a - bt \quad (2)$$

where  $a, b =$  constants characteristic of a species and  $t =$  temperature in  $^{\circ}\text{C}$ . The coefficient " $a$ " is the intercept (usually  $EMR$  at  $0^{\circ}\text{C}$ ), whereas " $b$ " is the slope coefficient. Both these parameters depend on body size and climatic adaptation of the bird. A review of a number of such equations describing the actual cost of thermoregulation in various birds shows that the coefficient " $b$ " increases regularly with increasing body weight. Using data collected by Kendeigh (1970), but excluding arctic species, we investigated the correlation between the coefficient " $b$ " and body weight ( $r = 0.9$ ). This correlation was then fitted to the equation of the exponential function.

$$b = 0.06514 W^{0.3625} \quad (3)$$

( $P < 0.001$ , fig. 2). Substituting equation (1) for " $a$ ", equation (3) for " $b$ ", and " $30 - t$ " for " $t$ " (taking into account that a temperature of  $30^{\circ}\text{C}$  was assumed as the starting point) in equation (2) as well as changing the negative sign to a positive one, we obtained a general expression of the existence energy of a passerine bird in relation to ambient temperature and body weight as

$$EMR = 1.572 W^{0.6210} + 0.06514 W^{0.3625} (30 - t) \quad (4)$$

where  $EMR$  = existence energy in kcal/bird-day,  $W$  = body weight in g,  $t$  = ambient temperature in °C.

Equation (4) was used to calculate the mean 24-hr energy requirements of each species studied for a complete year. The body weight of birds was determined from specimens obtained in the study area (Głowaciński, unpubl.) or was estimated from data in the literature (Szczepski and Kozłowski 1953, Ferens 1967, 1971). All calculations bearing on thermoregulation were adjusted to mean monthly temperatures of the Niepołomice Forest for both study years (table 1). Existence energy calculated in this way is synonymous with assimilation and respiration. Food consumed as well as feces and urine (FU) produced were calculated from data in the literature on food utilization by various bird species (Kendeigh 1949, Davis 1955, Kale 1965, El-Wailly 1966, Diehl 1971, etc.). The average efficiency of utilization of various foods is 75%; therefore, consumption is about 130% of assimilation, whereas  $FU = C - A$ .

In the present paper we ignore feather production in the autumn molt of adults. Turček (1960, 1966) calculated that the plumage of small passerines makes up about 7% of their biomass. Using a maximum value of 5 kcal/g dry matter for feathers (Spector 1956), this autumn production probably does not exceed 50 kcal/ha in the habitats investigated. The energetic cost of molt (additional respiration) may be omitted (Blackmore 1969), since in small birds this cost is insignificant and compensated for by the simultaneous improvement of thermoregulation resulting from the new plumage.

*Production and respiration of nestlings.* The bioenergetics of reproduction are relatively poorly known in wild birds compared to poultry. Only a few data are available for passerines on the energetic costs of egg production and incubation and on the efficiency of biomass production in nestlings. However, these can be used to estimate the total reproductive costs of a bird community.

For each species we determined the mean number of broods per year and the number of eggs per clutch from information in the literature (Szczepski and Kozłowski 1953). We then estimated the number and biomass of eggs produced. Using caloric values of passerine eggs taken from El-Wailly (1966) and Pinowski (1967), we calculated the average cost of egg production in calories. We then assumed that mean breeding success in hole-nesters is 75%, in others 60% (Haart-

man 1951, Nice 1957, Mackowicz 1970, Mackowicz et al. 1970, Tyler 1972, Głowaciński 1973). Apparently, the majority of brood losses occurs soon after hatching (Mackowicz et al. 1970), and the number of young leaving the nest is about 75% and 60% of the eggs laid for hole-nesting and other species, respectively. The total production of young birds (as an increment of their body biomass) was estimated by subtracting the caloric value of the eggs from the caloric value of the young birds when they leave the nest. The latter value was based on the assumption that the body weight and body tissue caloric values of such young birds are the same as they are in adults. In a number of species the biomass of young birds actually has a lower caloric value than that of adults, but at the same time young birds weigh more due to a greater water content (Myrcha and Pinowski 1969). These differences tend to cancel each other. The caloric value of adult tissue averages about 2.0 kcal/g fresh weight (Kale 1965, Brisbin 1969, Szwykowska 1969, Myrcha and Pinowski 1970). Evaluations of the production efficiency of nestlings show that on the average this reaches about 20% of the total consumption by the nestlings during their growth period (Pinowski 1968: 18%, Diehl 1971: 22%). Thus, based on production by juveniles, the consumption of young birds during growth was estimated according to  $C_{juv.} = 5 P_{juv.}$ . Total biomass produced during the breeding season includes egg production by adults and biomass production by young. A value including increased energy expenditure by parent birds for egg production, incubation, and increased activity during the feeding of young was added to the cost of breeding. To simplify the calculation, these costs were divided equally between the sexes. It was assumed that the cost of egg production is 142% of the caloric value of the egg and that the energetic cost of incubation in a small passerine bird is 30% of the existence energy for the whole incubation period (El-Wailly 1966). The gathering of large amounts of food for growing fledglings also requires increased energy expenditure by adults. This expenditure was estimated to be 15% of the total assimilation of the young, assuming that this cost is similar to the cost to adult birds of finding their own food (cf. Weiner 1972). The total cost of breeding borne by adult birds was arbitrarily divided among the three months of the breeding period (April, May, June) according to the breeding phenology of the species. Thus 15% of the reproductive cost

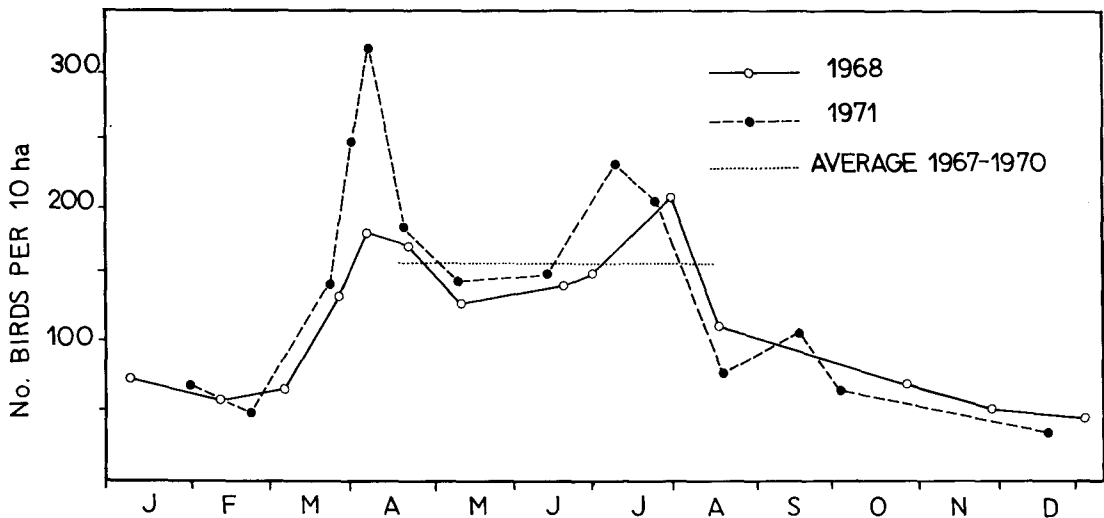


FIGURE 3. Numbers of birds/10 ha in the forest studied over a year.

was added to the values for respiration of adult birds in April, 55% in May, and the remaining 30% in June.

*Bioenergetics of the population and energy flow through a bird community.* Values of bioenergetic parameters estimated for an average individual of each species over a year were converted into measures for whole-species populations based on field data of their numbers during 1968 and 1971. It was thus possible to evaluate the energy flow through the whole community in successive months, and also for a whole year.

Calculations were made for 40 species of birds. Up to 3.5% of the passerines were not clearly identified during the field census.

These were grouped as "species not determined," and their average body weight was designated arbitrarily at 25 g.

Calculations were made on the Odra computer in the Mathematics Center of Jagiellonian University.

## RESULTS AND DISCUSSION

### COMPOSITION AND ABUNDANCE OF THE AVIFAUNA

Species with a mean annual abundance of less than 0.1 individuals/10 ha were excluded from our treatment of energy flow through the bird community. Thus, the bird population of the deciduous Niepołomice Forest comprises 40 species, 32 of which nest in the study area.

TABLE 2. Species comprising the avifauna of the Niepołomice Forest during 1968 and 1971. N = number of individuals per 10 ha of oak-hornbeam forest.

Species	1968			1971		
	N	Percent	Stay (mon.)	N	Percent	Stay (mon.)
<i>Parus caeruleus</i>	22.6	20.2	12	19.7	17.4	12
<i>Parus major</i>	13.7	12.3	12	14.4	12.7	12
<i>Sitta europaea</i>	12.9	11.5	12	9.1	8.0	12
<i>Fringilla coelebs</i>	7.6	6.8	5	10.0	8.8	8
<i>Erithacus rubecula</i>	5.9	5.3	8	7.7	6.8	8
<i>Ficedula albicollis</i>	4.2	3.8	4	3.8	3.3	3
<i>Parus palustris</i>	4.5	4.0	12	3.4	3.0	9
<i>Coccothraustes coccothraustes</i>	7.8	7.0	10	2.9	2.5	5
<i>Sturnus vulgaris</i>	3.7	3.3	5	3.4	3.0	4
<i>Emberiza citrinella</i>	1.5	1.3	6	5.3	4.7	7
<i>Certhia familiaris</i>	3.7	3.3	12	3.2	2.8	11
<i>Dendrocopos major</i>	3.2	2.9	12	3.5	3.1	12
<i>Turdus merula</i>	2.2	2.0	7	4.2	3.7	10
Other species <sup>a</sup>	18.3	16.3		22.2	20.2	
Total	111.8	100.0		112.8	100.0	

<sup>a</sup> *Turdus philomelos*, *Anthus trivialis*, *Phylloscopus sibilatrix*, *Sylvia atricapilla*, *S. borin*, *Phylloscopus collybita*, *Muscicapa striata*, *Luscinia luscinia*, *Streptopelia turtur*, *Garrulus grandarius*, *Columba palumbus*, *Cuculus canorus*, *Oriolus oriolus*, *Aegithalos caudatus*, *Troglodytes troglodytes*, *Dendrocopos medius*, *D. minor*, *Picus canus*, *Regulus regulus*, *Passer montanus*, *Dryocopus martius*, *Locustella fluviatilis*, *Caprimulgus europaeus*, *Carduelis carduelis*, *Crex crex*, *Turdus musicus*, *Phasianus colchicus*. \* denotes species not nesting in the study area.

TABLE 3. Assimilation (= energy flow) of the bird community in the oak-hornbeam forest in kcal  $\times 10^3$ /ha-year.

	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1968	4.5	2.9	5.7	13.0	18.6	13.4	8.9	4.5	4.1	3.8	2.6	2.0	84.2
1971	3.3	2.5	7.4	14.9	16.7	12.3	10.3	3.9	4.8	4.1	3.2	2.3	85.8
Average	3.9	2.7	6.6	14.0	17.7	13.0	9.6	4.2	4.5	4.0	2.9	2.1	85.0

The abundance of breeding birds during the investigation was about 80 pairs/10 ha (80.4 pairs/10 ha in 1968 and 79.7 pairs/10 ha in 1971). The mean annual abundance of birds in these years was 111.8 and 112.8 individuals/10 ha respectively (table 2).

The majority of the population consists of about ten species. Paridae alone (Blue Tit, *Parus caeruleus*; Great Tit, *P. major*; Marsh Tit, *P. palustris*) comprise 32–33% of all individuals. A detailed population analysis for individual species is given elsewhere (Głowaciński 1975).

Seasonal changes in the abundance of birds in the forest (fig. 3) and general annual population for the years studied are extremely similar. The differences consist mainly of small phenological shifts and changes in population numbers and intensity of seasonal migration.

Qualitatively, the composition of the population studied is very similar to that of the avifauna in other regions of southern Poland (Ranoszek 1969) and Czechoslovakia (Pikula 1968, Ferianc et al. 1970). A quantitative comparison of bird populations is much more difficult and applicable only to the breeding season. Material from other areas in the Wrocław Wojvodship suggests (Ranoszek 1969, Tomiałojć 1970) that breeding bird populations in oak-hornbeam stands along the Odra River and along the Vistula River are very similar. For example, in 1967, 81.3 pairs nested in a 10-ha area of oak-hornbeam forest between the towns of Wrocław and Legnica while 82.7 pairs/10 ha were found in the same habitat in the Niepołomice Forest (Ranoszek 1969). In an old oak-hornbeam forest near Legnica, the density of birds reached 100 pairs/10 ha (Tomiałojć 1970), which is the same number in oak-hornbeam forest in the Niepołomice Forest if only stands more than 100 years old are considered. More birds (138 pairs/10 ha) nest in the oak-hornbeam forests of Switzerland (Glutz von Blotzheim 1962). Oak-hornbeam forest is one of the most densely populated forest habitats of Europe (Novikov 1960, Oelke 1966). However, the bird density in the Niepołomice Forest, rela-

tive to other oak and oak-hornbeam forests, seems to be less than average, probably because ecotone effects were eliminated from this work because of the secluded location of the study area. These conditions were not met in all works used for comparison. Nevertheless, the avifauna of the Niepołomice Forest may be considered representative of oak-hornbeam forest avifaunas in Central Europe.

*Energy flow through a bird community.* Table 3 gives data on assimilation for the whole community by month and year. An allowance for breeding costs was added to values for April, May, and June. Mean energy flow (= assimilation) through a bird community in oak-hornbeam forest amounts to  $85.0 \times 10^3$  kcal/ha-year. However, more than 52% of this fell in the three months of the breeding season. All of the production (table 4), which in 1968 and 1971 amounted to 4.5 and  $3.9 \times 10^3$  kcal/ha-year ( $\bar{x} = 4.2 \times 10^3$  kcal/ha-year), respectively, occurred in this same period also. Thus, production accounts for nearly 5% of the total assimilation of this bird community. Converted into biomass the annual production averaged 2.1 kg/ha-year.

Table 4 summarizes energy consumption and assimilation, energetic content of feces and urine, and community respiration and production. Total consumption reached a mean of  $113.1 \times 10^3$  kcal/ha-year. Assuming that the average caloric value of food is about 1.7 kcal/g fresh weight (Diehl 1971, Witkowski, pers. comm.), the extraction of biomass from the ecosystem reaches about 66.5 kg/ha-year. During April, May, and June, this extraction must have been 11.0, 13.8, and 10.0 kg/ha-month, respectively.

Changes of individual elements of the en-

TABLE 4. Energy balance of the bird community in oak-hornbeam forest in kcal  $\times 10^3$ /ha-year.

Year	Con- sumption C	Assimi- lation A	Feces and Urine FU	Respi- ration R	Pro- duction P
1968	112.0	84.2	27.8	79.7	4.5
1971	114.1	85.8	28.3	81.9	3.9
Average	113.1	85.0	28.1	80.8	4.2

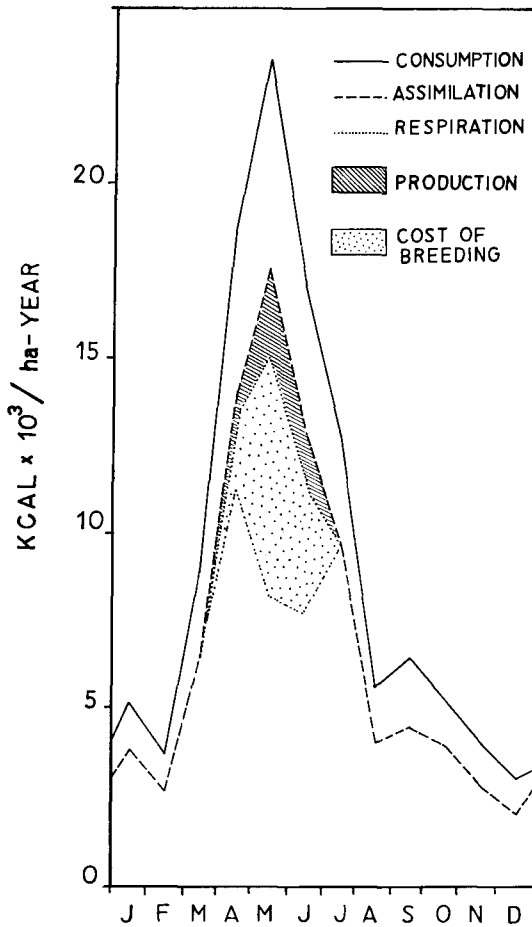


FIGURE 4. Energy flow through a bird community in oak-hornbeam forest.

ergy balance characteristic of a bird community in oak-hornbeam forest are shown in figure 4. Variations in the abundance and phenology of individual species and also in temperature regimes during successive years become negligible if the community is considered as a whole.

Individual species differ in their relative participation in the total energy flow through a bird community (table 5). The largest percentage of community assimilation is accomplished by populations of *Parus caeruleus* (12.1%), *Parus major* (10.2%), and Nuthatch (*Sitta europaea*) (8.2%). The next seven species together account for 38.5% of total assimilation, whereas the remaining 30 species contribute only 31.0%.

Production accounts on the average for 4.9% of the total assimilation, but within populations of individual species this value varies over a wide range. For example, *Parus caeruleus* contributes 3.0%, *P. major*, 3.1%, and *Sitta europaea*, 0.8%, whereas *Ficedula albicollis* may contribute as much as 7.1% and Tree Pipit (*Anthus trivialis*), 7.5%. The rea-

TABLE 5. Participation of individual species in energy flow through the bird community.

Species	Assimilation (kcal $\times 10^3$ /ha-year)	Percent of whole community assimilation
<i>Parus caeruleus</i>	10.3	12.1
<i>Parus major</i>	8.7	10.2
<i>Sitta europaea</i>	6.9	8.2
<i>C. coccothraustes</i>	5.7	6.7
<i>Fringilla coelebs</i>	5.3	6.3
<i>Sturnus vulgaris</i>	5.0	5.9
<i>Dendrocopos major</i>	4.7	5.5
<i>Turdus merula</i>	4.6	5.4
<i>Erethacus rubecula</i>	3.8	4.5
<i>Turdus philomelos</i>	3.6	4.2
Other species	26.4	31.0
Total	85.0	100.0

sons for this disparity are differences in production values for a single pair (juveniles/clutch and broods/year), and differences in length of stay in the area investigated. Migrating species draw a significant part of their existence energy from outside the ecosystem studied, whereas all of their production occurs during their stay in the oak-hornbeam forest.

The energy stored by birds in connection with biomass production is mainly exported from the study area. After leaving the nest, the young disperse immediately, often away from the point of origin; subsequently, most species migrate to other climate zones. The number of birds breeding each year is nearly the same. Because data concerning adult mortality in the study area are not available, it is not possible to estimate what part of production is exported from the ecosystem. It is possible to estimate biomass turnover by dividing production by the standing crop of the community during the period of preparation for breeding (Kale 1965). During 1968 and 1971, the standing crops of the community were 1.06 and 1.05  $\times 10^3$  kcal/ha, respectively. Thus, the index of biomass turnover was successively 4.2 and 3.7 ( $\bar{x} = 4.0$ ). These values are nearly the same as those (5.1–6.0) for a population of Tree Sparrow (*Passer montanus*) (Pinowski 1968), but they are quite different from the low indices of biomass turnover (0.5–1.8) given for Long-billed Marsh Wren (*Telmatodytes palustris*) (Kale 1965). It seems that not only great production but also high mortality are responsible for the relatively rapid turnover of biomass in the bird community of oak-hornbeam stands in the Niepołomice Forest, as is the case with *Passer montanus* near Warsaw (Pinowski 1968). The results presented in this study also may be compared with the figures cal-

culated by Holmes and Sturges (1973) for a northern hardwood bird community. The maximum bird density during the spring is similar in both ecosystems, but the mean annual numbers and biomass are lower in the northern hardwoods. Therefore, the values for assimilation ( $50.6 \times 10^3$  kcal/year) and respiration ( $50.0 \times 10^3$  kcal/year) for the hardwood bird community are lower than in the Niepołomice Forest. The estimate of the annual production given by Holmes and Sturges (1973) is very low (about  $0.6 \times 10^3$  kcal/ha-year). This last value was derived only from standing crop data, however, and may be an underestimate. The annual assimilation of birds in both ecosystems reaches about 0.1% of the primary production.

No other data for direct comparison of energy flow through bird communities in various ecosystems are available. The few studies of this kind are either incomplete or they concern single populations. For example, Odum et al. (1962) studied energy flow through an American old field ecosystem taking into account only one dominant bird species, Savannah Sparrow (*Passerculus sandwichensis*). The population of these birds stays in that region only for about 150 days per year, assimilating in that period  $36.0 \times 10^3$  kcal/ha at an average density of 10 individuals/ha. Production was  $0.4 \times 10^3$  kcal/ha-season (0.9% of assimilation). However, these results were perhaps too low, since in calculation of energy requirements, only the standard metabolic rate was used. Pinowski (1968) evaluated energy flow through a population of *Passer montanus* in a cultivated field in central Poland. This population averaged 4.5 individual/ha. Assimilation reached  $26.0 \times 10^3$  kcal/ha-year, but production was 280 kcal/ha-year (0.93% of assimilation). A population of *Telmato-dytes palustris* in the salt marshes of Georgia (Kale 1965) had a density of 97 individuals/ha, and energy flow was not less than  $880 \times 10^3$  kcal/ha-year, with a production of  $4.6 \times 10^3$  kcal/ha-year (1.9% of assimilation). West and DeWolfe (1974) investigated energy flow through a bird community in Alaskan tundra, where birds remain only about 100 days each year. Assimilation was investigated in habitats of greater (3.3 individuals/ha) and lesser (1.3 individuals/ha) population densities. It measured 4.95 and  $1.80 \times 10^3$  kcal/ha-year, respectively. As various assumptions and methods were employed to obtain the estimates cited, it is difficult to arrive at conclusions concerning their value for comparisons with the present study.

It is very difficult to ascertain accurately the level that birds of oak-hornbeam forest occupy in the trophic chain of the ecosystem. The qualitative food requirements of different species are different and subject to change, even though most species feed mainly on insects during spring and summer.

The quantitative participation of birds in their role of consumers of the first, second, and higher orders in the energy flow through the ecosystem of oak-hornbeam forest is quite important. According to the general model of Medwecka-Kornaś et al. (1974), in 1968 the forest stand investigated took up  $2.603 \times 10^6$  kcal/ha-season (April–November) in the form of photosynthetic active radiation (PhAR). Plants took up only  $133 \times 10^6$  kcal/ha of this amount; the rest of the energy was dispersed. Birds assimilated only 0.08% of gross primary production from the ecosystem. Small rodents, being on nearly the same trophic level, took up  $0.122 \times 10^6$  kcal/ha, i.e., 0.09% of the energy received by the forest during the same period. Energy assimilation by the decomposers and first order consumers was markedly higher. Forest invertebrates and litter microorganisms assimilated about  $14.9 \times 10^6$  kcal/ha (about 11% of the energy from the producers), butterflies and moths (mainly *Tortrix viridana*) feeding on trees about  $1.4 \times 10^6$  kcal/ha (about 1% of the energy), and deer, only  $0.16 \times 10^6$  kcal/ha (0.12% of energy).

As an indicator of energy capacity, one may use the ratio of production to consumption (P/C) expressed as a percent. For the bird community it averaged 3.7%; for populations of small rodents the mean value over a four-year cycle reached about 2.4%. Thus it seems that production is even more expensive for small rodents than it is for birds. Even higher consumption indices are found in consumers of the first order, i.e., insects. For *Tortrix viridana* the value was about 40%, for other butterflies feeding in tree stands, about 30% (Medwecka-Kornaś et al. 1974).

When considering the significance of birds in the ecosystem of oak-hornbeam forest, it should be stressed that during the spring and summer, when consumption is most intense, birds feed primarily on insects, especially butterflies. It may be assumed, that these insects (larva, pupa, winged form) comprise at least 50% of the food of the entire bird community each year. Butterfly production in the Niepołomice Forest is about  $500 \times 10^3$  kcal/ha. Therefore, it may be assumed that each year birds eliminate 10–12% of the population of insects harmful to trees.



## SUMMARY

The consumption, assimilation (= energy flow), respiration, and production in a multi-species bird community of an oak-hornbeam forest in southern Poland were estimated. The calculations of bioenergetics involved 40 bird species. Using the mapping method during the breeding season and the strip census for the rest of the year, abundance and bird community dynamics were investigated. The average density of breeding birds was 80 pairs per 10 ha, whereas the yearly mean was 112 birds per 10 ha. On the basis of data from the literature a formula was derived for calculating the existence energy for birds (EMR, kcal/bird-day) in relation to body weight ( $W$ , g) and ambient temperature ( $t$ , °C):

$$EMR = 1.572 W^{0.6210} + 0.06514 W^{0.3625} (30 - t).$$

The equation was employed and, while taking into account the energy cost of reproduction, energetic parameters were calculated successively for individuals, a population, and the whole bird community. The total consumption averaged  $113.1 \times 10^3$  kcal/ha-year. The extraction of energy from the ecosystem by birds was exceptionally high during the breeding season (April–June) because the birds effect more than 50% of their total annual consumption during this period.

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