# Forest Ecosystems in Industrial Regions

Studies on the Cycling of Energy
Nutrients and Pollutants in the Niepołomice Forest
Southern Poland

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Chapter 4

# Energy and Matter Flow Through Consumers in the Niepołomice Forest Ecosystem

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the lowest levels in the forest, may be of much importance. This holds true especially for young tree stands (Bobek et al. 1972, Fruziński et al. 1975). The cervids commonly prefer tree species which are the main components of forest ecosystems, hence economically important. In this way, they may affect forestry very disadvantageously (Haber et al. 1975).

Wild boar activities are of high but variable significance, especially on the forest floor. Their mode of feeding contributes to an acceleration of matter cycling and stimulates the development of soil and litter invertebrates (Haber 1969). On the other hand, their activities are destructive of the herb layer (cf. Bratton 1974). An unequivocal evaluation of their impact on forest ecosystems is barely achievable at the moment because of the lack of adequate quantitative data.

### 4.3.3 Energy and Matter Flow Through Bird Populations

Z. Głowaciński, J. Kozłowski, and J. Weiner

The Niepołomice Forest is a mosaic of different habitats. The bird assemblages are therefore described from a gradient-typological perspective, with age variation among forests taken into account. The main habitats are: alder forests, oak-hornbeam forests, pine forests with oaks and birches, moist pine forests, and meadows.

In all, 180 bird species have been recorded in the Niepołomice Forest, of which 60% are known to breed (Głowaciński 1975, 1978, 1981). Very rare species do not play any significant role in energy and matter flow. This study considers only those species with population densities not less than 0.1 pairs $ha^{-1}$.

Energy flow through bird populations has been estimated for all the main habitats. The parameters have been analyzed using a computer simulation model (Głowaciński and Weiner 1977, 1980, 1983, Weiner and Głowaciński 1975). To this end, the abundance of juveniles and adults was derived from field observations on population density, phenology, death rate, and breeding success in particular species. Various ecological and bioenergetic data were taken from the available literature.

Of the five main habitats investigated (forests from 75 to 100 years old), the largest bird assemblage occurs in the oak-hornbeam forest; the pine forest is half as rich in birds (Table 4.15). The dominant species are *Fringilla coelebs* and *Anthus trivialis,* associated with *Erithacus rubecula, Parus caeruleus,* and *P. major* (Table 4.15). Meadows are relatively simple in ecological structure, and the bird assemblage there is between 5 and 11 times less rich in the number, but only half as poor in biomass as in the mature forest ecosystems (Table 4.15).

The avifauna is very unstable and largely homogeneous in winter. Only a single winter bird colony has been recognized in the whole Niepołomice Forest. It is dominated by titmice. The bird biomass in winter approximates 200 g $ha^{-1}$, which is equivalent to 1,600 kJ $ha^{-1}$ (Table 4.16).

The energy flow (or assimilation) through a breeding bird colony in mature forests ranges from 250 to $585 \times 10^3$ kJ $ha^{-1}$ in the breeding season depending on the habitat. Ecological efficiency, however, is very even and ranges from 2.1 to

**Table 4.15.** Abundance (N) and standing crop (Sc) of birds in the main habitats of the Niepołomice Forest in the breeding season. (Głowaciński 1975, Głowaciński and Weiner 1977, 1983). For each habitat three dominant species are listed

| Ecosystem | Bird species | N | | Sc | |
|---|---|---|---|---|---|
| | | Pairs per 10 ha | % | $g\ ha^{-1}$ | $kJ\ ha^{-1}$ |
| Meadow | *Alauda arvensis* | 3.3 | 46.7 | 23.1 | 184.9 |
| | *Anthus pratensis* | 1.7 | 23.3 | 5.8 | 46.0 |
| | *Coturnix coturnix* | 0.5 | 7.0 | 10.0 | 80.6 |
| | Other species[a] | 1.6 | 23.0 | 86.8 | 691.9 |
| | Total | 7.1 | 100.0 | 125.7 | 1003.4 |
| Alder forest | *Emberiza citrinella* | 8.1 | 11.0 | 45.4 | 361.1 |
| | *Fringilla coelebs* | 8.1 | 11.0 | 32.4 | 257.9 |
| | *Erithacus rubecula* | 6.3 | 8.5 | 21.6 | 171.5 |
| | Other species[a] | 51.9 | 69.5 | 279.9 | 2236.1 |
| | Total | 74.4 | 100.0 | 379.3 | 3026.6 |
| Oak-hornbeam forest | *Ficedula albicollis* | 10.8 | 13.5 | 31.3 | 249.4 |
| | *Fringilla coelebs* | 9.1 | 11.3 | 36.4 | 289.8 |
| | *Parus caeruleus* | 8.2 | 10.2 | 20.5 | 163.2 |
| | Other species[a] | 52.2 | 65.0 | 464.3 | 3696.3 |
| | Total | 80.3 | 100.0 | 552.5 | 4398.7 |
| Pine mixed forest | *Anthus trivialis* | 8.1 | 12.7 | 37.3 | 296.6 |
| | *Erithacus rubecula* | 6.0 | 9.4 | 20.5 | 163.4 |
| | *Fringilla coelebs* | 6.0 | 9.4 | 24.0 | 191.1 |
| | Other species[a] | 43.6 | 68.5 | 287.8 | 2541.0 |
| | Total | 63.7 | 100.0 | 369.6 | 2942.1 |
| Fresh pine forest | *Fringilla coelebs* | 7.5 | 20.7 | 30.0 | 238.8 |
| | *Anthus trivialis* | 4.7 | 13.0 | 21.6 | 172.1 |
| | *Phylloscopus collybita* | 2.3 | 6.4 | 4.2 | 33.0 |
| | Other species[a] | 21.7 | 59.9 | 177.4 | 1411.9 |
| | Total | 36.2 | 100.0 | 233.2 | 1855.8 |

[a] The full list is given in the cited publications

2.4% (Table 4.21). Apart from the breeding season, the energy flow is much lower. The total annual energy flow through the birds is $660 \times 10^3\ kJ\ ha^{-1}$.

The energy flow through the birds is lower by a factor of 3 to 7 in the meadows, but the ecologic efficiency is considerably higher and reaches 3.5% (Table 4.17). This is due to the greater share of species with higher birth rates and greater population densities. Following cutting in the deciduous forest the ecologic efficiency may be as high as 7% (Głowaciński and Weiner 1977).

The energy balances of bird populations of the deciduous and coniferous forests are widely different from each other in the breeding season. The energy flow is much higher in the former. The standing crop is twice as high there as in the coniferous forest. Furthermore, a maximum is achieved in 15-year-old deciduous

**Table 4.16.** Abundance (N) and standing crop (Sc) of a winter bird community in the Niepołomice Forest. (Głowaciński and Weiner 1977)

| Species | N | | Sc | |
|---|---|---|---|---|
| | Indiv. per 10 ha | % | $g\ ha^{-1}$ | $kJ\ ha^{-1}$ |
| *Parus major* | 12.5 | 20.7 | 23.6 | 187.9 |
| *Coccothraustes coccotheraustes* | 10.0 | 16.6 | 53.0 | 421.9 |
| *Sitta europaea* | 9.4 | 15.6 | 19.9 | 158.4 |
| *Parus caeruleus* | 9.2 | 15.2 | 11.5 | 91.5 |
| *Certhia* sp. | 4.1 | 6.8 | 3.9 | 31.1 |
| *Parus palustris* | 3.5 | 5.8 | 4.0 | 31.8 |
| Other species | 11.7 | 19.3 | 86.9 | 691.9 |
| Total | 60.4 | 100.0 | 202.8 | 1614.5 |

**Table 4.17.** Energy budget and ecological efficiency of the main bird communities of the Niepołomice Forest (energy budget of migratory birds from unpublished data of Weiner and Głowaciński) C = consumption, A = assimilation, E = excretion, R = respiration, P = production, P/A = ecological efficiency

| Ecosystem | C | A | E | R | P | P/A |
|---|---|---|---|---|---|---|
| Breeding season (150 days) ($kJ \times 10^3\ ha^{-1}\ season^{-1}$) | | | | | | |
| Wet meadow | 115.5 | 86.6 | 28.9 | 83.6 | 3.0 | 3.5 |
| Alder-forest | 646.1 | 484.6 | 161.5 | 474.6 | 10.0 | 2.1 |
| Oak-hornbeam forest | 780.3 | 585.2 | 195.1 | 571.0 | 14.2 | 2.4 |
| Mixed pine forest | 587.1 | 440.3 | 146.8 | 429.6 | 10.7 | 2.4 |
| Fresh pine forest | 333.7 | 250.3 | 83.4 | 244.5 | 5.8 | 2.3 |
| Weighted mean[a] (without meadow) | 443.4 | 332.6 | 110.8 | 324.9 | 7.7 | 2.3 |
| Nonbreeding season (215 days) ($kJ \times 10^3\ ha^{-1}\ season^{-1}$) | | | | | | |
| Mean (without meadow) | 148.6 | 111.9 | 36.7 | 111.9 | 0.0 | |
| Whole year ($kJ \times 10^3\ ha^{-1}\ yr^{-1}$) | | | | | | |
| Mean (without meadow) | 592.0 | 444.5 | 147.5 | 436.0 | 7.7 | |

[a] Weighted mean of various age classes of various forest communities

forests, but only in mature coniferous forests. In the climax, however, the standing crop of birds is fairly constant in these forest ecosystems.

The energy flow through the birds in the Niepołomice Forest falls to only $50 \times 10^3$ kJ $ha^{-1}$ in winter. The standing crop, however, is only slightly lower than in spring and summer in the coniferous forests.

The energy balances of the forest nesting birds are given in Fig. 4.9. Ecological succession from cutting (1 year old) to climax (over 150 years old) is taken into account. The energy flow increases at variable rates during secondary succession (Głowaciński and Weiner 1977, 1980, 1983). Bird productivity is much higher in

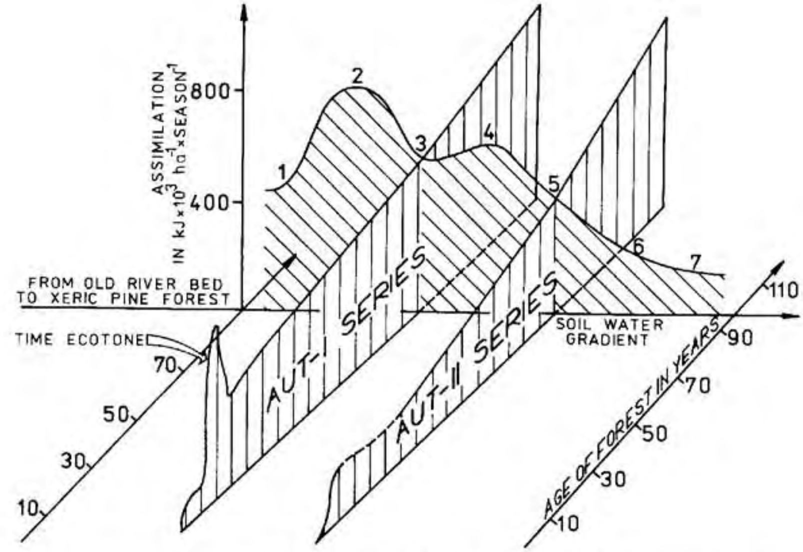


**Fig. 4.9.** Three-dimensional pattern of energy flow through breeding bird communities in the Niepołomice Forest. *1* moist alder forest; *2* alder forest × oak-hornbeam forest; *3* oak-hornbeam forest; *4* oak-pine forest; *5* mixed pine forest; *6* fresh pine forest; *7* xeric pine forest; *AUT I* ecological succession of oak-hornbeam forest; *AUT II* ecological succession of pine forest

forests developed on moderately humid and transitional sites (alder-oak forest, oak-hornbeam forest, oak-pine forest) than in those on dry (pine forest) and wet sites (alder forest). Energy flow attains a maximum in alder-oak forests (assimilation equal to $851.8 \times 10^3$ kJ ha$^{-1}$ in the breeding season), and exceeds by a factor of 5 that in dry pine forests (Głowaciński and Weiner 1983). This is shown in the diagram of energy flow through bird assemblages at various successional stages (Fig. 4.9).

The average energy flow through the avifauna has been estimated taking into account typological variation of the habitats and age variation of the tree stands. The total energy flow averages $440 \times 10^3$ kJ ha$^{-1}$ in the breeding season and $150 \times 10^3$ kJ ha$^{-1}$ in the nonbreeding season, providing the total annual flow of $600 \times 10^3$ kJ ha$^{-1}$. At least 75% of the bird diets are accounted for by insects (Graczyk 1974, Oko 1975, Sikora 1975, Markiewicz 1978). Consequently, one may assume that the birds consume some $450 \times 10^3$ kJ ha$^{-1}$ in the form of insects. Under the additional assumption that 50% of the bird diets are accounted for by butterflies (mostly *Tortrix viridana*), whose production is known (Bandoła-Ciołczyk and Witkowski 1976, and Sect. 4.2), one may conclude that the birds utilize 2–10% of production of the latter, mostly in May and June.

The energetic impact of bird populations on the deciduous and coniferous forests does not exceed 0.5% of primary production.

Having estimated the energy flow through birds, the flow of specific elements can be computed as well. To this end, data on the chemical composition of bird bodies and food are required. The body composition of two small insectivorous

**Table 4.18.** Body composition in the blackcap (*Sylvia atricapilla*) and the great tit (*Parus major*) (Ambroziak 1979; Białecka 1979). Fat content as percent proportion of dry weight; N, P, K, Ca contents as percent proportions of dry weight without fat

| Species and sex | Water | Fat | N | P | K | Ca |
|---|---|---|---|---|---|---|
| *Sylvia atricapilla*, females | 66.5 | 15.8 | 9.3 | 2.8 | 1.3 | 3.9 |
| *Sylvia atricapilla*, males | 66.8 | 16.0 | 9.6 | 3.0 | 1.3 | 4.2 |
| *Parus major*, females | 69.8 | 11.6 | 10.5 | 2.5 | 1.1 | 4.1 |
| *Parus major*, males | 67.5 | 16.2 | 11.2 | 2.8 | 1.1 | 5.0 |
| Average | 67.5 | 14.9 | 10.2 | 2.8 | 1.2 | 4.3 |

birds, the blackcap (*Sylvia atricapilla* L.) (Ambroziak 1979) and the great tit (*Parus major* L.), is given in Table 4.18. The figures are almost the same for both species. Hence, these values can be extrapolated for the remaining species. Concentrations of nitrogen, phosphorus, potassium, and calcium are given in percentage proportion of dry biomass without fat, because fat contents are highly variable among individuals. Considerable changes in body composition have been observed in great tit females during the period of egg deposition and incubation (Białecka 1979); therefore, the values are averaged over the whole nesting season.

Using these data and also assuming that the feathers (13% nitrogen dry weight) account for 9% of the total biomass, the amounts of particular elements maintained in bird bodies have been computed. There is less than 10 g nitrogen $ha^{-1}$, 3 g calcium, and even smaller amounts of potassium and phosphorus (Table 4.23). The amounts of those elements assimilated during a single breeding season can be estimated by multiplying standing crop by biomass turnover rate. The latter coefficient approximates 3 $yr^{-1}$, but the amounts of assimilated elements exceed the average annual level by a factor of 5 because the standing crop of birds is much lower in winter than in the breeding season. This estimate is also biased by nest mortality. However, Bieszczad-Kosch (1979) demonstrated that except for calcium, the concentration of the elements in birds' bodies investigated does not change during postembryonic development. The concentration of calcium in juveniles, especially those 3 to 7 days old, is very low. Even in juveniles leaving the nest it is still much lower than in adults. Calcium, however, is also the main constituent of egg shells. The amounts contained in egg shells counterbalance the difference in calcium concentrations between juvenile and adult birds. Hence, the estimate of element assimilation by birds in the process of production may be sufficiently reliable.

Depending on the age of the forest, the birds assimilate during production 13–90 g nitrogen, 3–17 g phosphorus, 1–7 g potassium, and 4–27 g calcium $ha^{-1}$ in the oak-hornbeam forest. In the coniferous forests these values are still lower. Average values for the whole Niepołomice Forest area: 35 g nitrogen, 7 g phosphorus, 3 g potassium, and 11 g calcium $ha^{-1}$ (Table 4.19). Bird consumption in terms of energy is given in Table 4.17. The estimates provided above follow from

**Table 4.19.** Flow of elements through bird communities of various ecosystems near maturity in the Niepołomice Forest

| Ecosystem | Standing crop Sc | | | | Production P | | | | Consumption C | | | | Excretion E | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | P | K | Ca | N | P | K | Ca | N | P | K | Ca | N | P | K | Ca |
| Breeding season (150 days) (g $ha^{-1}$ $season^{-1}$) | | | | | | | | | | | | | | | | |
| Meadow | 4.7 | 0.9 | 0.4 | 1.4 | 14.0 | 2.6 | 1.1 | 4.1 | 711 | 31 | 96 | 10 | 706 | 30 | 95 | 6 |
| Alder forest | 14.0 | 2.7 | 1.1 | 4.2 | 46.4 | 8.8 | 3.8 | 13.8 | 3,976 | 171 | 535 | 54 | 3,962 | 160 | 534 | 40 |
| Oak-hornbeam forest | 20.4 | 3.9 | 1.7 | 6.1 | 66.2 | 15.5 | 5.4 | 19.7 | 4,802 | 207 | 646 | 65 | 4,781 | 203 | 644 | 45 |
| Mixed pine forest | 13.7 | 2.6 | 1.1 | 4.1 | 49.7 | 2.4 | 4.0 | 14.8 | 3,613 | 156 | 486 | 49 | 3,600 | 153 | 485 | 34 |
| Fresh pine forest | 8.6 | 1.6 | 0.7 | 2.6 | 26.9 | 5.1 | 2.2 | 8.0 | 2,054 | 89 | 276 | 28 | 2,045 | 87 | 276 | 20 |
| Weighted mean (without meadows) | 10.9 | 2.1 | 0.9 | 3.3 | 35.5 | 6.7 | 2.9 | 10.6 | 2,729 | 118 | 367 | 37 | 2,698 | 115 | 364 | 26 |
| Nonbreeding season (215 days) (g $ha^{-1}$ $season^{-1}$) | | | | | | | | | | | | | | | | |
| Weighted mean (without meadows) | 8.8 | 1.7 | 0.7 | 2.6 | 0.0 | 0.0 | 0.0 | 0.0 | 844 | 36 | 114 | 11 | 844 | 36 | 114 | 11 |
| Weighted mean (without meadows) | 9.7 | 1.9 | 0.8 | 2.9 | 35.5 | 6.7 | 2.9 | 10.6 | 3,573 | 154 | 481 | 48 | 3,542 | 151 | 478 | 37 |

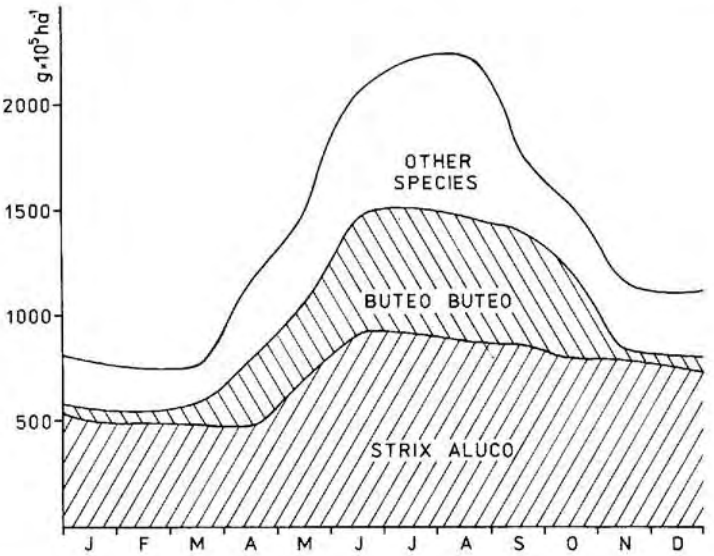


**Fig. 4.10.** Seasonal variation in standing crop of raptorial birds in the Niepołomice Forest. *Strix aluco* tawny owl; *Buteo buteo* common buzzard

the assumption that the birds feed mostly on insects, especially in the breeding season. The concentrations of specific elements in insects have been assumed as follows: 4.6% of the biomass is accounted for by nitrogen, 0.6% by phosphorus, 0.2% by potassium, and 0.02% by calcium (Spector 1956, Kozłowski unpubl.).

The total consumption of specific elements and the amounts returned to the ecosystem in the form of feces and urine are provided in Fig. 4.16 and Table 4.19. The amounts of elements consumed are strongly dependent on the successional stage of the forest, with a maximum usually achieved in mature forests. Annually, the birds consume 6 kg nitrogen, 260 g phosphorus, 800 g potassium, and 80 g calcium $ha^{-1}$ in mature oak-hornbeam forest (Fig. 4.16). The averages for the whole Niepołomice Forest are much lower and approximate 3.5 kg nitrogen, 150 g phosphorus, 480 g potassium, and 50 g calcium $ha^{-1}$ annually (Table 4.19). Almost the total consumed elements are rapidly evacuated with feces and urine. The birds seem to accelerate considerably the rate of matter, and especially nitrogen, cycling in the ecosystem investigated.

The impact of birds on forest ecosystems exceeds by far that of bioenergetics and matter cycling. It is largely related to food selection, as it depends on which insect species are eaten and what is the role of prey species in the ecosystem. Furthermore, birds eat and/or destroy buds and seeds of trees and other plant species, and as well transport seeds and fruits (e.g., the Turdidae). A quantitative estimate of these effects on the forest ecosystem is difficult and exceeds the scope of this study.