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Dynamics of the abundance and consumption of birds of prey in the Niepołomice Forest

[with 5 text—figs]

Dynamika liczebności i konsumpcja ptaków drapieżnych Puszczy Niepołomickiej

Abstract. Sixteen species of birds of prey from the orders *Falconiformes* and *Strigiformes* were recorded from the Niepołomice Forest in 1977—1987, twelve of them belonging to its breeding avifauna. The Tawny Owl, Buzzard and Goshawk were distinctly numerically dominant. The most interesting fact was the nesting of the Ural Owl and Tengmalm's Owl in the Forest. In 1978 and 1983 breeding pairs censuses were made and the data thus obtained were used to compute the annual dynamics of biomass and consumption of the whole community of birds of prey for these two years and to evaluate their influence on the prey population inhabiting the wooded areas. It was found that distinct pressure was exerted by the birds of prey on two rodent species, the bank vole and the field vole. No effect of their predation upon other small mammals and birds was proved.

CONTENTS

I. INTRODUCTION

The present state of the avifauna of the Niepołomice Forest — perhaps with the exception of birds of prey — is comparatively well known. Most of the papers dealing with it have appeared in the last twenty years. Before this period only fragmentary information obtained from partial and often accidental observations was published, although the Forest is situated in close vicinity to Kraków. That was the case towards the end of the nineteenth cen-

tury (KROMER 1894; RZEHAK 1894, SCHAUER 1878) and even 60 years later (KANIA 1964, KWIATEK 1963, TWARÓG 1964).

The first work based on systematic studies was a quantitative analysis of the avifauna in the south-western region of the Forest (KANIA 1968), whereas GŁOWACIŃSKI'S (1975a) comprehensive faunistic-ecological outline contained an already full description of the avifauna of the whole Forest area. Further publications are given but to selected problems of avian ecology. A succession of bird communities against the gradient changes of forest communities was described by GŁOWACIŃSKI (1972, 1975b and 1981) and GŁOWACIŃSKI & JARVINEN (1975), GŁOWACIŃSKI & WEINER (1977 and 1980) and WEINER & GŁOWACIŃSKI (1975) dealt with the bioenergetics of birds in the pine forests and oak-hornbeam forests entering into the Niepołomice Forest complex. The results of studies on energy and matter flow through populations of small birds as well as birds of prey are given in other publications (GŁOWACIŃSKI et al. 1984, GRODZIŃSKI & WASILEWSKI 1984).

In all the hitherto published studies birds of prey were treated only as one of the components of the avifauna of the Forest, without being given special attention. It should however be emphasized that our knowledge of the occurrence and abundance of most of raptorial species throughout the country is very incomplete (TOMIAŁOJĆ, 1990). The results obtained so far in the Niepołomice Forest do not reflect the actual state, for the studying of this group of birds needs individual methods. The data provided by studies carried out on the occurrence and numbers of the birds of prey in the Forest and on the energy and matter flow through their populations should not be treated as full either (GRODZIŃSKI & WASILEWSKI, l.c.).

The need for studies on birds of prey is also indicated by the fact that these birds are under strong pressure of human activity, direct or indirect; the latter kind manifests itself in profound changes resulting in degradation of the habitats in which they live. The tree stands of the Niepołomice Forest are just such an environment, harried by the action of industrial dusts and gases emitted by the metallurgical plants of the Lenin Steel Works (GRODZIŃSKI et al. 1984). Four to nine tons of dust fall monthly on each square kilometre of this forest, containing also heavy metals: iron — 360 kg, zinc — 26 kg, magnesium — 10 kg, lead and copper — 5 kg each, nickel — 3 kg and cadmium — 1.3 kg. However, the most sinister is the fall of sulphur oxides in so large amounts that annually they give 6.3 g/m^2 of pure sulphur. Another degrading factor in the Forest is excessive tree felling, leading in consequence to a too radical rejuvenation of the stands (ĆWIKOWA et al. 1984).

The role played by birds of prey in the biotopes inhabited by them suggests itself in the discussion of the ecological aspect of these birds. Many investigators concerned themselves with this problem, but the influence of the birds of prey on the population of prey living in wooded areas is presented only in single papers (GOSZCZYŃSKI 1983, HUHTALA 1976, SOUTHERN & LOVE 1968 and 1982, WIDEN 1985 and partly also RYSZKOWSKI et al. 1971). On the other

hand, most of the papers are given to the role of birds of prey in agrocenoses or in open areas, only adjacent to forest complexes. The species studied most frequently in this respect were as follows: Buzzard *Buteo buteo* (CZARNECKI & FOKSOWICZ 1954, GOSZCZYŃSKI & PIŁATOWSKI 1986, PINOWSKI & RYSZKOWSKI 1962, SLÁDEK 1961, TRUSZKOWSKI 1976), Goshawk *Accipiter gentilis* (GOSZCZYŃSKI & PIŁATOWSKI l.c.; KENWARD 1977, OPDAM et al. 1977) and Tawny Owl *Strix aluco* (SOUTHERN 1954, WENLAND 1972, 1980), whereas GOSZCZYŃSKI (1973, 1977) deals with the effect of the whole community of raptors in a population of prey.

Some birds, which from the ecological point of view also occupy the niche of „predators", have been omitted from the present study. The Raven *Corvus corax* and Black Stork *Ciconia nigra*, whose numbers and consumption have already been preliminarily evaluated (GRODZIŃSKI & WASILEWSKI 1984) belong to such species in the Forest area — at least in some periods of the year. However, the difficulties encountered in isolating such groups of birds unambiguously caused that the present study is confined to the birds of prey in the systematic sense of this term only.

The purpose of this work was to appraise the influence of the birds of prey of the orders *Falconiformes* and *Strigiformes* upon the population of prey inhabiting the tree stands of the Niepołomice Forest. The indirect task of this work comprises studies on the qualitative composition and abundance of these birds, the evaluation of the annual dynamics of their biomass and consumption and the investigation of the composition of their diet.

Here I wish to express my heartfelt thanks to Dr T. TOMEK of the Institute of Systematics and Evolution of Animals, P.A.Sc., for her enormous work connected with the identification of the bird remains from Tawny Owls' pellets. I also thank Dr A. NADACHOWSKI, Dr A. RUPRECHT, Dr Z. SZYNDLAR and Dr Sc. B. WOŁOSZYN for their help with determining the remaining vertebrates. I am very much indebted to Prof. B. PETRYSZAK for his determination of the insects found in the food of the Tawny Owl.

I owe also my sincere thanks to Prof. A. GÓRECKI for his valuable remarks and help with the elaboration of the results concerning bioenergetic problems, to Mr P. MIELCZAREK for his help during field study and to Mr R. CZUCHNOWSKI for giving me access to his unpublished materials.

II. STUDY AREA AND METHODS

The Niepołomice Forest is situated in the forks of the rivers Vistula and Raba, about 20 km east of Kraków (50°07'N and 20°23'E) and it is about 11 000 ha in area. It is the greatest of the extant forest complexes in this part of the country and it extends eastwest over a space of 18 km and north-south 13 km (in its broadest place). The brook Drwinka, a right-bank tributary of the Vistula, divides the Forest into two parts. The northern part lies lower, on the ren-

dzina flood-plain bench of the Vistula, and is composed of three complexes: Grobla — 1500 ha in area, Grobelczyk — 260 ha and Koło — 220 ha. The southern part, situated higher, on the sand plain of the fluviatile fan of the Raba, forms a single big complex of an area of 8870 ha (Fig. 1).

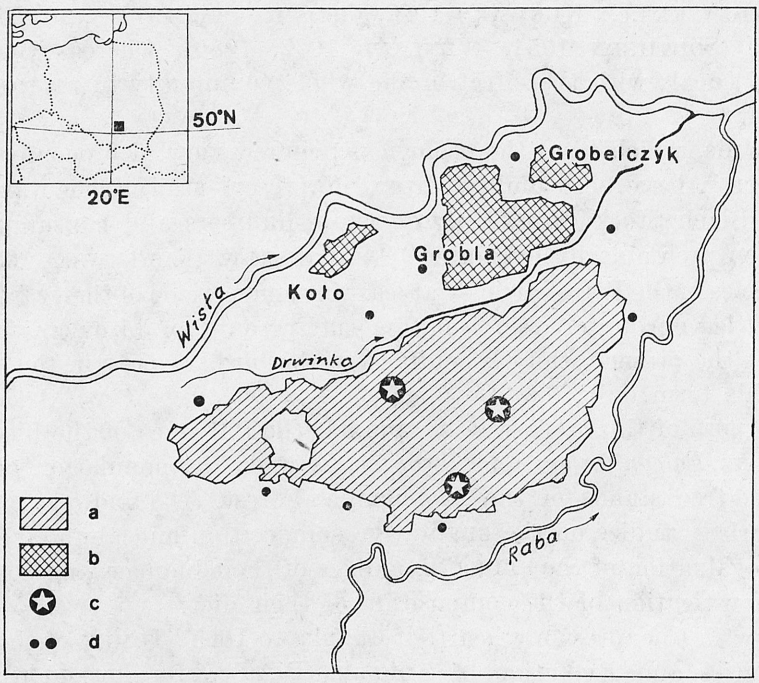

Fig. 1. The simplified map of the Niepołomice Forest and its situation in the territory of Poland. a — pine forests, b — oak-hornbeam forests, c — approximate places where Tawny Owls' pellets used for analysis were found, d — villages and towns

Detailed geobotanical characterizations of the Niepołomice Forest have already been presented in many botanical papers (Bednarz 1981, Ćwikowa et al. 1984, Denisiuk & Medwecka-Kornaś 1976, Ferchmin & Medwecka-Kornaś 1976 and others). A more general description, comprising only characterizations of the tree stands, will suffice here for further considerations.

The pine *Pinus silvestris*, occurring in 71% of the forest area, is the commonest tree in it; oaks, *Quercus robur* and *Q. sessilis*, are met with in 17% of the area and alders, *Alnus glutinosa* and *A. incana* in 9%. The pine forest *Pino-Quercetum*, which covers about 52% of the Forest area, is dominant. Depending on substratum and configuration of the land, it may either occur in places as a fresh pine forest *Vaccinio myrtilli-Pinetum* or pass into a dry pine forest *Cladonio-Pinetum* on sandy eminences. The oak-hornbeam forest *Tilio-Carpinetum* occupies 13% of the area and a transitional form between the fresh pine and the oak-hornbeam forest nearly 35%. Other associations, such as,

for instance, alder carrs *Circaeo-Alnetum* and wet alderwoods *Carici elongate-Alnetum* cover very small areas. Deciduous forests, mainly oak-hornbeam forests, having their natural character in places, grow in the northern part of the Forest complex. Plantations prevail in the southern part, which for the most part consists of pine forests and transitional forms between pine and oak-hornbeam forests (Fig. 1).

Owing to excessive wood cutting, carried on for tens of years, the structure of the tree stands is not very favourable. Only about 35% of the stands lie within the age group from 50 to 100 years, whereas the remaining stands, forming a huge majority, are 21 to 50 years old or still younger (Ćwikowa et al., l.c.). As a result, worse and worse nesting conditions are provided for many species of diurnal and nocturnal birds of prey. The radical rejuvenation of the forests may be one of the causes of the decrease in the number of these birds, which has already been observed in some regions of the country. In the last tens of years the incessantly progressing dewatering of the Forest has been increasingly distinct (Bzowski 1973). It has a harmful effect upon the biotopic conditions, limiting the area that favours natural productive stands.

The climate of the Forest is typical of the submontane lowlands and basins of the Tarnów region. The vegetative season with temperatures exceeding +5°C is long and lasts above 220 days. The mean daily temperature for five winter months, from November throughout March is 0°C, for April and October 8°C and for the remaining five months, from May throughout September 16°C (Hess 1969).

The presented data concerning the tree stands and basic meteorological parameters were indispensable to the preparation of this work. On the other hand, all the observations of the birds of prey in the Niepołomice Forest were referred to one of two typical forest habitats, i.e. pine and oak-hornbeam forests. They differ widely both in the numbers of birds of prey and in the density of their potential prey animals. On the other hand, thermal conditions drastically changed the expenditure of energy in the birds of prey and their food requirements. This is just for this reason that the seasons of winter and summer and the short transitional periods were taken into account in this study.

This study was carried out from 1977 to 1987 in the coniferous complex, 8870 ha in area, and two deciduous complexes — Grobla and Grobelczyk — covering 1760 ha, both together. The third, smallest, complex — Koło — most distant from the remaining parts of the Forest, was omitted. Field observations made in 1977, prior to the period of systematic investigation carried out from 1978, were used to work out the methods and to obtain preliminary results. Seeing that the number of pairs of nesting raptors was to constitute the point of departure for further study, field observations were concentrated in the pre-breeding and breeding seasons, i.e. from March to June, every year. In the remaining periods of the year observations were conducted considerably less intensively and this is probably why members of some species of rapto-

rial birds visiting the Forest sporadically and staying in it for a short time, far less important besides to the present work, were not observed. In winter months assessments were made only at the edge of the forest, where the birds of prey chiefly accumulated, which had been found during the preliminary study carried out throughout the forest complex.

Recording of the breeding pairs of diurnal birds of prey was done in two ways. The first of them consisted in searching for old nests in winter and next examining them and their close neighbourhood in the breeding season. The second method, applied in the pre-breeding and breeding seasons, was based on repeated assessments made by an observer wandering on foot or by bicycle along the roads and aisles of the forest. The distance covered daily was usually about 30 km. All the birds of prey observed or heard, their behaviour and traces of feeding were recorded and the results were plotted on a map. It appeared that the points representing the places of particular observations clustered together and particular clusters were distant from each other. It was assumed that the lines surrounding such clusters represented the borders of breeding areas, which was confirmed by the fact that in most cases occupied nests were later found in such areas acknowledged to be breeding areas. In each successive season the starting point of appraisal was the checking of the nests from the preceding year.

The estimation of the number of breeding owl pairs was performed in a similar manner. Night assessments along the roads and passable aisles in the whole area of the Forest were made several times a year, in March and April. Starting from 1982, tape recordings were used to elicit calls from the owls also in the period of their poor vocal activity. In the case of the Tawny Owl, fairly regularly distributed all over the Niepołomice Forest, the counts of breeding sties were made more frequently but only in selected areas. In the oak-hornbeam forests such a region, situated in the central part of the Grobla complex, is 650 ha in area; it consitutes 40% of the complex. In the pine forests it was a belt extending across the complex, about 2200 ha in area or nearly 25% of their total area.

In order to estimate the influence the birds of prey exercise upon the population inhabiting the Forest it was necessary to get familiar with the diet of these birds and, above all, that of the Tawny Owl, evidently numerically dominant. In searching out the places where these birds had ejected pellets, we came across many difficulties and only a systematic examination of the feeding racks for deer made it possible to find three such sites in the coniferous complex of the Niepołomice Forest. Each of them was at least 2 km away from the edge of the forest, which practically excluded the possibility of contact of these birds with the fields and meadows surrounding it. The remains of prey (vertebrates and insects) from about 180 pellets were collected and identified.

The methods for calculation of biomass and consumption and their dynamics are given at the beginning of the sections devoted to respective problems.

III. THE OCCURRENCE AND NUMBERS OF BIRDS OF PREY

The occurrence of 16 species of birds of prey from the orders *Falconiformes* and *Strigiformes* was observed in the Niepołomice Forest during the present study, carried out in 1977—1987 (Table I). A systematic list of these birds is given below; its arrangement and nomenclature follow the keys to the vertebrates of Poland, part IVa, Birds, *Non-Passeriformes* (FERENS 1967).

Table I

List of breeding and visiting birds of prey occurring in the Niepołomice Forest in the years of studies here and the earlier data recorded till 1972

	Data from 1977—1987	Data from before 1972
breeders	*Accipiter gentilis* (LINNAEUS, 1758) *Accipiter nisus* (LINNAEUS, 1758) *Milvus migrans* (BODDAERT, 1783) *Aquila pomarina* BREHM, 1831 *Buteo buteo* (LINNAEUS, 1758) *Pernis apivorus* (LINNAEUS, 1758) *Falco subbuteo* LINNAEUS, 1758 *Falco tinnunculus* LINNAEUS, 1758 *Strix aluco* LINNAEUS, 1758 *Strix uralensis* PALLAS, 1771 *Asio otus* (LINNAEUS, 1758) *Aegolius funereus* (LINNAEUS, 1758)	*Accipiter gentilis* (LINNAEUS, 1758) *Accipiter nisus* (LINNAEUS, 1758) *Milvus milvus* (LINNAEUS, 1758) *Buteo buteo* (LINNAEUS, 1758) *Falco subbuteo* LINNAEUS, 1758 *Falco tinnunculus* LINNAEUS, 1758 *Strix aluco* LINNAEUS, 1758 *Asio otus* (LINNAEUS, 1758)
visitors	*Milvus milvus* (LINNAEUS, 1758) *Aquila chrysaëtos* (LINNAEUS, 1758) *Buteo lagopus* (BRUNNICH, 1762) *Athene noctua* (SCOPOLI, 1769)	*Circus cyaneus* (LINNAEUS, 1766) *Circus pygargus* (LINNAEUS, 1758) *Circus aeruginosus* (LINNAEUS, 1758) *Milvus migrans* (BODDAERT, 1783) *Haliaeëtus albicilla* (LINNAEUS, 1758) *Aquila chrysaëtos* (LINNAEUS, 1758) *Aquila pomarina* BREHM, 1831 *Buteo lagopus* (BRUNNICH, 1762) *Pernis apivorus* (LINNAEUS, 1758) *Circaëtus gallicus* (GMELIN, 1788) *Pandion haliaëtus* (LINNAEUS, 1758) *Falco peregrinus* TUNSTALL, 1771 *Asio flammeus* (PONTOPPIDAN, 1763) *Aegolius funereus* (LINNAEUS, 1758)

Falconiformes

Accipiter gentilis (LINNAEUS, 1758) — Goshawk. It occurred as a breeding in both the oak-hornbeam and pine forests, but in the coniferous complex most of its nests were placed on the southeastern borders of the forest. A constant increase in its number was observed during the ten-year study, from 4 pairs in 1978 to 16 in 1987 (CZUCHNOWSKI, typescript).

Accipiter nisus (LINNAEUS, 1758) — Sparrow Hawk. It nested in the Fo-

rest regularly but in very small numbers and only in the coniferous complex at that. In the study period its number ranged from 1 to 3 pairs.

Milvus migrans (BODDAERT, 1783) — Black Kite. During the study period this bird was observed several times but exclusively in the spring season. In 1983 a pair was found nesting in the deciduous complex. This breeding ended in the departure of one young bird from the nest.

Milvus milvus (LINNAEUS, 1758) — Red Kite. During the whole study period one individual, flying between the pine forests and oak-hornbeam forests, was seen only once, on 9 April 1987.

Aquila chrysaëtos (LINNAEUS, 1758) — Golden Eagle. At present it visits the Forest very rarely. In the spring of 1987 a dead bird in immature plumage was found on the northern boundary of the pine forests with meadows.

Aquila pomarina BREHM 1831 — Lesser Spotted Eagle. In 1986 a pair nested in the Gibiel Reserve in the northern part of the pine forests. Their breeding was successful and one juvenile left the nest. In the following year no birds of this species were observed nesting, although two adult individuals were seen circling between the pine and oak-hornbeam forests on 2 May.

Buteo buteo (LINNAEUS, 1758) — Buzzard. It is the most numerous diurnal bird of prey and it nests throughout the territory of the Forest. In successive years of the study its number underwent fluctuations, the highest number of breeding pairs being found in 1983 (Table II).

Buteo lagopus (BRUNNICH, 1762) — Rough-legged Buzzard. It visited the Forest irregularly. It was observed only in 6 winter seasons and even then most frequently in the north of the pine forests. There were never seen more than two birds at the same time.

Pernis apivorus (LINNAEUS, 1758) — Honey Buzzard. It was very rarely met with in the Forest. Nevertheless, one pair nested in the Grobla complex in 1979 and 1980. However, we failed to find whether the breeding was successful. Only one individual, flying over the meadows amidst the pine forests, was observed in 1982.

Falco subbuteo LINNAEUS, 1759 — Hobby. This bird nested in the pine forests regularly except for the years 1978 and 1981, when only migrants were observed. In spring, exactly in May, though irregularly, it visited also the region of oak-hornbeam forests, but its nesting in the deciduous complex was not recorded. Every year starting from 1982 a pair occupied the nest used by Ravens in early spring.

Falco tinnunculus LINNAEUS, 1758 — Kestrel. Nowadays it occurs in very small numbers in the Forest. Two or three pairs nest on its boundary with adjacent meadows and fields every year. No winterning individuals were seen.

Strigiformes

Athene noctua (SCOPOLI, 1769) — Little Owl. It was observed only several times at the northern edge of the pine forests. The individuals observed were visitors coming from the villages neighbouring upon the Forest.

Strix aluco LINNAEUS 1758 — Tawny Owl. It is the commonest and most numerous species of the birds of prey in the study area. The greatest concentration of breeding pairs was found in the oak-hornbeam forests, especially in the oldest stands situated in the central part of the Grobla complex. In the pine forests it was most frequently met with in their south-eastern part (Table II).

Strix uralensis PALLAS, 1771 — Ural Owl. This faunistic element is new to the Niepołomice Forest. First observed by GŁOWACIŃSKI (1981), starting from 1978 it nested regularly in the coniferous complex in slowly but constantly incereasing numbers. Nests of six pairs were found and breeding effects were checked in 1987 (CZUCHNOWSKI, typescript). This bird was sporadically heard also in the oak-hornbeam forests, where however its nesting was not observed.

Asio otus (LINNAEUS, 1758) — Long-eared Owl. It was found to breed in small numbers in the study area but only in 7 seasons, probably because of the scarcity of places suitable for its nesting. On the other hand, breeding was regularly observed in poplar plantations and copses outside the administrative boundary of the Forest. Nomadic flocks were seen in the area of the Forest every winter. In the 1977/1978 season, from December throughout February, a group of 12 birds stayed in one and the same place at the western end of the pine forest, where 16 individuals were also observed in the winter of 1982/1983.

Aegolius funereus (LINNAEUS, 1758) — Tengmalm's Owl. One pair nested in the western part of the coniferous complex, on the boundary between an old pine forest and a young birch stand from 1980 to 1984. The nest was placed in a tree-hole of a Black Woodpecker at a height of about 8 m in a pine-tree. In 1983 and 1985 the occurrence of another pair was found at the eastern end of the pine forest, not far from the place where remains of an individual were come across in 1965 (KANIA 1968). The voice of Tengmalm's Owl was also heard twice in the area of the aok-hornbeam forests in May 1983.

The survey above shows that 12 species belonged to the breeding fauna of the Forest, whereas another 4 species only visited it. Such a breeding to visiting species ratio is due, among other things, to the fact that, as has already been mentioned, in the field study more attention was given to searching out breeding birds, which better characterize the biotope of the Forest; they are of essential significance in further bioenergetic considerations and determine the pressure exerted upon the prey population. Six of the breeding species — Buzzard, Goshawk, Sparrow Hawk, Kestrel, Tawny Owl and Ural Owl — nested in the Forest in all the years of study. The Hobby nested in 8 seasons, the Long-eared Owl in 7, Tengmalm's Owl in 6 and the Honey Buzzard in 2. The Lesser Spotted Eagle and Black Kite were found breeding only in one season. A comparison of the results obtained with the data published by GŁOWACIŃSKI (1975a) in his faunistic-ecological study, in which he compiles

the results of his own 6-year investigation and the data from literature, is given in Table I. Only two species included in that publication, the Spotted Eagle *Aquila clanga* PALLAS, 1811 and the Lesser Kestrel *Falco naumanni* FLEISCHLER, 1817, the identification of which has been called in question by the Faunistic Commission, are here omitted. This comparison shows that at present the number of the nesting species of raptorial birds is larger, which is caused chiefly by the fact that in previous studies carried out in the Forest this group of birds did not receive adequate attention, for it is hardly probable that birds of prey should find better and better conditions of breeding in the Forest biotope permanently degraded under strong pressure of industrial pollution and excessive exploitation of old tree stands.

The species whose breeding in the Niepołomice Forest was found for the first time include the Black Kite, Honey Buzzard, Ural Owl, Tengmalm's Owl and Lesser Spotted Eagle. It is probable that this last species is not quite a new breeder in the Forest, for a pair nesting in the area of oak-hornbeam forests in 1968 and identified as Spotted Eagles may have been Lesser Spotted Eagles, in fact. Particularly interesting is the occurrence of two species in the Forest: the Ural Owl and Tengmalm's Owl, which from the geographical point of view are Siberian elements in the Palaearctic. In the territory of Poland they are very rare species and their occurrence is not yet quite well known. The Ural Owl nests locally in the south of Poland, where it is relatively numerous in the Carpathians, especially in their eastern part. Another region of its occurrence is Mazuria; however, it may well be that it is also present in other parts of the country. The breeding sites of Tengmalm's Owls are known from the Sudetes and Carpathians and from the north of Poland, that is, from the Białowieża and Augustów Forests and from the middle section of the Baltic coast. Its nesting was exceptionally found in the lowlands of Silesia (TOMIAŁOJĆ 1990). The breeding sites of these birds situated nearest to the Niepołomice Forest are in the Carpathians, about 40 km away, and so it is highly probable that some individuals from the mountains visited the study area and perhaps even settled in it.

Visiting birds recorded before 1972 were more numerous (GŁOWACIŃSKI 1975a) but, as has already been mentioned, in the present investigation most attention was focussed upon breeding birds. Furthermore, some earlier observations refer to the birds met with in unwooded biotopes, often even outside the administrative boundaries of the Forest.

In addition to the qualitative data, information about the abundance of particular species was gathered during the present study. The large size of the study area and insufficient means (a small number of observers) made it impossible to carry out the breeding pairs census more than twice in the whole area, in 1978 and 1983.

The species that appeared distinctly numerically dominant are the Tawny Owl, Buzzard and, in some measure, also the Goshawk. The results presented

in Table II indicate that the abundance of some species increased noticeably in the five years dividing these two censuses. This is particularly true of the Goshawk, in which a threefold increase was observed and in the Buzzard, with a nearly twofold increase. In the case of the Tawny Owl the number obtained in the area of pine forests in 1978 may have been somewhat underestimated, because the method used then was less accurate than that in 1983. If the number of Buzzards in 1983 was the highest of all obtained throughout the study period, the numbers of the Goshawk and, especially, Ural Owl went on growing in following years. And so in 1987 as many as 16 nests of the Goshawk were detected in the Forest and 6 broods of the Ural Owl were found and examined. The only species whose numbers have decreased over a space of the last 20 years is the Kestrel, but this tendency is general in Poland (TOMIAŁOJĆ, l.c.). The remaining species are not numerous enough to allow a statement on the direction of changes.

The numbers of birds of particular species dominant in the Forest are also very high in the Polish scale. For comparing the findings from the Niepołomice Forest with the numbers of some raptorial birds in other regions of the country I used information given by TOMIAŁOJĆ (1990) in his book „Ptaki Polski — rozmieszczenie i liczebność" (Birds of Poland — distribution and abundance).

As regards the Buzzard, the greatest density, 56.4 pairs 100 km², has hitherto been recorded from the 55-km² area of the Barycz Valley, next 30.6 pairs/100 km² from the 450-km² area of the Iława Lake District and 19.5 pairs/100 km² from the 230-km² area of the Wkrzańska Forest. In the Niepołomice Forest its density was 17.8 pairs/100 km² in 1978 and 32.9 pairs/100 km² in 1983.

In the Goshawk the greatest known density of breeding pairs, 12.9 pairs/100 km², was found in the 350-km² area of the Kampinos Forest and 11.5 pairs/100 km² in a 120-km² area near Skierniewice. In the Niepołomice Forest 3.7, 11.2 and 15.0 pairs were nesting per 100 km² in 1978, 1983 and 1987, respectively. The last of these values is one of the greatest obtained for large areas in this country.

In the case of the Tawny Owl the greatest density of breeding pairs was observed in an old oak-hornbeam stand in the Białowieża Forest, where it was about 2 pairs/100 ha, whereas in the Niepołomice Forest it was about 1.5 pairs/100 ha also in oak-hornbeam forests in the study period. In the pine-woods of the Białowieża Forest 0.5—1.0 pair nested in 100 ha and in similar but younger stands in the Niepołomice Forest 0.3—0.6 pair.

The comparison above indicates that the Niepołomice Forest, despite its continuous degradation, still provides a relatively favourable biotope for rather common birds of prey and also for some rarer ones, e.g. Ural Owls.

Table II

Number of pairs of all birds of prey nesting in the pine and oak-hornbeam forests and in the whole area of the Niepołomice Forest in 1978 and 1983 and their densities per 100 ha

Species	Pine forests 8870 ha				Oak-hornbeam forests 1760 ha				Whole area 10630 ha			
	No. of pairs		Pairs/100 ha		No. of pairs		Pairs/100 ha		No. of pairs		Pairs/100 ha	
	1978	1983	1978	1983	1978	1983	1978	1983	1978	1983	1978	1983
Buteo buteo	14	27	0.15	0.30	5	8	0.28	0.45	19	35	0.17	0.33
Milvus migrans	—	—	—	—	—	1	—	0.05	—	1	—	0.01
Accipiter gentilis	3	9	0.03	0.10	1	3	0.05	0.17	4	12	0.04	0.11
Accipiter nisus	2	2	0.02	0.02	—	—	—	—	2	2	0.02	0.02
Falco subbuteo	—	2	—	0.02	—	—	—	—	—	2	—	0.02
Falco tinnunculus	3	1	0.03	0.01	—	1	—	0.05	3	2	0.03	0.02
Strix aluco	27	50	0.30	0.56	25	26	1.41	1.47	52	76	0.49	0.71
Strix uralensis	1	3	0.01	0.06	—	—	—	—	1	3	0.01	0.03
Asio otus	—	1	—	0.01	—	1	—	0.05	—	2	—	0.02
Aegolius funereus	—	2	—	0.02	—	—	—	—	—	2	—	0.02

IV. DYNAMICS OF BIOMASS OF BIRDS OF PREY

An estimation of the numbers of breeding pairs of the raptorial birds was the first step on the way to find their biomass in its seasonal aspect. However, the determination of biomass dynamics for particular species in the first place required knowledge of their abundance changing in the course of the year. The number of individuals entering upon breeding constituted the point of departure. Owing to marked mortality this number dwindles during the period between the breeding season and the end of the year. On the other hand, the number of birds that start breeding, e.g. in April, is lower than that found in January for losses caused by mortality occur also at the beginning of the year. The experiential determination of the size and rate of losses over so large an area was impossible and therefore the data concerning annual death rate were obtained from literature. NEWTON (1975) gives these data for the Sparrow Hawk, LUNDBERG & WESTMAN (1984) for the Ural Owl and HUHTALA & SULKAWA (1976) for the Goshawk. As regards the remaining species, the mean annual mortality was drawn from general monographs (GLUTZ 1971; CRAMP 1980, 1985). The highest annual mortality of adult birds, about 60%, is given for the Sparrow Hawk and the lowest, about 10%, for the Ural Owl. It oscillates about 30% for the remaining birds of prey occurring in the Niepołomice Forest. Young birds in the first year of life exhibit a similar mortality of about 60% in all the species under study.

It was computed what percentage of the birds that had undertaken breeding died within one month and the figure obtained was subtracted from the basic value in successive months on the assumption that the changes proceed linearly. In the resident birds, as has already been mentioned, the subtraction of this figure every month from the quantitative state in January reduces it to the initial state found in the field in the breeding season. In the case of young the losses sustained during their stay in the nest were left out but it was assumed that the population increases in the breeding season only by the number of young departing from the nest. The mean number was adopted for all the nests of a given species. The data obtained for the Buzzard, Goshawk and Ural Owl in the Niepołomice Forest were complemented with information drawn from literature (BELSKIY 1962; CRAMP, l.c.; GLUTZ, l.c.; NEWTON 1976).

In addition to the number of individuals, changing over the space of a year, the mean body weights of adults obtained from CRAMP'S (l.c.) publication made the basis for estimating the biomass of particular species. Information about the body weight of nestlings on the consecutive days of their postembryonic development and the length of time needed for them to attain the final body weight is provided by BELSKIY (1962) for the Long-eared Owl and Kestrel and by HEINROTH and HEINROTH (1927) and NIETHAMMER (1938) for the remaining species. Data on breeding phenology were collected during field studies.

Table III

Seasonal changes of biomass in g/100 ha in three numerically dominant species of birds of prey and in the remaining species together in the pine and oak-hornbeam forests in the Niepołomice Forest in 1978

	Species	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Pine forests	*S. aluco*	350.0	334.8	319.6	304.4	456.6	528.4	563.1	540.6	517.4	494.9	471.8	449.2
	B. buteo	39.4	39.4	92.0	276.2	414.3	545.5	525.8	506.0	486.3	311.0	59.2	39.4
	A. gentilis	72.8	68.5	64.2	64.2	101.7	137.1	132.8	124.2	117.8	111.4	105.0	98.5
	Remaining species	118.8	110.7	35.3	41.2	51.6	72.8	88.5	84.6	79.8	62.2	70.1	68.1
	Total	581	553	511	686	1024	1284	1310	1255	1201	979	698	655
Oak-hornbeam forests	*S. aluco*	1625.0	1562.5	1491.4	1420.4	2130.6	2465.9	2627.8	2522.7	2414.7	2309.6	2201.7	2096.6
	B. buteo	99.4	99.4	165.5	497.1	745.7	979.3	944.6	909.7	875.0	560.1	99.4	—
	A. gentilis	113.3	113.3	107.9	107.9	170.0	226.7	221.3	210.5	205.1	194.3	188.9	178.1
	Remaining species	—	—	—	—	—	—	—	—	—	—	—	—
	Total	1837	1775	1765	2025	3046	3672	3794	3642	3495	3064	2490	2275

Table IV

Seasonal changes of biomass in g/100 ha in three numerically dominant species of birds of prey and in the remaining species together in the pine and oak-hornbeam forests in the Niepołomice Forest in 1983

	Species	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Pine forests	*S. aluco*	648.2	620.0	591.9	563.7	845.5	978.0	1042.8	1000.5	958.3	914.3	873.7	831.4
	B. buteo	19.7	19.7	355.1	532.6	799.0	1052.5	1012.1	977.5	940.1	451.3	39.4	39.4
	A. gentilis	214.2	203.5	192.8	192.8	299.9	401.6	385.6	369.5	353.4	337.4	321.3	305.2
	Remaining species	127.7	123.3	79.6	78.8	131.8	169.8	191.7	192.3	171.4	160.0	135.8	129.6
	Total	1010	966	1220	1368	2076	2602	2632	2540	2423	1863	1370	1305
Oak-hornbeam forests	*S. aluco*	1698.8	1625.0	1551.1	1477.2	2215.9	2563.0	2732.9	2622.1	2511.3	2400.5	2289.7	2178.9
	B. buteo	—	—	530.3	795.4	1193.2	1571.0	1515.9	1461.4	1406.9	676.1	—	—
	A. gentilis	367.0	354.4	323.8	323.8	512.8	690.9	669.3	626.4	593.7	561.3	529.0	496.6
	Remaining species	—	—	34.1	160.2	190.0	257.9	294.9	287.2	126.6	95.4	68.2	63.0
	Total	2066	1970	2439	2756	4112	5083	5213	4997	4638	3733	2887	2738

For the presentation of the annual dynamics of biomass its value was computed for successive months. If a group of birds stayed in the Forest for a part of a month, which happened to some migrating species and nestlings that had hatched, for instance, in the middle of a month, the biomass was calculated for the actual period. And so, when, e.g. four Hobbies of a total biomass of 960 g appeared in the Forest in mid-May, the monthly value of the biomass of this species was 480 g.

In computing biomass, migrants turning up for a short stay were omitted, while the wintering species, e.g. small nomadic flocks of Long-eared Owls and single Common Buzzards and Rough-legged Buzzards were taken into account.

The biomass of the three most numerous species and all the other species together in the pine and oak-hornbeam forests is given (in g/100 ha) in Table III and Fig. 2 for 1978 and in Table IV and Fig. 3 for 1983. The dominance of the Tawny Owl, Buzzard and Goshawk is striking, for the other species do not even form 10% of the total biomass and in 1978 these three dominant species made up the total biomass in the oak-hornbeam forests. In the annual cycle its value clearly begins to rise in May, when newly hatched —young birds add to the size of the population, and it reaches a maximum in the second half of June and in July (Figs. 2 and 3).

The maximum value of biomass of all the birds of prey together was 3.8 kg/100 ha in 1978 and 5.2 kg/100 ha in 1983 in the oak-hornbeam forests and 1.3 kg/100 ha in 1978 and 2.6 kg/100 ha in 1983 in the pine forests.

As regards the Tawny Owl, the highest value of biomass was noted in July: 46.2 kg in 1978 and 48.1 kg in 1983 over an area of 1760 ha of the oak-hornbeam forests and 49.9 and 92.5 kg, respectively, in the pine forests (8870 ha). In the case of the Buzzard it was 17.2 kg in 1978 and 27.6 kg in 1983 in the

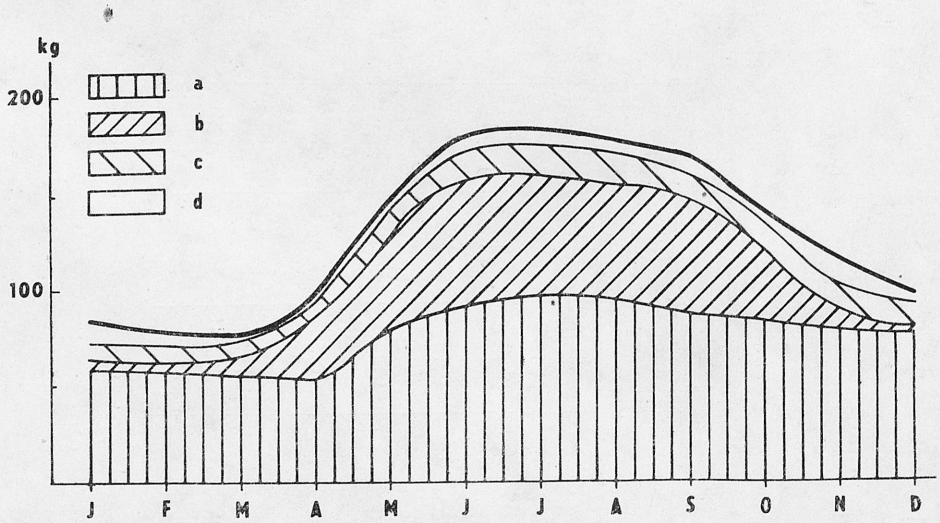

Fig. 2. Seasonal changes in biomass (in kg) in three numerically dominant species of birds of prey and in all the remaining ones together in the whole area of the Niepołomice Forest in 1978. 1 — Tawny Owl, b — Buzzard, c — Goshawk, d — all remaining species together

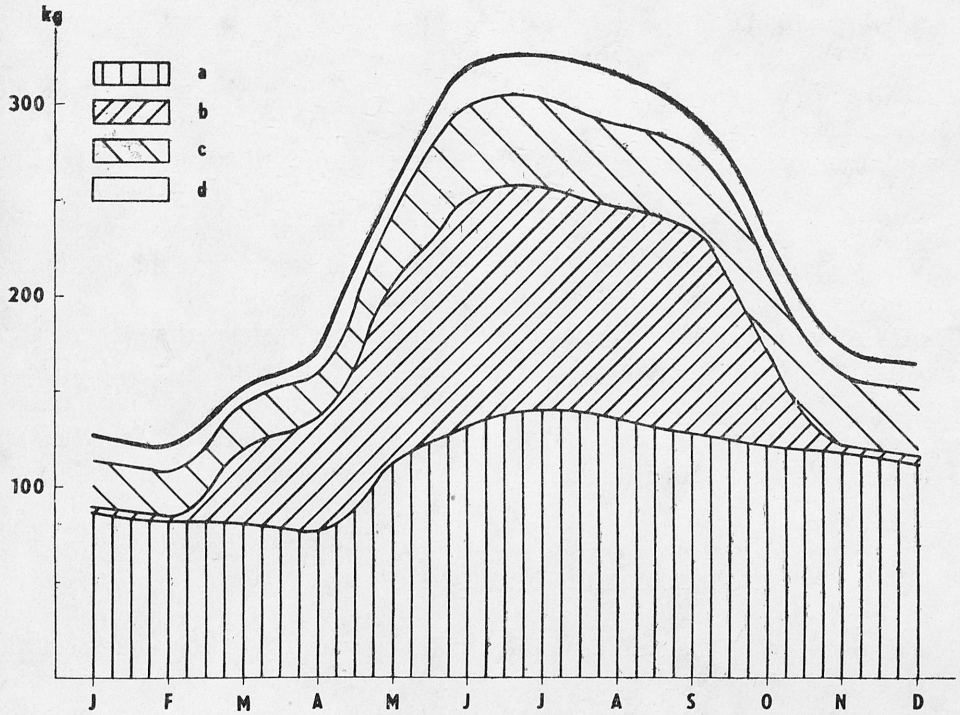

Fig. 3. Seasonal changes in biomass (in kg) in three numerically dominant species of birds of prey and in all the remaining ones together in the whole area of the Niepołomice Forest in 1983. Explanations of symbols as in Fig. 2

oak-hornbeam forests and, respectively, 48,3 and 93.3 kg in the coniferous complex. The biomass of the Goshawk reached 3.9 kg in 1978 and 12.1 kg in 1983 in the oak-hornbeam forests and 12.1 and 35.6 kg in the respective years in the pine forests.

A comparison of the values of biomass per unit of area in the pine and oak-hornbeam forests indicates clearly that the deciduous complex provides the more attractive habitat for the birds of prey. The quantity of biomass per 100 ha in it was three times as large as in the pine forests in 1978 and twice as large in 1983. In addition to the greater food resources of the oak-hornbeam forests, their smaller area and the shape, causing an increase in the length of the forest outline, were also favourable to birds of prey, for they secured them easier contact with the fields and meadows surrounding them than did the pine forests and thus created attractive habitats in so far as food is concerned. How important this is can be judged by the fact that most of the nests of Buzzards and Goshawks in the pine forests were grouped in their peripheries.

Regarding resident species, few in number and characterized by poor breeding success, the annual cycle of biomass dynamics indicates that at the beginning of the year and towards its end the values of biomass are similar. In the Sparrow Hawk in the whole area of the pine forests it was 960 g in January

1983 and about 1000 g in December in the same year. In the case of Tengmalm's Owl, whose breeding success was greater, the biomass in the same area was about 600 g (5 individuals) in January and about 1000 g (8 individuals) in December. This being so, the noticeable increase of their numbers in successive years may be due exclusively to the imigration of birds from other regions whereas the rise in mortality may cause the disappearance of small populations of these species. In more abundant species the value of biomass towards the end of the year is distinctly greater than at its beginning, which may influence the further increase in their numbers in following years.

The total value of the biomass of the birds of prey is perhaps somewhat underestimated, since the young birds of the previous year do not mate and so do not behave demonstratively or defend their territories. Under such circumstances it was very hard to detect them in the large area of the Niepołomice Forest and sure enough some of them were not included in calculations.

V. CONSUMPTION OF BIRDS OF PREY

The knowledge of the number of individuals, varying in the course of the year, and the body weight of raptors made the basis also for the evaluation of their consumption and, in consequence, their effect upon the population of prey. The equations for the daily energy budget (DEB) of non-passerine birds living at liberty (KENDEIGH et al. 1977) were employed in calculation. These equations permit us to compute the value of daily energy budget for two ambient temperatures:

$$DEB = 8.059\ W^{0.50} \quad \text{for } 0°C$$
$$\text{and } DEB = 1.079\ W^{0.67} \quad \text{for } 30°C$$

where W represents the body weight.

On the basis of the meteorological data from many years it was calculated that in the Niepołomice Forest the mean winter temperature (November—March) is 0°C, the mean temperature of April and October 8°C and that of the remaining five months (May—September) 16°C (HESS 1969). Because in the equations above the value of DEB is given for 0 and 30°C, the intermediate values were calculated on the assumption that it changes linearly.

Next the coefficient of food assimilation was applied in calculation of consumption, the daily energy budget being increased appropriately. The value of this coefficient adopted for all the birds of prey was that obtained experientially for the Tawny Owl, i.e. 85% (METCHEVA 1986). For instance, in the Tawny Owl weighing 500 g the daily energy budget (DEB) at the temperature of 0°C is 753 kJ/individual/day and the consumption (C) — 866 kJ/individual/day or 1.7 kJ/gram/day. In this way consumption in successive months of the year was calculated for the changing standing crops of particular species, allowances being made for changes of temperature.

Table V

Seasonal changes of consumption in kJ/day/100 ha in three numerically dominant species of birds of prey and in the remaining species together in the pine and oak-hornbeam forests in the Niepołomice Forest in 1978

	Species	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Pine forests	*S. aluco*	601	575	549	433	535	619	660	634	606	704	810	771
	B. buteo	51	51	119	300	381	502	484	466	448	338	77	51
	A. gentilis	91	86	81	67	89	120	117	109	103	116	132	123
	Remaining species	175	173	71	71	67	98	123	115	110	101	81	76
	Total	918	885	820	871	1072	1339	1384	1324	1267	1259	1100	1021
Oak-hornbeam forests	*S. aluco*	2789	2682	2560	2022	2498	2890	3080	2957	2830	3288	3779	3599
	B. buteo	129	129	215	541	687	902	870	838	806	609	129	—
	A. gentilis	142	142	135	113	149	199	194	185	180	203	237	223
	Remaining species	—	—	—	—	—	—	—	—	—	—	—	—
	Total	3060	2946	2910	2676	3334	3991	4135	3980	3816	4100	4145	3822

Table VI

Seasonal changes of consumption in kJ/day/100 ha in three numerically dominant species of birds of prey and in the remaining species together in the pine and oak-hornbeam forests in the Niepołomice Forest in 1983

	Species	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Pine forests	*S. aluco*	1113	1064	1016	802	991	1146	1222	1173	1123	1301	1500	1427
	B. buteo	25	25	461	580	736	969	932	900	866	491	51	51
	A. gentilis	269	255	242	202	263	353	339	325	310	353	403	383
	Remaining species	242	235	141	120	162	213	243	246	215	222	237	226
	Total	1652	1579	1860	1704	2152	2681	2736	2644	2514	2367	2191	2087
Oak-hornbeam forests	*S. aluco*	2916	2789	2663	2103	2598	3004	3204	3090	2944	3417	3930	3740
	B. buteo	—	—	688	866	1099	1447	1396	1346	1296	736	—	—
	A. gentilis	461	434	407	339	451	607	588	550	522	587	664	624
	Remaining species	—	—	75	226	224	314	356	344	198	183	151	140
	Total	3377	3223	3833	3534	4372	5372	5544	5330	4960	4923	4745	4504

The consumption in the annual cycle, in kJ/day/100 ha, for the whole populations of the three dominant species and for the population of all the remaining raptorial species together is presented for 1978 and 1983 in Tables V and VI. The results obtained for both the pine and the oak-hornbeam forests indicate a distinct dominance of the Tawny Owl. Only in summer months (June—August) the size of the consumption of the Buzzard comes near to that of the Tawny Owl, especially in the coniferous complex. Unlike the Tawny Owl, the Buzzard, as a migrant, hardly ever appears in the area of the Forest in winter months (November—February) and this strongly affects the size of its annual consumption, which is far smaller than the consumption of the former species. The consumption of migrating birds first keeps at the same level or it rises slowly from the moment when the first individuals appear in the Forest until they reach the number established by counting the breeding pairs. The further increase in consumption is connected with reproduction and reaches a peak when the young birds flegde. Later, the consumption decreases till the time of departure (Table V and VI, Figs. 4 and 5).

As regards the resident species, during the annual cycle consumption first decreases, having a minimum in April, which is due to higher ambient temperatures than in winter and, what follows, smaller expenditure on thermoregulation. In the nesting season it rises to attain a high value in July. After a gentle fall induced by a decrease in the number of birds owing to the deaths of some of them, another increase in consumption takes place and has a maximum towards the end of November. It is brought about by a fall in temperature

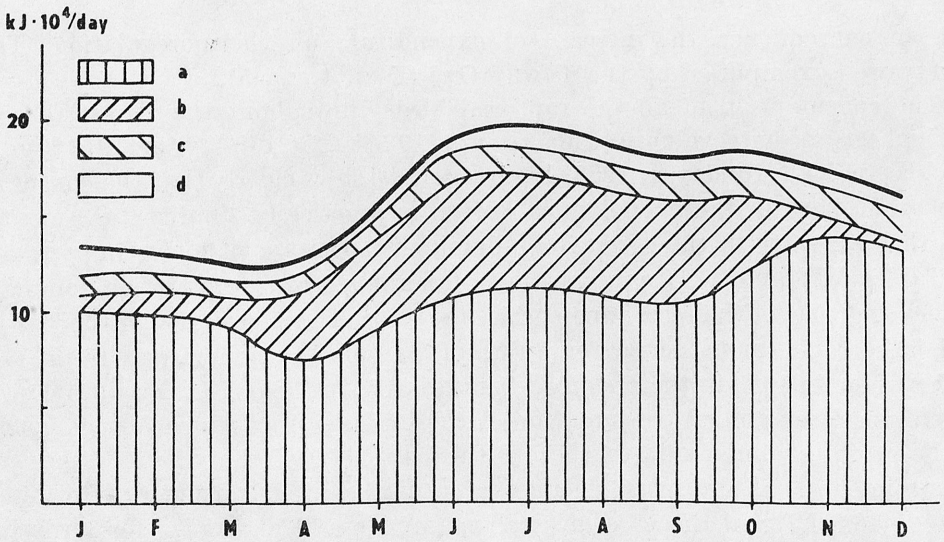

Fig. 4. Seasonal fluctuations in consumption (in kJ × 10^4/day) in three numerically dominant species of birds of prey and in all the remaining ones together in the whole area of the Niepołomice Forest in 1978. Explanations of symbols as in Fig. 2

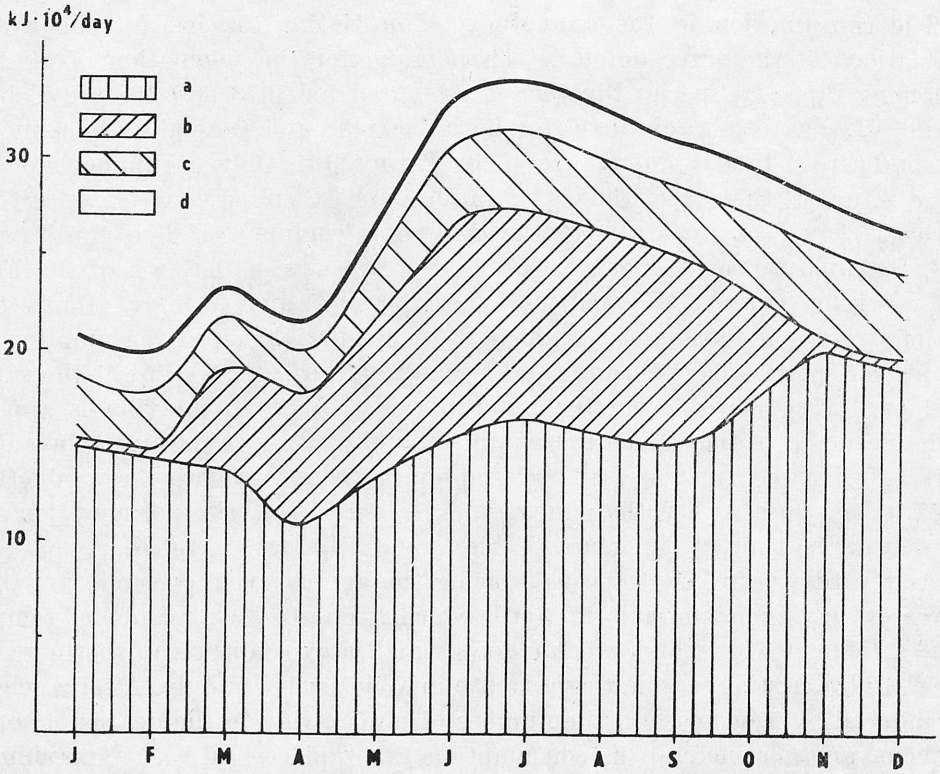

Fig. 5. Seasonal fluctuations in consumption (in kJ × 10^4/day) in three numerically dominant species of birds of prey and in all the remaining ones together in the whole area of the Niepołomice Forest in 1983. Explanations of symbols as in Fig. 2

and, in consequence, the increase of expenditure on thermoregulation. This is very well exemplified by the Tawny Owl (Figs. 4 and 5).

The consumption of all the raptorial birds throughout the Forest reaches the highest absolute value in July. It was 19.5 kJ × 10^4/day in 1978 and as much as 34 kJ × 10^4/day in 1983. Figures 4 and 5 show clearly that the consumption of Buzzard in the Niepołomice Forest is practically limited to 8 months and that its value in the case of non-dominant species is of minor importance.

Tables VII and VIII present the total annual consumption of dominant species and that of the remaining species together. The superiority of the Tawny Owl is here enormous, since the value of its consumption ranges from 53% of the whole in 1983 in the pine forests up to 81% in the oak-hornbeam in 1978. Contrarwise, the annual consumption of the birds of prey which do not belong to the group of dominants reaches at the best 10% of the whole in the pine forests in 1978. If the mean energy value of the prey consumed determined at about 6.3 kJ/g in the case of small mammals and at 8 kJ/g for birds has been taken into account and consumption converted to biomass, it appears that the raptor population of the Niepołomice Forest ate about 9 tons in 1978 and nearly 15 tons in 1983.

Table VII

Total annual consumption in kJ × 10^6 and in kJ/ha in three numerically dominant species of birds of prey and in the remaining species together in the pine and oak-hornbeam forests and in the whole area of the Niepołomice Forest in 1978

Species	Pine forests			Oak-hornbeam forests			Whole area		
	kJ × 10^6	kJ/ha	%	kJ × 10^6	kJ/ha	%	kJ × 10^6	kJ/ha	%
Strix aluco	20.281	2286	56.1	18.735	10645	81.4	39.016	3671	65.9
Buteo buteo	8.862	1000	24.5	3.145	1787	13.7	12.007	1130	20.3
Accipiter gentilis	3.341	377	9.2	1.128	640	4.9	4.469	418	7.5
Remaining species	3.698	414	10.2	—	—	—	3.698	347	6.3
Total	36.182	4077	100.0	23.008	13072	100.0	59.190	5566	100.0

Table VIII

Total annual consumption in kJ × 10^6 and in kJ/ha in three numerically dominant species of birds of prey and in the remaining species together in the pine and oak-hornbeam forests and in the whole area of the Niepołomice Forest in 1983

Species	Pine forests			Oak-hornbeam forests			Whole area		
	kJ × 10^6	kJ/ha	%	kJ × 10^6	kJ/ha	%	kJ × 10^6	kJ/ha	%
Strix aluco	37.472	4223	53.0	19.498	11076	67.7	56.970	5358	57.2
Buteo buteo	16.516	1862	23.4	4.777	2712	16.6	21.293	2000	21.4
Accipiter gentilis	9.991	1126	14.1	3.341	1896	11.6	13.332	1251	13.4
Remaining species	6.762	762	9.5	1.192	678	4.1	7.954	749	8.0
Total	70.741	7973	100.0	28.808	16362	100.0	99.549	9358	100.0

In order to verify the results presented, the size of consumption established on the basis of the equations for daily energy budget given by KENDEIGH et al. (1977) was compared with the data from other sources. And so METCHEVA (1986) studied the daily energy budget and consumption of the Tawny Owl experientially and obtained 498 kJ/individual/day for the temperature of 20°C. This result is nearly identical with the value calculated from the equations, which is 510 kJ/individual/day for the same temperature. CESKA (1980), too, gives a similar resutlt for the Tawny Owl at an unspecified temperature; it is 515 kJ/individual/day.

Some equations for computing the daily energy budget of birds of prey are published also in other studies (BENNET & HARVEY 1987, NAGY 1987). The results obtained with them resemble those presented in this paper.

On the other hand, information from other works suggests that the now-obtained value of consumption is somewhat overestimated. GOSZCZYŃSKI (1983) and LOVE (1980) write that the daily requirements of the Tawny Owl are about 55 g/individual/day, that is, on the average about 350 kJ/individual/day. This value is about 40% lower than the value assumed in the present work, nevertheless it is still of the same order of magnitude. SIMEONOV (1963, after CRAMP 1985) however gives a different value of the daily requirements of the Tawny Owl in the winter season, namely, 73 g/individual/day. Converted to energetic units it is about 460 kJ/individual/day and therefore also about 40% lower than the result obtained for winter temperatures in the present study.

In the case of the Buzzard CRAMP (1985) and GOSZCZYŃSKI (1983) estimate the daily requirements at 90 g/individual/day, although the first of these authors finds it 50% higher for young birds. If the first of these values has been assumed, the consumption computed in the present paper also appears to be overestimated by nearly 40%.

Regarding other species, only NEWTON'S (1973) findings for the Sparrow Hawk can be used as the basis for comparisons. He writes that one pair of these birds annually eat about 1200 prey individuals of the size of a Sparrow *Passer domesticus*, which makes nearly 50 g/individual/day or about 400 kJ/individual/day. Comparatively, the requirements of the Sparrow Hawk at the temperature of 16°C calculated in the present study was 340 kJ/individual/day and therefore these two values are nearly identical. The requirements computed for the temperature of 8°C were about 420 kJ/individual/day and so they were higher only by 5%.

It should however be emphasized that with the exception of the paper by METCHEVA (1986) all the cited pieces of information about the annual consumption of birds of prey and their food requirements are rather general and merely of the estimative nature.

Summing up, the bioenergetic calculations based on the empirical equations drawn from literature, presented in this paper, seem to be correct and the estimates of the consumption of the birds of prey in the Niepołomice Forest fit to be employed in further considerations.

VI. DIET OF THE TAWNY OWL

The knowledge of the diet of raptorial birds was the basis for appraising their contribution to the energy flow through the biocenosis of the woodlands of the Niepołomice Forest. The data concerning abundance as well as tables VII and VIII show that more than a half of the consumption of all the birds of prey falls to the Tawny Owl. As the territories of this species do not exceed 30—40 ha (SOUTHERN 1970), most of the individuals living in the Forest, espe-

cially in its coniferous complex, have no contact with the meadows and fields surrounding it and their consumption is limited to the wooded areas. In the other birds of prey prevailing in number — the Buzzard and Goshawk — part of consumption comes from open areas (GOSZCZYŃSKI & PIŁATOWSKI 1986, OPDAM et al. 1977, SLÁDEK 1961).

This being so, the study was focussed on the diet of the Tawny Owl. The data were obtained from an analysis of about 180 pellets collected at three sites in the middle part of the coniferous complex. The distance of these sites from the forest edge was at the least 2 km, as the crow flies, which practically excluded the contact of these individuals with the potential prey occurring in open areas. The sites where the pellets were gathered were situated in tree stands which were transitional between fresh pine forests and oak-hornbeam forests and so the results arrived at are in some measure representative of both these complexes.

A list of the vertebrate species which go to the making of the Tawny Owl's diet is given in Table IX. The mean body weight of adult prey vertebrates in this diet, needed to compute their biomass, was assumed on the basis of keys to birds (FERENS 1967; 1971) and mammals (PUCEK 1984). Only the data concerning the mean body weight of the bank vole *Clethrionomys glareolus* refer to individuals of various age caught just at the Niepołomice Forest (BOBEK 1973).

The most numerous of the vertebrate species falling a prey to the Tawny Owl was the bank vole, whose individuals formed 28% of the total number of prey and the biomass 23% of the total biomass. The remaining species were distinctly less numerous: field voles *Microtus agrestis* constituted nearly 6% of the prey number and above 7% of their biomass. Shrews also made up 7% of the total biomass but as much as 25% of the number of individuals. Summarily, the list of mammals includes 12 species and 330 individuals, that is, nearly 70% of the total number of prey vertebrates and above 53% of their biomass (Table IX).

The presence of a bat *Myotis bechsteini* very rare in the territory of Poland, in the diet of the Tawny Owl in the Niepołomice Forest is very interesting from the faunistic viewpoint. Remains of three muskrats *Ondatra zibethicus* were found in pellets for the first time in this country, whereas in other regions of the Palaearctic this species had already been found in the food of this raptor (CRAMP 1985).

Of birds, thrushes — the genus *Turdus* — were represented most numerously in the pellets, numbering 15 individuals, 8 of which were Song Thrushes *Turdus philomelos*. To be sure, they all together formed scarcely 3% of the prey individuals, but above 10% of their biomass. Another bird species, represented among the prey individuals by a similar number, was the Great Spotted Woodpecker *Dendrocopos major* — nearly 2% of the total number, but above 6% of the biomass of the prey. The remaining 25 avian species were met with in the pellets in very small numbers. The list of birds contains 27 species all

Table IX

Numbers of individuals and biomass of ver tebrate species found in pellets of the Tawny Owl *Strix aluco* in three localities studied in the Niepołomice Forest in 1978—1979

Species	No. of individuals	%	Biomass in g	%
1	2	3	4	5
Sorex araneus LINNAEUS, 1758	71	14.98	497.0	5.05
Sorex minutus LINNAEUS, 1766	55	11.60	165.0	1.68
Sorex sp.	3	0.63	15.0	0.15
Talpa europaea LINNAEUS, 1758	2	0.42	190.0	1.93
Myotis bechsteini (KUHL, 1818)	1	0.21	10.0	0.10
Myotis brandti (EVERSMANN, 1845)	1	0.21	6.0	0.06
Clethrionomys glareolus (SCHREIBER, 1786)	134	28.27	2 278.0	23.17
Arvicola terrestris (LINNAEUS, 1758)	4	0.84	320.0	3.25
Microtus agrestis (LINNAEUS, 1761)	27	5.70	729.0	7.42
Microtus arvalis (PALLAS, 1779)	3	0.63	60.0	0.61
Ondatra zibethicus juv. (LINNAEUS, 1766)	3	0.63	450.0	4.58
Apodemus flavicollis (MELCHIOR, 1834)	5	1.05	120.0	1.22
Apodemus sp.	10	2.11	230.0	2.34
Mus musculus LINNAEUS, 1758	1	0.21	15.0	0.15
Muridae indet.	10	2.11	180.0	1.83
Total of mammals — 12 species:	330	69.6	5 256.0	53.6
Cuculus canorus LINNAEUS, 1758	1	0.21	105.0	1.07
Dendrocopos major (LINNAEUS, 1758)	8	1.69	640.0	6.51
Hirundo rustica LINNAEUS, 1758	3	0.63	48.0	0.49
Anthus trivialis (LINNAEUS, 1758)	2	0.42	46.0	0.47
Motacilla alba LINNAEUS, 1758	1	0.21	21.0	0.21
Motacilla flava (LINNAEUS, 1758)	1	0.21	18.0	0.18
Motacilla sp.	1	0.21	19.0	0.19
Oriolus oriolus (LINNAEUS, 1758)	1	0.21	73.0	0.74
Sturnus vulgaris LINNAEUS, 1758	1	0.21	77.0	0.78
Sylvia atricapilla (LINNAEUS, 1758)	2	0.42	36.0	0.37
Sylvia borin (BODDAERT, 1783)	3	0.63	54.0	0.55
Sylvia communis LATHAM, 1787	2	0.42	28.0	0.28
Sylvia curruca (LINNAEUS, 1758)	1	0.21	12.0	0.12
Sylvia sp.	2	0.42	28.0	0.29
Phylloscopus collybita (VIEILLOT, 1817)	1	0.21	8.0	0.08
Phylloscopus sibilatrix (BECHSTEIN, 1793)	2	0.42	16.0	0.16
Phylloscopus sp.	11	2.32	88.0	0.89
Regulus sp.	1	0.21	6.0	0.06
Ficedula hypoleuca (PALLAS, 1764)	4	0.84	52.0	0.53
Ficedula sp.	4	0.84	52.0	0.53
Muscicapa striata (PALLAS, 1764)	9	1.90	153.0	1.56
Erithacus rubecula (LINNAEUS, 1758)	6	1.26	102.0	1.04
Phoenicurus phoenicurus (LINNAEUS, 1758)	1	0.21	16.0	0.16
Turdus philomelos C. L. BREHM, 1831	8	1.69	520.0	5.29
Turdus merula LINNAEUS, 1758	2	0.42	164.0	1.67
Turdus iliacus LINNAEUS, 1766	3	0.63	186.0	1.89
Turdus sp.	2	0.42	140.0	1.42
Parus major LINNAEUS, 1758	7	1.47	126.0	1.28

Table IX cont.

1	2	3	4	5
Parus caeruleus LINNAEUS, 1758	3	0.63	36.0	0.37
Parus palustris LINNAEUS, 1758	1	0.21	10.0	0.10
Parus sp.	2	0.42	26.0	0.26
Sitta europaea LINNAEUS, 1758	3	0.63	69.0	0.70
Carduelis carduelis (LINNAEUS, 1758)	2	0.42	32.0	0.32
Fringilla coelebs LINNAEUS, 1758	6	1.26	126.0	1.28
Aves — indet.	6	1.26	192.0	1.95
Total of birds — 27 species:	113	23.8	3 325.0	33.8
Rana temporaria (LINNAEUS, 1758)	31	6.50	1 240.0	12.61
Total of vertebrates — 40 species:	474	100.0	9 821.0	100.0

together but only 113 individuals, forming 24% of the total number of prey individuals and 34% of their biomass (Table IX).

The common frog *Rana temporaria* was the only but fairly abundant amphibian species, represented by 31 individuals, i.e. 6% of the number of prey individuals and 12% of their biomass.

Some pellets contained exclusively or nearly exclusively remains of insects. Many of these remains were successfully identified and the number of individuals was established. Table X gives a list of these insects. The commonest was *Calosoma inquisitor* with its 106 individuals, followed by *Geotrupes stercorarius*, 47 individuals, and *Carabus nemoralis*, 26.

In considering the occurrence of vertebrates in the Tawny Owl's diet, one may notice differences between the results now obtained and the data from other studies carried out in the territory of Poland. They are mainly due to the fact that these last studies deal with the diet of the Tawny Owl either from urban areas (BOCHEŃSKI jun. 1990, BOGUCKI 1967) or from fields and other open areas, only bordering upon forest complexes (CAIS 1963, JASKOWSKI 1956, KOCHAN 1978, KOWALSKI & LESIŃSKI 1988, KULCZYCKI 1964, SKURATOWICZ 1950). Even in his work on mammals of the Piska Forest KOWALSKI (1961) dealt with pellets collected outside the boundary of the forest. SERAFIŃSKI (1954), to be sure, studied the composition of the Tawny Owl's diet in forest areas and yet in the pellets gathered by him such species as the House Sparrow *Passer domesticus* and house mouse *Mus musculus*, occurred in large numbers and the common vole *M. arvalis* was dominant in respect of abundance and very distinctly at that. This indicates that, living at the edge of the forest, the Tawny Owl hunted in open and synanthropic areas.

It was calculated that in the food analysed in the above-quoted works treated jointly the species which dominated in respect of the number of individuals were the common vole with its 20% and the house mouse, 12%, among mammals and the House Sparrow, above 4%, among birds, and so the field and synanthropic species hardly encountered in the food of the Tawny Owl in the Niepołomice Forest. On the other hand, in the diet compiled for the

Table X

Remains of insects found in pellets of the Tawny Owl *Strix aluco* in the Niepołomice Forest in 1978—1979

Species	No. of individuals
Calosoma inquisitor (LINNAEUS, 1758)	106
Carabus convexus FABRICIUS, 1775	11
Carabus nemoralis O. F. MULLER, 1764	26
Carabus arcensis HERBST, 1784	2
Carabus violaceus LINNAEUS, 1758	1
Cychrus caraboides (LINNAEUS, 1758)	1
Pterostichus sp.	4
Agonum sp.	1
Dytiscidae indet.	2
Nicrophorus humator OLIVIER, 1790	1
Nicrophorus sp.	1
Staphylinus sp.	1
Anatis ocellata (LINNAEUS, 1758)	1
Tenebrionidae indet.	1
Geotrupes stercorarius (LINNAEUS, 1758)	47
Geotrupes spiniger (MARSHAM, 1802)	1
Melolontha melolontha (LINNAEUS, 1758)	10
Prionus coriarius (LINNAEUS, 1758)	2
Chrysomelidae indet.	1

Tawny Owl on the basis of those works the forest forms, the bank vole with its about 5% and soricids, nearly 10%, which in the Niepołomice Forest belong to dominant ones, are comparatively few in number.

The common feature of the results presented in those works and those obtained in the Niepołomice Forest is however the low proportion of rodents from the genus *Apodemus*, which in both cases reach about 3% of the number of prey items as well as the similar number of field voles — about 5%. The percentages of frogs *Rana* sp. in the Tawny Owl's consumption in these two cases are comparable; in the present study they account for above 6% of the number of prey individuals and in the works quoted for about 10%.

The low proportion of rodensts from the genus *Apodemus* in the food of the Tawny Owl in the Forest is puzzling, since these mice are its basic prey in other regions of the Palaearctic. It can be seen from SOUTHERN's (1954) classical work that the genus *Apodemus* accounts for 21—23% of the prey biomass. SOUTHERN & LOVE (1968, 1982) write that, if there are similar numbers of bank voles and *A. sylvaticus* in their feeding grounds, Tawny Owls give preference to the latter species and under some circumstances can consume 30—75% of the population of these mice. Yellow-necked field mice are the Tawny Owl's main food in some regions of Germany, where they may form 36—48% of the number of its prey items (WENLAND 1980). In WENLAND'S (1972) opinion, if there are few yellow-necked field mice in the feeding ground, the Tawny

Owl may replace them by eating more birds. A very small number of yellow-necked field mice but fairly numerous birds in the Tawny Owl's diet in the Niepołomice Forest might support this explanation. However, this does not prove true, for the yellow-necked field mouse is the second most numerous species of rodents in this area, being outnumbered only by the bank vole. In the pine forests it makes 14.3% of the whole population of rodents and in the oak-hornbeam forests even 26% (GÓRECKI 1984a).

The relatively large number of field voles in the list of the Tawny Owl's prey is noteworthy. These voles constitute above 7% of the biomass obtained. They must be particularly preferential food, for they occur in very small numbers in the Niepołomice Forest. In the composition of the rodent community of the pine forests they account for 1% and in the oak-hornbeam forests only 0.25% (GÓRECKI l.c.). SERAFIŃSKI (1954) however found that there are discrepancies between the results of field studies in the occurrence of the field vole and its presence in the Tawny Owl's pellets. During his two-year investigation of the fauna of small mammals, he failed to capture a single field vole, whereas he found as many as 15 individuals in the pellets.

It is also interesting that shrews and so animals of a very small body mass, 5—7 g, constituted a great proportion of prey (25% of all items); meanwhile GOSZCZYŃSKI (1977) shows that about 90% of the Tawny Owl's prey were animals weighing 11 to 50 g, while the lighter ones — just of the size of shrews — formed less than 1% of its composition.

In the case of birds, the quantity of resources did not decidedly influence the numbers of individuals falling a prey to the Tawny Owl. All of the species dominant in the pine complex of the Niepołomice Forest, e.g. the Chaffinch *Fringlla coelebs*, Tree Pipit *Anthus trivialis*, Starling *Sturnus vulgaris*, Great Tit *Parus major* and warblers *Phylloscopus* sp. (GŁOWACIŃSKI 1975a, 1981) to be sure, entered into the composition of the Tawny Owl's food but they were represented in it by very small numbers of individuals. Some preference can be noticed for the Great Spotted Woodpecker, which, being only a subdominant in the Forest, occurred in the Tawny Owl's hunting grounds all the year round. The numbers of individuals found for the Tawny Owl's particular prey species evidence its preference for thrushes. Singular species of the genus *Turdus* do not belong to the group of dominants of the Niepołomice Forest and besides, except for the Blackbird, occur in its area only for about 7 months. This notwithstanding, above 10% of all the biomass of the Tawny Owl's prey was composed of thrushes. This preference does not seem to have been connected with the size of prey, because apart from relatively big thrushes (about 70 g) very small species (about 8 g) were also taken, e.g. those of the genus *Phylloscopus* (14 individuals) and *Regulus* sp.

The contents of some pellets show that in summer months the Tawny Owl consumed also a certain number of insects. However, we failed to evaluate their biomass and contribution to the energetic value of the total consumption accurately. Out of the insects identified, *Geotrupes* sp., *Carabus nemoralis* and,

above all, *Melolontha melolontha* are mentioned also in other works (CRAMP 1985, UTTENDÖRFER 1939), in which there is however not a hint on the occurrence of *Calosoma inquisitor*, the predominant beetle in the Tawny Owl's food in the Forest. In the gradation period of *Tortrix viridana* large numbers of that beetle go up an infested tree to feed on the larvae of the parasite. It is probably then that they are eaten up by Tawny Owls. In the season of mass outbreak of some insect species, e.g. the cockchafer *M. melolontha*, they may become the main component of the diet for a short time (UTTENDÖRFER l.c.) but their proportion in the annual consumption is still inconsiderable.

A comparison of the compositions of Tawny Owls' food from three sites situated in the coniferous complex of the Niepołomice Forest shows no essential differences. In each of them the percentage share of all the three dominant prey species — bank voles, field voles and shrews — calculate together was almost the same, ranging between 60 and 70% of the number of all prey items. The number of field voles eaten at particular sites oscillated between 6 and 8% and slight differences were revealed at comparison between the numbers of shrews and voles found in the food. In a sample composed of the greatest number of prey individuals and therefore the most representive one, small insectivorous mammals and voles occurred in the same percentages. At the other two sites in considerably less abundant samples the 30% advantage of one or the other group of prey was observed.

The foregoing data show that the composition of the Tawny Owl's food examined in the Niepołomice Forest differs from that given for other regions of Poland. This evidences that Tawny Owls inhabiting the interiors of forests have a completely different diet than have the individuals which occur in open and synanthropic areas.

VII. INFLUENCE OF BIRDS OF PREY ON THE POPULATION OF PREY INHABITING WOODED AREAS

Knowing the size of consumption of the birds of prey in the Niepołomice Forest and the composition of the Tawny Owl's food, which constitutes its greatest proportion, we were in a position to evaluate their influence upon the prey population of the wooded areas. The knowledge of the composition and productivity of the community of small mammals and birds inhabiting the tree stands of the Forest was also utilized in this evaluation (GÓRECKI 1984a, GŁOWACIŃSKI et al. 1984).

The bank vole dominates very distinctly among the rodents of the Forest; its numbers reach 81.7% of the whole community of rodents in the pine forests and 65.7% in the oak-hornbeam forests. The genus *Apodemus* makes up 15.6% of the rodents in the pine forests and as much as 33.5% in the oak-hornbeam forests. As can be seen, the whole population of rodents in the Forest consists virtually only of these two forms.

In the pine forests the total net annual production of the rodent community averaged 3704 kJ/ha or 588 g/ha, of which 3028 kJ/ha or 480 g/ha fell to the bank vole, 578 kJ/ha or 91 g/ha to the genus *Apodemus* and only 33 kJ/ha or 5 g/ha to the field vole. The main role in the consumption of these rodents was played by the Tawny Owl, in which, as has been stated in the preceding section, small mammals formed 53.6% of the biomass consumed. In 1978 the Tawny Owl took 525 kJ/ha or 83 g/ha in the pine forests and so 17% of the annual production. The Buzzard was another bird of prey that limited the number of bank voles, which made up about 5% of the biomass of its food (GOSZCZYŃSKI & PIŁATOWSKI 1986, SLÁDEK 1961). In the year in question the Buzzard gained only 50 kJ/ha or 8 g/ha, that is, 1% of the population in the pine forests and as regards the remaining raptors, the consumption of this vole was of minor importance. In 1983, owing to a greater density of raptorial birds, their effect upon prey was also more distinct. The Tawny Owl consumed 971 kJ/ha or 154 g/ha per annum, that is, 32% of the population and the Buzzard took 93 kJ/ha or 14 g/ha and so 3%. Both these species together consumed therefore 35% of the net annual production of the bank vole in the pine forests.

In the case of the genus *Apodemus* the Tawny Owl caught 80 kJ/ha or 12 g/ha in 1978. This was nearly 14% of the annual production of the forest-inhabiting population. In 1983 the Tawny Owl's consumption was greater and it destroyed 147 kJ/ha or 23 g/ha, that is, 25% of the annual production of these rodents in the pine forests.

The third species predominating in the Tawny Owl's food was the field vole. Its proportion in the annual consumption in the year of the less abundant occurrence of these owls was 160 kJ/ha or 25 g/ha, whereas in the year of their greater abundance as much as 295 kJ/ha or 47 g/ha. Both these values considerably exceed the mean annual production of the field vole in the pine forests per 1 ha of the Forest area. It should however be emphasized that this species lives chiefly in wood plantations and young woods and so it occurs insularly and its density examined in older tree stands may be misleading when converted to the values for the area of the whole Forest. Besides, it may well be that the pellets examined came from the gradation period of this rodent in the Niepołomice Forest (these phenomena were not checked at present). At any rate, the high proportion of field voles in the Tawny Owl's diet clearly indicates that this bird of prey has a particular preference for them (Table XI).

In the area of the oak-hornbeam forests the total net annual production of the rodent community averaged 5940 kJ/ha or about 940 g/ha, of which about 620 g/ha fell to the bank vole, 315 g/ha to the genus *Apodemus* and only 2 g/ha to the field vole. As in the pine forests, the Tawny Owl played the main role in the reduction of the number of rodents also in the oak-hornbeam forests. It can be seen from Table XI that in 1978 it took 388 g/ha and so 62% of the annual production of the bank vole. In the same year the Buzzard's consumption reduced the size of the population of the bank vole by another

Table XI

Net annual production, in kJ/ha × year, of rodents dominating in the diet of the Tawny Owl *Strix aluco* in the Niepołomice Forest (on the basis of GÓRECKI's 1984a data), the size of its consumption, limiting this production, in kJ/ha × year, and the percentage of the rodent population killed

Year	Species	Pine forests			Oak-hornbeam forests		
		Rodent production	Consumption		Rodent production	Consumption	
		kJ/ha × year		% of population	kJ/ha × year		% of population
1978	*Clethrionomys glareolus*	3028	525	17	3920	2448	62
	Apodemus sp.	578	80	14	1989	370	18
	Microtus agrestis	33	160	?	12	745	?
1983	*Clethrionomys glareolus*	3028	971	32	3920	2547	65
	Apodemus sp.	578	147	25	1989	387	19
	Microtus agrestis	33	295	?	12	775	?

2%. All together 64% of the annual production of this rodent was destroyed. In 1983 the influence of the raptors was still greater. In the oak-hornbeam forests the Tawny Owl consumed 65% of bank vole production yearly and the Buzzard 3%, which add up to 68%, by which value the total annual production of this rodent was theoretically decreased.

As regards rodents from the genus *Apodemus*, 18% of their annual production was destroyed by the Tawny Owl in the oak-hornbeam forests in 1978 and 19% in 1983.

In the oak-hornbeam forests, as in the pine complex, the proportion of the field vole in the Tawny Owl's consumption conspicuously exceeded the estimates of resources (GÓRECKI 1984a). The example of the Niepołomice Forest seems to confirm GOSZCZYŃSKI's (1983) suggestion that the influence of birds of prey — especially that of the Tawny Owl — on the populations of wood rodents is greater than generally supposed. The strong influence of the Tawny Owl on the mortality of bank voles is emphasized in various papers. GOSZCZYŃSKI (1983) writes that it may destroy up to 45% of the production of this rodent in forest areas. SOUTHERN & LOVE (1982) found that Tawny Owls may take 20 to 35% of the standing crop of the bank vole. The results obtained in the oak-hornbeam complex of the Niepołomice Forest are higher by far than these values. Evaluations of the Tawny Owl's food composition were carried out on the basis of analyses of pellets collected in the central parts of the Forest. They had been produced by owls that had no or only very meagre contact with the fields surrounding the Forest. Other Tawny Owls, inhabiting the edges of the forest, could avail themselves of prey living in open areas. In consequence, the size of consumption computed in this study perhaps contains an overestimated proportion of forest rodents.

As for the rodents of the genus *Apodemus*, a comparison of the present findings with the data from literature shows opposite results. The percentage of their annual production taken by the Tawny Owl was relatively low and ranged between 14 and 25%, whereas according to SOUTHERN & LOVE (1982), under some circumstances it can consume 35—76% of the standing crop of *A. sylvaticus*.

In considering the proportion of the field vole in the Tawny Owl's consumption, we are struck by the fact that it noticeably exceeds the resources found in the Forest area. The data concerning the abundance of small rodents (GÓRECKI 1984a) were established allowing for the mosaic pattern of the plant cover (timber forests, young woods, plantations, clearings). This notwithstanding, the capture methods applied might to a certain degree bring about an underestimation of the numbers of field voles. In the forests of both types its density calculated for a unit of area is small and its occurrence is probably confined to the area of plantations and young woods, suggesting that the Tawny Owl's hunt is distinctly selective. This is also confirmed by other studies. SOUTHERN (1954) writes that the proportion of field voles in the biomass of the Tawny Owl's food is 8—12%. Also in the works on the Tawny Owl's food in the territory of Poland, quoted in the preceding section, the field vole averages above 4% of the number of prey individuals captured and in the case of the Piska Forest even 15% (KOWALSKI 1961). Since individuals of the field vole are relatively heavy (about 27 g), its proportion in the biomass of prey is still greater.

Summing up, it may be stated that in the case of wood rodents, birds of prey, chiefly Tawny Owls, exert strong pressure on two species: the bank vole and the field vole. It should be also kept in mind that in the area of oak-hornbeam forests the role played by the consumption of raptorial birds in the limitation of the abundance of the species mentioned above is overestimated, for the raptors living at the edge of this complex of the Forest may take a large proportion of their prey in open areas.

The size of the population of insectivorous mammals in the Niepołomice Forest had not hitherto been given detailed studies and for this reason it was difficult to evaluate the pressure exercised on it by birds of prey. However, adopting the data on the mean annual number of individuals in an area of 1 ha in other regions of Poland (PUCEK 1969) we found it possible to make an attempt at such evaluation. It turned out that both in the pine forests and in the oak-hornbeam forests, more abounding in shrews, the monthly consumption of the Tawny Owl reduces the mean annual number of insectivorous mammals by about 5% and so the consumption of the birds of prey seems to have no significant influence on their population.

It was considerably more difficult to estimate the effect of the birds of prey on the avifauna inhabiting the stands of the Niepołomice Forest. Various bird species constitute above 33% of the Tawny Owl's consumption evaluated in the present paper. According to GOSZCZYŃSKI & PIŁATOWSKI (1986)

and SLÁDEK (1961), about 60% of the Buzzard's consumption is composed of birds and so is as much as 95% of the Goshawk's. However, if in the case of the Tawny Owl, as evidenced by its diet in the Forest, the greater part of consumption comes from wooded areas, as regards the Buzzard and especially the Goshawk, more than 50% of the prey birds are captured in open areas. Preliminary estimates of the composition of the Goshawk's food in the Niepołomice Forest show that pigeons, especially the Domestic Pigeon, prevail in it. This agrees with the data presented in their work by GOSZCZYŃSKI and PIŁATOWSKI (l.c.), who state that above 50% of the biomass of food consists of pigeons. A similar percentage of the Goshawk's food formed by pigeons is given also by OPDAM et al. (1977). As regards the Buzzard, about half the birds consumed also come from unwooded areas (GOSZCZYŃSKI & PIŁATOWSKI, l.c.). In this connection it has been assumed that as far as the Tawny Owl is concerned, the whole consumption made up of birds comes from the forest area, whereas in the case of the Buzzard and Goshawk only a half of it.

The basis employed to evaluate the influence of these species upon the population of birds living in the stands of the Niepołomice Forest consisted of the data on the standing crop of birds calculated for a unit of area (GŁOWACIŃSKI et al. 1984). The evaluation was made for two periods: in winter, when the density of birds in the Forest is the lowest and towards the end of spring, when it is high. Also the size of the raptors' consumption composed of birds was estimated for January and June on the basis of the previously discussed energetic requirements and food composition.

In January the standing crop of the bird population was estimated at 1624 kJ/ha or 203 g/ha, whereas the monthly consumption of the three raptorial species numerically dominant in the Forest, was 8 g/ha or 4% of resources in the pine forests in 1978. And so in this period the birds of prey ate half a bird of the size of a Great Tit in an area of 1 ha in the pine forests. In 1983 also in the pine forests the monthly consumption of the birds of prey was 117 kJ/ha and so 7% of resources. They therefore ate a nearly whole bird of the size of a Great Tit from an area of 1 ha.

In the oak-hornbeam forests the birds of prey consumed about 320 kJ/ha, that is, 20% of individuals in January 1978. The bird population was therefore reduced by two birds of the size of a Great Tit each per 1 ha during that month. In 1983 the size of consumption was nearly the same — 22% of resources. And so it may be assumed that during 4 winter months the bird population decreases in the pine forests by 16—28% of the initial resources. With the calculated size of consumption, the bird population in the oak-hornbeam forests would undergo a complete annihilation within 5 months. The conclusion suggests itself that either a much larger part of consumption than assumed comes from areas surrounding these forests or the authors of the work quoted underestimated the size of the bird population.

In June the standing crop of the bird population in the pine forests was estimated at 2942 kJ/ha or 369 g/ha. In 1978 the three dominant species of

birds of prey consumed 4% of resources during that month, which means that the birds of prey ate less than one bird of the size of a Chaffinch from an area of 1 ha monthly. In 1983 their consumption reached 31 g/ha or 8% of the bird population. This is an equivalent of 1.5 birds of the size of Chaffinch. It may be therefore assumed that during four summer months the reduction of the bird population in the pine forests ranged from 16 to 24% of their standing crop.

In June but in the area of oak-hornbeam forests and so in the biotope characterized by a greater number of birds their standing crop reached 4398 kJ/ha or 552 g/ha. In 1978 the monthly consumption of the dominant birds of prey was 395 kJ/ha or 9% of the standing crop. This was equivalent to the capture of 2.3 birds of the size of a Chaffinch each in an area of 1 ha. In 1983 the monthly consumption attained a higher value, namely, about 11% of the standing crop. Under such circumstances the raptors took 3 birds of the size of a Chaffinch each in an area of 1 ha during the month of June.

The global consumption of the Tawny Owl, Buzzard and Goshawk in the area of oak-hornbeam forests decreases the standing crop of birds by 36—44% during four summer months. As in the winter season, the value of consumption seems to be overestimated, which is also suggested by a higher percentage of prey from open areas in the food of these raptors.

The lack of detailed information about the food composition of the Buzzard and Goshawk in the Niepołomice Forest and about the abundance of particular prey species does not permit an evaluation of the influence of these raptors upon them. It seems however that wood gallinaceans are the only group of birds upon which pressure, however indeterminate, may be exerted. This group is predominant in the Goshawk's food in the Scandinavian forests (Huhtala 1976, Widen 1985) and so it may well be that in the Niepołomice Forest the very small number of Hazel Grouse *Tetrastes bonasia* and the disappearance of the vestigial population of Black Grouse *Lyrurus tetrix* are the effect of the pressure exerted upon them by the Goshawk.

The foregoing considerations have boiled down to a discussion of the influence exercised on the prey population by those three numerically dominant species of birds of prey. The role of the remaining birds of prey seems to be of minor importance and only in the winter season their consumption may be conducive in increasing the losses of the community of small birds nomadizing in the territory of the Niepołomice Forest.

In addition to vertebrates, the birds of prey's diet comprised also various species of insects. However, the production of this group in the Forest is by two orders of magnitude greater than that of all warm-blooded consumers (Witkowski & Borusiewicz 1984) and so the consumption of the birds of prey practically has no influence upon their abundance.

The community of birds of prey of the Niepołomice Forest, which is a complex already devastated to a considerable extent, is however characterized by a wealth of species, which besides occur in fairly large numbers. An increase,

taking place lately, in the numbers of some species is probably not accidental and may have been brought about by a change in the age structure of the Forest, connected with a greater proportion of plantations and young woods, more abounding in avian prey, in the forest area. At the same time the content of heavy metals, emitted in the vicinity of the Forest, in the bodies of prey is not yet so high as to have a toxic effect on the birds of prey consuming them (SAWICKA-KAPUSTA & KOZŁOWSKI 1984). However, the role of the birds of prey in the biocenosis of the Niepołomice Forest is not only trophic. The problems of the action of consumers on the function of ecosystems, also with regard to their non-energetic influence on the matter flow, are striking and have been dealt with by many investigators (e.g. BATZLI 1978, WIENER 1975). Nevertheless, as can be seen from the works referred to, attempts to balance these processes have failed definitively so far. An attempt at such a balance for the Niepołomice Forest has been made by GÓRECKI (1984b), and his data are used for all further comparisons.

The present paper shows that the standing crop of the community of birds of prey ranges from nearly 10 to 52 g/ha over a span of a year; this constitutes about 10% of the standing crop of the community of small birds, which changes in a similar way. At the same time this is scarcely about 0.5% of the biomass of all the warm-blooded consumers living in the Niepołomice Forest. Their consumption is however distinctly greater than would be suggested by their proportion in the community of warm-blooded animals, forming nearly 3% of the total consumption from the trophic level of the first and the second order.

The birds of prey also join in the processes of acceleration of the matter flow and contribute significantly to the flow of biogens. In particular, the species which take food partly outside the boundaries of the forest and discharge it in the form of excrements in the area of the Forest add somewhat to the quantity of biogens in its biocenosis. To be sure, the estimated level of biogens in the production of the birds of prey is about 1% of the level for all the warm-blooded consumers, yet if their excretion is considered only for three elements — nitrogen, phosphorus and potassium — the role of these birds is rather significant. Regarding each of those elements, the birds of prey excrete above 5% of the global amount contained in the excrements of all the warm-blooded consumers. And so the role that they play in the action favouring the development of plants and decay of litter is great enough to be noticed.

As a result, in addition to the unambiguous influence of the birds of prey upon some species of forest rodents, they also contribute to a series of processes which add up to the function of the ecosystems in the Niepołomice Forest.

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STRESZCZENIE

Badania nad ptakami drapieżnymi prowadzono w latach 1977—1987 na terenie Puszczy Niepołomickiej, położonej w bliskim sąsiedztwie Krakowa (ryc. 1). Obszar ten (około 11 000 ha) leżący w strefie działania skażeń emitowanych przez Kombinat Metalurgiczny i dewastowany nadmiernymi wyrębami okazał się jednak stosunkowo dobrym siedliskiem dla pospolitszych gatunków ptaków drapieżnych. Stwierdzono występowanie na terenie Puszczy 16 gatunków ptaków z rzędów *Falconiformes* i *Strigiformes*, z których 12 należało do awifauny lęgowej. Porównanie uzyskanych wyników z wcześniejszymi danymi wykazało, że zwiększyła się liczba gatunków lęgowych, mniejsza natomiast niż uprzednio jest liczba gatunków przelotnych (tab. I).

W roku 1978 i 1983 przeprowadzono na terenie borów i grądów Puszczy inwentaryzację wszystkich par lęgowych całego zespołu ptaków drapieżnych (tab. II). Gatunkami wyraźnie dominującymi liczebnie okazały się: *Strix aluco*, a w dalszej kolejności — *Buteo buteo* i *Accipiter gentilis*. Ich liczebność w przeliczeniu na powierzchnię 100 km^2 należy do najwyższych spośród stwierdzonych na terenie kraju. Z faunistycznego punktu widzenia najbardziej interesujące było stwierdzenie gnieżdżenia się *Strix uralensis* i *Aegolius funereus*, należących w Polsce do gatunków bardzo nielicznych.

Ocena liczebności ptaków drapieżnych w okresie lęgowym oraz dane o ich śmiertelności były podstawą do oszacowania dynamiki liczebności poszczególnych gatunków. W ten sposób obliczano dla kolejnych miesięcy roku stan biomasy w g/100 ha u gatunków dominujących i całego zespołu ptaków drapieżnych (tab. III i IV). Wielkość biomasy w cyklu rocznym zaczyna wzrastać

wyraźnie w maju, gdy pojawiają się osobniki młode i osiąga maksimum w drugiej połowie czerwca i w lipcu (ryc. 2 i 3).

Znajomość zmieniającej się podczas roku liczby osobników i ciężaru ich ciała pozwoliły również na oszacowanie ich konsumpcji. W obliczeniach oparto się na równaniach określających wielkość dobowego budżetu energetycznego ptaków z grupy *Non-Passeriformes*, przy uwzględnieniu wartości współczynnika asymilacji. Wielkość konsumpcji (w kJ/doba/100 ha) w cyklu rocznym przedstawiono w tabeli V i VI. Największą wartość konsumpcji stwierdzono u puszczyka i zbliżoną u myszołowa — w miesiącach letnich. Dynamika konsumpcji w cyklu rocznym związana jest nie tylko ze zmianą liczby osobników, ale także ze zmianami temperatury. Obniżenie się jej zwiększa wydatki na termoregulację i powoduje zwiększenie konsumpcji (ryc. 4 i 5). Całkowita roczna konsumpcja gatunków dominujących liczebnie i pozostałych przedstawiona jest w tabeli VII i VIII. Dominacja puszczyka jest ogromna, gdyż w zależności od rodzaju drzewostanu i roku badań, wielkość jego konsumpcji wahała się od 53% do 81% konsumpcji całego zespołu ptaków drapieżnych.

Główną rolę w konsumpcji ptaków drapieżnych odgrywał *S. aluco*, zbadano więc skład jego pokarmu. Materiał do tych badań zebrano z trzech stanowisk położonych wewnątrz Puszczy, co praktycznie wykluczało kontakt z terenami otwartymi osobników składających wypluwki. Spośród kręgowców blisko 70% liczby ofiar i 53% ich biomasy przypadało na drobne ssaki, a 24% liczby ofiar i 34% ich biomasy na ptaki (tab. IX). Ofiarą najliczniej odławianą była nornica ruda *Clethrionomys glareolus* — 28% liczby osobników i 23% całej zjadanej biomasy. Wśród owadów znalezionych w wypluwkach najliczniej spotykany był chrząszcz — *Calosoma inquisitor* (tab. X).

Poznanie wielkości konsumpcji ptaków drapieżnych oraz składu pokarmu *S. aluco*, mającego w niej największy udział, pozwoliło na ocenę ich wpływu na populację ofiar zasiedlających tereny leśne. Skład i produktywność zespołu drobnych ssaków i ptaków, a więc potencjalnych ofiar, były badane na terenie Puszczy Niepołomickiej w okresie bezpośrednio poprzedzającym niniejsze badania. Konsumpcja drapieżników zmniejsza od 17% do ponad 60% zasoby populacji *Cl. glareolus*, a jeszcze większa presja wywierana jest na *Microtus agrestis*, którego zasoby stwierdzone na terenie Puszczy są wielokrotnie niższe od jego wyliczonego udziału w konsumpcji *S. aluco* (tab. XI). Nie stwierdzono natomiast istotnego wpływu drapieżników na inne drobne ssaki i ptaki.

Oprócz jednoznacznego wpływu na populację niektórych gryzoni leśnych ptaki drapieżne włączają się również w cały szereg procesów składających się na funkcjonowanie ekosystemów Puszczy Niepołomickiej.

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