

Małgorzata PIOTROWSKA and Tomasz WESOŁOWSKI

The breeding ecology and behaviour of the chiffchaff *Phylloscopus collybita* in primaeval and managed stands of Białowieża Forest (Poland)

PIOTROWSKA M., WESOŁOWSKI T. 1989. The breeding ecology and behaviour of the chiffchaff *Phylloscopus collybita* in primaeval and managed stands of Białowieża Forest (Poland). Acta orn. 25: 25–76.

The study was carried out with varying intensity during 1975–83. Intensive observations on partially colour-ringed birds were carried out in two primaeval forest plots (ash-alder = AA and oak-hornbeam = OH habitat) in 1976–79 and within two managed forest plots (OH and coniferous = CON habitat) in 1978–82. Densities were lowest in primaeval OH and CON, intermediate in managed OH and CON and highest in AA. Densities fluctuated within fairly narrow limits. First males arrived on April 3–9, first females about three weeks later. Only males were site-tenacious, one third of them came back in the following seasons. Average territory size in AA was over four times lower than in primaeval OH. Males were usually monogamous, but several cases of polygyny were recorded, all but one in AA. Nests were built on the ground or low above it. Egg-laying period was May 2 – July 6–7, commencement of laying varied among seasons. About 70% of females participated in second broods. First clutches contained most frequently six eggs, clutch size decreased over a season. Nestling losses were caused mostly by predation and desertion. Nests with young were two, three times more frequently predated than nests with eggs. Nestling losses were highest in primaeval OH and lowest in AA. Production of young was highest in AA, intermediate in managed OH and CON and lowest in primaeval OH.

A comparison of the ecology and behaviour of birds breeding in primaeval and equivalent managed stands reveals that they do not differ except for much higher densities in the managed stands and, in OH, better nesting success in the managed stands.

M. Piotrowska, Research Institute on Environmental Development,
20-007 Lublin, Pstrowskiego 12, Poland.

T. Wesołowski, Department of Avian Ecology, Wrocław University,
50-335 Wrocław, Sienkiewicza 21, Poland.

Экология размножения и этология *Phylloscopus collybita* в первичных и вторичных древостоях Беловежской пуцы (Польша)

Исследования проводились с различной интенсивностью с 1975 до 1983 годов. Интенсивные наблюдения над птицами, которые частично были окольцованы цветными кольцами, велись в 1976–79 годах на двух площадках в первичном лесу (пойменный лес и груд) а в 1978–82 годах на двух площадках леса, в котором велось лесное хозяйство (груд и бор). Наиболее низкая плотность наблюдалась в первичном боре и груде, средняя — в освоенном боре и груде, а наиболее высокая — в пойменном лесу. Плотности изменялись в относительно небольших

пределах. Первые самцы прилетали 3–9 апреля, первые самки примерно через три недели. Только самцы возвращались в места предыдущего гнездования, около одной третьей из них возвращалась в очередные сезоны. Средняя величина гнездовой территории в пойменном лесу была примерно в четыре раза меньше чем в первичном груде. Самцы были обычно моногамны, но констатировано также несколько случаев полигинии, все кроме одного в пойменном лесу. Гнезда находились на земле либо низко над землей. Кладки происходили в период со 2 мая до 6 или 7 июля, сроки начала гнездования были различны по отдельным годам. Около 70% самок приступало к повторным кладкам. Первые кладки содержали обычно 6 яиц, величина кладки уменьшалась по мере течения сезона. Главные факторы, вызывающие потери в гнездах — это хищничество и оставление гнезд. Гнезда с выводками в два-три раза чаще уничтожались хищниками чем гнезда с яйцами. Самые высокие потери в гнездах наблюдались в первичном груде, а самые низкие в пойменном лесу. Самую высокую продуктивность молодых констатировали в пойменном лесу, среднюю — в освоенном груде в боре, а самую низкую в первичном груде.

В экологии и этологии птиц, гнездящихся в первичных древостоях, не обнаружено различий по сравнению с аналогичного типа освоенными древостоями, за исключением значительно более высоких плотностей в освоенных древостоях и более высокой эффективности гнездования в освоенном груде.

Introduction	26
Study area	27
Material and methods	30
Results	35
Densities, fluctuations in numbers	35
Behaviour	36
Spring arrival, settlement pattern	36
Site tenacity	38
Territorial and other behaviour of males	39
Male pairing success, sex ratios	45
Behaviour of females	46
Breeding ecology	47
Nests, nest sites	47
Timing of breeding, length of breeding season	53
Clutch size	57
Breeding losses	59
Partial breeding losses	59
Total nesting failures	60
Production of young	65
Discussion	66
Habitat distribution of the chiffchaff	66
Optimal habitat of the chiffchaff	68
Managed versus primaeval habitats	69
Life-history tactics	70
Acknowledgements	71
References	72
Streszczenie	73

INTRODUCTION

Most of lowland forests in the temperate zone have undergone deep anthropogenic transformations. Thus, it is almost impossible to collect data on temperate woodland birds, which could serve for valid, unconfounded by anth-

ropogenic influences, comparisons with materials collected in other climatic zones. This conviction led to the start of a long-term programme of bird studies in the Białowieża National Park, in which the last fragments of a European primaeval lowland forest are preserved (TOMIAŁOJĆ *et al.* 1984). Some population data on *Troglodytes troglodytes*, *Phylloscopus sibilatrix* and woodpeckers have already been published (WESOŁOWSKI 1981, 1983, 1985. WESOŁOWSKI and TOMIAŁOJĆ 1986).

The chiffchaff, a small warbler, was chosen as another species for an intensive study, as it is relatively common in a variety of habitats, and it breeds low above the ground. The latter feature greatly facilitated the data collection. Observations in the Park were carried out by Tomasz WESOŁOWSKI. Their aim, apart from a mere gathering of basic information on the breeding habits of the chiffchaff in the primaeval forest, was also an attempt to answer the following questions:

- what factors affected the habitat distribution of this species
- which habitat was optimal for it
- did the chiffchaff possess any adaptations for breeding in the optimal habitat.

Intensive management in the Białowieża Forest started as late as the twentieth century and mature stands are still mostly of natural origin, even in its managed parts. This offered another unique chance, a possibility to be found usually only somewhere in a tropical rain forest or in remote parts of a Siberian taiga – to study the impact of first-step anthropogenic transformations on bird numbers, ecology and behaviour. Thus, when an opportunity arised, it was decided to carry out a study of the chiffchaff in the managed parts of the Forest as well. This was done by Małgorzata PIOTROWSKA.

Though field data had been collected separately, it was later decided that they should be analysed jointly. This resulted in the preparation of this comparative paper.

STUDY AREA

The Białowieża Forest complex (total area 1250 km²) is situated on the Polish-Soviet border. Its western part belongs to Poland (580 km², Fig. 1). Biogeographically it falls within the mixed forest zone, containing at least some admixture of the spruce *Picea excelsa* in almost all the types of tree stands.

The Forest represents a relic remnant of the vast lowland forests which once covered great parts of temperate Europe. Its present unique features result from its considerable size, great compactness and exceptionally good state of preservation (FALIŃSKI 1977, TOMIAŁOJĆ *et al.* 1984). Though traces of human presence from as early as the Neolithic period are known, intensive timber-cutting did not start there before the beginning of this century. The majority of tree-stands in the Polish part are now under management, but a 47.5 km² block of best preserved primaeval stands has been strictly protected within the Białowieża National Park. Within the Park only a very limited human activity is allowed. The activity consists in clearing fallen trees from few forest roads, visits of guided tourist groups and scientific observations.

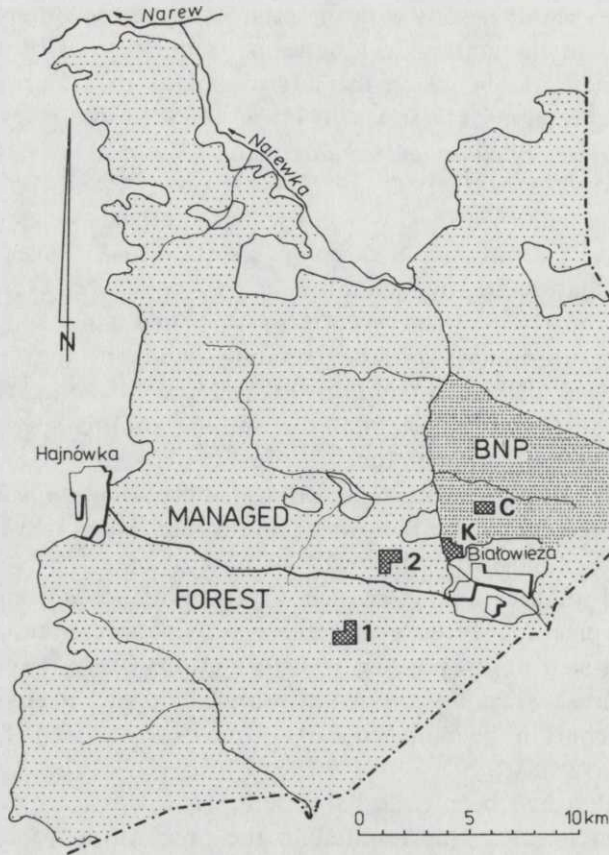


Fig. 1. A map of the Polish part of the Białowieża Forest showing localization of the intensive study plots. Sparcely dotted – managed stands, densely dotted – primaeval stands protected within Białowieża National Park (=BNP), squared – the plots: K – ash-alder primaeval, C – oak-hornbeam primaeval, 1 – coniferous managed, 2 – oak-hornbeam managed

Ryc. 1. Mapa polskiej części Puszczy Białowieżskiej z zaznaczoną lokalizacją powierzchni próbnych. Obszary rzadko kropkowane – las zagospodarowany, gęsto kropkowane – las pierwotny chroniony w Białowieżskim Parku Narodowym, kratkowane – powierzchnie próbne: K – pierwotny łęg, C – pierwotny grąd, 1 – zagospodarowany bór, 2 – zagospodarowany grąd

The stands preserved in the Park are distinguished from those in other temperate forests by the following features: they are multistoreyed, mixed-species, uneven-aged, composed of trees reaching unusual heights (the tallest spruces reach 55 m, several other species 42–45 m) and contain large amount of dead timber and uprooted trees. Detailed descriptions of the habitats and plots studied in the Park, as well as their photos, are given in TOMIAŁOJĆ *et al.* (1984), thus only a brief review of the most important feature of the main habitats studied (*i.e.* ash-alder, oak-hornbeam and coniferous) is presented in Table 1.

The mature stands in the managed Forest part are still similar to the primaeval ones. They are mostly of natural origin (self-sown), and have remained multi-species and uneven-aged. However, dead and fallen trees are removed from the stands. Hence, the main difference between the primaeval and managed stands stems

Table 1. Characteristic features of various types of *Phylloscopus collybita* primaeval habitats in the Białowieża National Park
 Tabela 1. Cechy charakterystyczne różnych typów siedlisk pierwotnych zasiedlanych przez pierwiosnka w Białowieżskim Parku Narodowym

Habitat type Typ siedliska	Ash-alder Łęg <i>Circaeo-Alnetum</i>	Oak-hornbeam Grąd <i>Tilio-Carpinetum</i>	Coniferous Bór <i>Peucedano-Pinetum</i>
Tree layer	Composed of <i>Alnus glutinosa</i> , <i>Fraxinus excelsior</i> and <i>Picea excelsa</i> ; open canopy, tree crowns usually not in touch	Composed of <i>Carpinus betulus</i> , <i>Tilia cordata</i> , <i>Quercus robur</i> , <i>Acer platanooides</i> and <i>Picea excelsa</i> ; close canopy, contiguous tree crowns form almost uninterrupted layer	Composed of <i>Picea excelsa</i> , <i>Pinus silvestris</i> and small admixture of deciduous trees; moderately close canopy
Warstwa koron	Złożona z olszy, jesionu i świerka, sklepienie luźne, korony drzew zwykle nie stykają się ze sobą	Złożona z grabu, dębu szypułkowego, klonu i świerka; stykające się korony krzew tworzą prawie nieprzerwaną warstwę	Złożona ze świerka, sosny oraz niewielkiej domieszki drzew liściastych, korony o umiarkowanym zwarciu
Shrub layer	Well developed, mainly <i>Ribes</i> spp. and <i>Padus avium</i>	Under-developed	Almost absent
Warstwa krzewów	Dobrze wykształcona, głównie porzeczki i czereemcha	Niedorozwinięta	Prawie brak
Ground layer	Well developed often more than 1 m high	Well developed, usually less than 0.3 m high	Very sparse, areas covered by dead needles or mosses predominate
Warstwa runa	Dobrze rozwinięta, często ponad 1 m wysokości	Dobrze rozwinięta, zwykle poniżej 0,3 m wysokości	Bardzo rzadka, przeważają obszary pokryte ześchłym igliwem lub mchami
Soil moisture Wilgotność podłoża	Very wet, swampy Bardzo mokre, bagienne	Moderately moist to dry Umiarkowanie wilgotne do suchego	Dry Suche

not so much from the differences in the structure of the mature stands, but from a much greater proportion of clearings and young tree plantations in the managed stands.

Coniferous and oak-hornbeam stands are managed according to two different schedules (WŁOCZEWSKI and ILMURZYŃSKI 1957). The coniferous habitat is cleared by cutting all trees from N–S oriented belts, 500 m long and 50–80 m wide. The clearings are replanted mostly with Scotch pine *Pinus silvestris* but young tree plantations also contain a substantial number of self-sown spruces and birches *Betula* spp. After 3–5 years such cutting is performed along a belt neighbouring the one cut formerly. This leads to a characteristic steplike appearance of the stands (cf. Fig. 7 and Photo 1).



Photo 1. Managed coniferous plot

Photo L. WILCZEK

Typical step-like pattern of distribution of different-aged stands (clear-cut area, young tree plantation, pole-aged stand and mature forest), resulting from management, is visible. The location of *Phylloscopus collybita* nest marked with the circle

Fot. 1. Typowy fragment powierzchni w borze zagospodarowanym

Widoczna schodkowa struktura drzewostanów (zrąb, młodniki, drągowizna i dojrzały drzewostan) będąca wynikiem gospodarki lesnej. Położenie gniazda pierwiosnka zaznaczono kółkiem

Clear-cutting is less frequently applied in the oak-hornbeam stands. The standard procedure there consists in selective cutting or removing all trees in small (0.08–0.2 ha), roughly circular plots. In gaps so created young oaks, *Quercus robur* as in the coniferous stands, tree-cutting is repeated every several years. This creates are planted and other free species are allowed to regenerate by self-seeding. Similarly a fine-grained mosaic of differently-aged patches, which imitates the process of gap regeneration in the primaeval stands.

MATERIAL AND METHODS

In the Park data were collected in 1975–83 with varying intensity. Censuses of breeding birds were carried out during the whole of this period (TOMIAŁOJC *et al.* 1984 and unpubl.). Censuses were made by means of the improved mapping method (TOMIAŁOJC 1980). The total area censused ranged from 187.5 to 358.1 ha in

different years. The study plots were situated in three types of climax stands differing structurally (Table 1). The period of field work was usually from 10 April till the end of June, so it covered mostly the period of the chiffchaff first brood. Only in 1978 were observations continued until the end of July.

Nests were located mostly during standard census work. All nests were checked to obtain data on clutch and brood size and to follow their fate. The number of visits was kept to a minimum in an attempt to minimize losses caused by the observer; whenever possible, the nests were checked from a distance. A total of 169 nests were found (Table 2).

Table 2. Number of birds ringed and number of *Phylloscopus collybita* nests found in primaeval (BNP) and managed stands in the Białowieża Forest

Tabela 2. Liczba zaobrączkowanych ptaków i znalezionych gniazd pierwiosnka w części pierwotnej (BPN) i zagospodarowanej Puszczy Białowiejskiej

Type of stand Typ drzewostanu	Number of birds ringed Liczba zaobrączkowanych ptaków				Number of nests found Liczba znalezionych gniazd
	Males Samce	Females Samice	Nestlings Pisklęta	Total Ogółem	
Primaeval Pierwotny	22	11	316	349	169
Managed Zagospodarowany	34	12	362	408	131
Total – Razem	56	23	678	757	300

An intensive programme of observations was executed in 1976–79 within a more limited area. It started in 1976 in a 12 ha part of plot K and in 23 ha in 1977–79 (Fig. 2). Most of this plot was covered by the ash-alder stand. Another plot – C – covering 48 ha of oak-hornbeam habitat was studied in 1977–79. Within these plots the birds were mist-netted and colour-ringed. In 1976–77 birds were caught in 60–70 mist-nets, regularly distributed over the plots, in other years more selective methods were applied (*cf* WESOŁOWSKI 1982 for details). The number of birds ringed is shown in Table 2.

Territorial males were provoked with play-backs of conspecific songs and their consecutive song-locations were plotted on large scale plans of the plots. This procedure was repeated on many visits to the plots, observations were put together on cumulative plans, and borders of territories of individual males were delineated. As neighbouring males, even when strongly stimulated, were singing at some distance from one another, usually not less than 20 m, the lines denoting borders of the territories were drawn 10 m (half of the minimum distance) outside the outermost places of singing of individual males.

In order to obtain data on pairing and breeding success of territory owners, the presence of females was checked in all territories, and every effort was made to locate all nests within the plots.

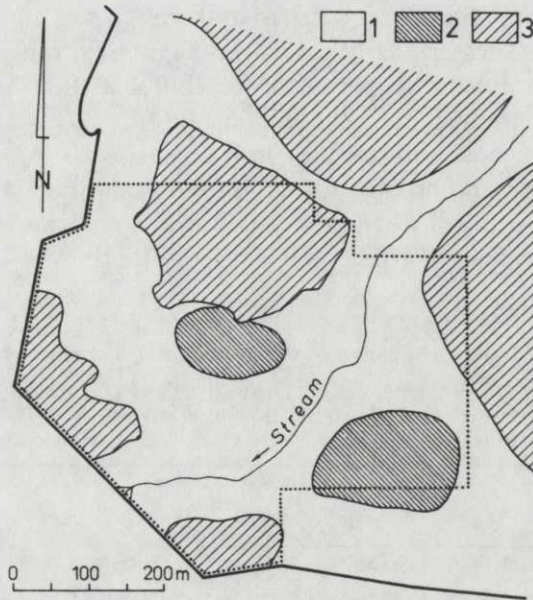


Fig. 2. Habitat structure of the plot K

1 – swampy ash-alder, 2 – about 80 years old alder stand developing after clear-cutting, 3 – dry oak-hornbeam stands. Area studied in 1977–79 marked with dotted line

Ryc. 2. Struktura siedliska na powierzchni K

1 – podmokłe drzewostany łęgowe, 2 – około 80-letni drzewostan olszowy na dawnym zrzebie, 3 – suche drzewostany gąrdowe. Powierzchnię, na której prowadzono obserwacje w latach 1977–79 zaznaczono linią kropkowaną

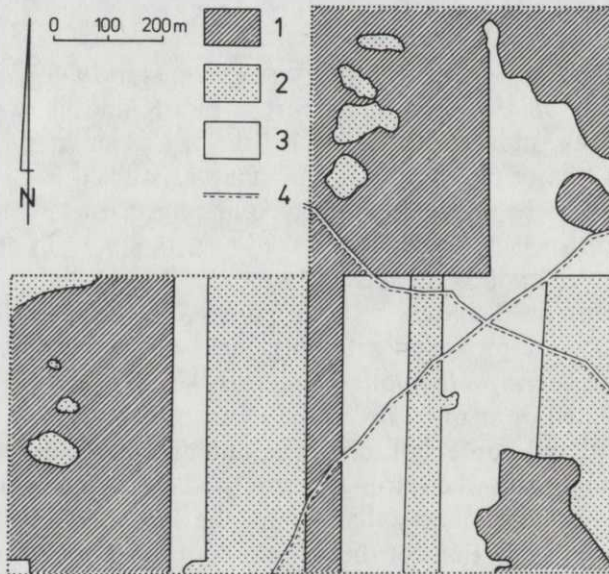


Fig. 3. Habitat structure of the managed coniferous plot

1 – tree stand over 50 years old, 2 – tree plantations 11–50 years old, 3 – tree plantations 1–10 years old, 4 – roads

Ryc. 3. Struktura siedliska powierzchni borowej w zagospodarowanej części Puszczy

1 – drzewostan ponad 50-letni, 2 – drzewostan w wieku 11–50 lat, 3 – uprawy i młodniki 1–10-letnie, 4 – drogi

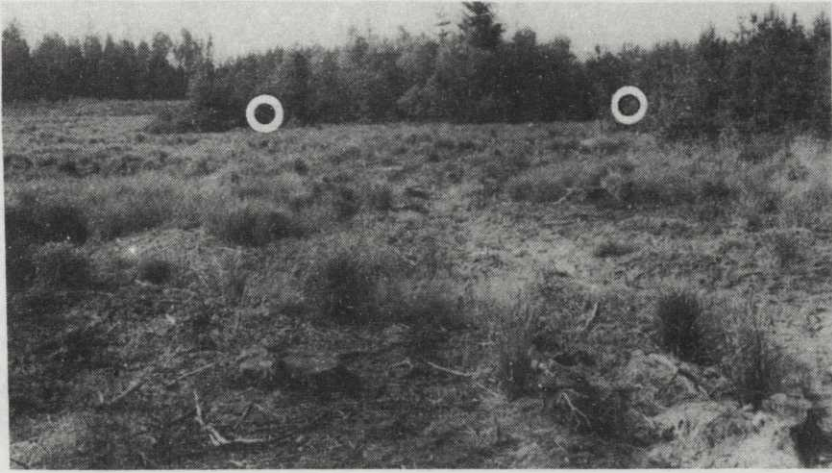


Photo L. WILCZEK

Photo 2. Managed coniferous plot

A patch of young coniferous trees containing a single tall spruce surrounded by clear-felled areas – the place which became accepted by a site-tenacious male. Position of *Phylloscopus collybita* nests marked with the circles

Fot. 2. Powierzchnia próbna w borze zagospodarowanym

Kępa młodych drzewek z pojedynczym wyższym świerkiem wśród zrębów – miejsce, które zostało zaakceptowane przez powracającego samca. Położenie gniazda pierwiosnka zaznaczono kółkami

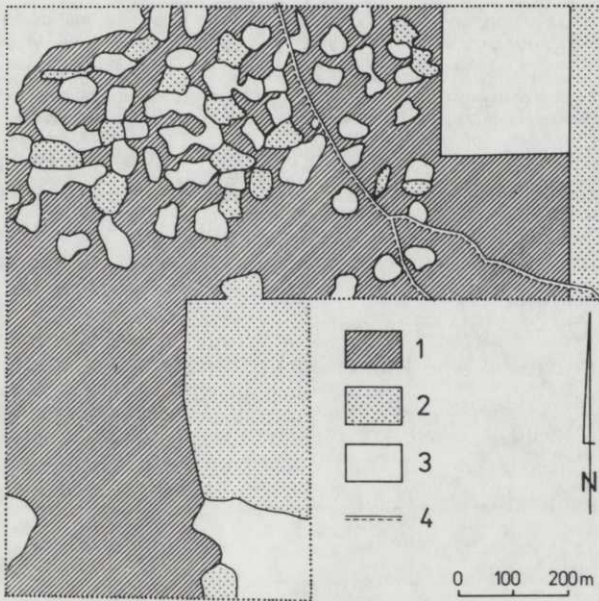


Fig. 4. Habitat structure of the managed oak-hornbeam plot

For explanations see Fig. 3

Ryc. 4 Struktura siedliska powierzchni grądowej w zagospodarowanej części puszczy

Objasnienia patrz ryc. 3

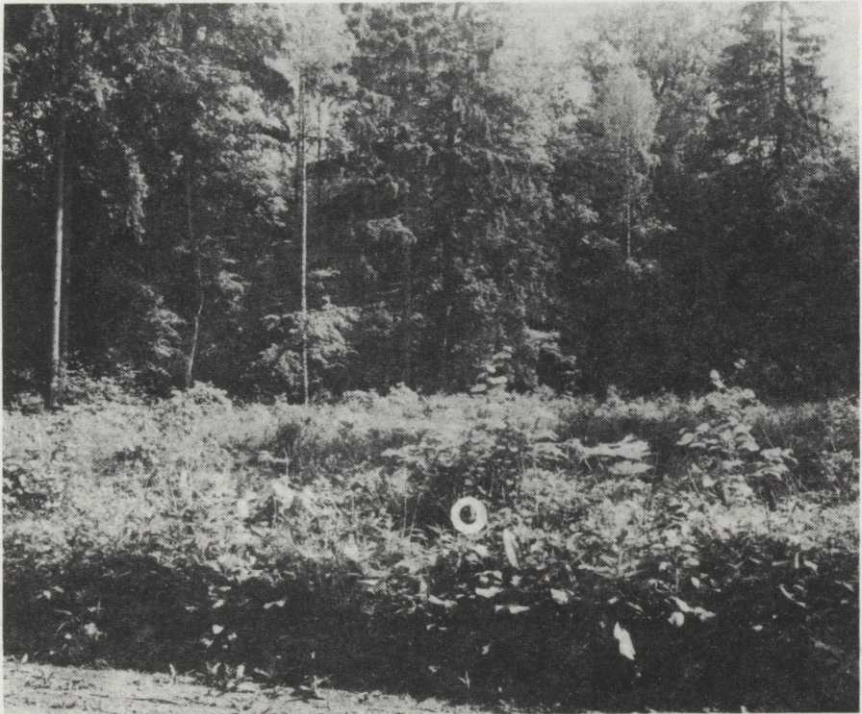


Photo L. WILCZEK

Photo 3. Managed oak-hornbeam plot

In the foreground — forest road and young tree plantation overgrown with dense bushes and luxuriant herbs. In the background — multi-layer, species rich mature tree stand. Position of *Phylloscopus collybita* nests marked with the circle

Fot. 3. Powierzchnia próbna w grądzie zagospodarowanym

Na pierwszym planie droga leśna i uprawa zarosła gęstymi krzewami i roślinnością zieloną. W tle dojrzały wielowarstwowy wielogatunkowy drzewostan łąkowy. Położenie gniazda pierwiosnka zaznaczono kółkiem

In the managed stands observations were carried out within two plots. They were chosen so as to represent typical habitats managed in a standard way. Mature stands covering parts of these plots were of natural origin and structurally resembled the equivalent primaeval ones.

The study in the managed forest began in 1978 in a 40 ha coniferous plot, enlarged in 1979–82 to 82.8 ha (Fig. 3, Photos 1 and 2). Another plot, covering 82.9 ha of oak-hornbeam habitat was studied in 1979–82 (Fig. 4, Photos 3 and 4). Data were collected between the end of March and the end of June (end of July in 1980).

Field procedures used in the managed stands were similar to those used in the National Park with one exception, *i.e.* play-backs of songs were not used for the delineation of males' territories. The number of birds ringed and numbers of nests found there are shown in Table 2.

RESULTS

Densities, fluctuations in numbers

In the primaeval forest the chiffchaff bred in highest densities in the swampy stands (Table 3). The highest density recorded within a single plot was 5.6 territories/10 ha. As follows from the Table, densities in the primaeval oak-hornbeam



Photo L. WILCZEK

Foto 4. Managed oak-hornbeam plot

Location of *Phylloscopus collybita* nest (encircled) built in a branch laying over a ditch, seasonally filled with water is shown

Fot. 4 Powierzchnia próbna w grodzie zagospodarowanym

Gniazdo pierwiosnka (obwiedzione kółkiem) zbudowane na gałęzi leżącej nad rowem sezonowo wypełnionym wodą

and coniferous stands were similar to each other and, on average, four to five times lower than in the ash-alder stands. The maximum densities in the oak-hornbeam and coniferous habitats amounted to 1.4 territ./10 ha. The densities in the managed stands were about two times higher than those in the respective primaeval habitats, reaching maximally 2.1 territ./10 ha. However, taking into account the fact that birds in the managed stands utilized roughly only a half of the available area (cf Fig. 7 and 8) it would appear that densities calculated for the area actually utilized were much higher, reaching the level found in the swampy stands. The densities recorded in other managed coniferous stands within the Białowieża Forest: 1.6–2.7 territ./10 ha. (PIOTROWSKA and WOŁK 1983) agree well with the materials presented here.

Data from other woodlands in Poland (Table 4) and from other parts in Central Europe (compiled by SCHÖNFELD 1978) fit well the pattern found in our data, *i. e.* that the chiffchaff breeds in the highest densities in swampy woods and in much lower densities in other types of tree-stands.

The numbers of the chiffchaff fluctuated in fairly narrow limits (Table 3), the coefficients of density variation in the ash-alder habitat and in the managed stands were in the range 5.6–12.3%. As the higher coefficients of variation found in the primaeval oak-hornbeam and coniferous stands (21 and 25% respectively) at least

Table 3. Densities (territories/10 ha) of *Phylloscopus collybita* in different habitats of the Białowieża Forest

Data from primaeval stands (following TOMIAŁOJC *et. al.* 1984 and unpubl.) show mean values calculated from all plots censused in the BNP in a given year and habitat. The number of plots censused (24-33 ha each) is shown in parentheses. Values for managed stands come from intensively studied plots.

Densities in the ash-alder stands were significantly higher ($p < 0.001$, *t* test) than in any other habitat. Densities in the managed oak-hornbeam and coniferous stands were significantly higher ($p < 0.001$, *t* test) than in the equivalent primaeval habitats. Other differences were non significant

Tabela 3. Zagęszczenie (terytoria/10 ha) pierwiosnka w różnych siedliskach Puszczy Białowieżskiej

Dane dla lasu pierwotnego przedstawiają przeciętne wartości z wszystkich powierzchni kontrolowanych w BPN w danym roku i siedlisku (wg TOMIAŁOJC i in. 1984 oraz nie publ.). Liczbę kontrolowanych powierzchni (każda wielkości 24–33 ha) podano w nawiasach. Dane dla lasu zagospodarowanego pochodzą z intensywnie badanych powierzchni.

Zagęszczenie w łągach było istotnie wyższe niż w jakimkolwiek innym siedlisku (test *t*, $p < 0,001$). Zagęszczenie w grądzie i borze zagospodarowanym było istotnie wyższe niż w odpowiednich typach siedlisk pierwotnych (test *t*, $p < 0,001$). Pozostałe różnice nie były istotne

Type of stand Typ drzewostanu	Year Rok	Ash-alder stands Łęgi	Oak-hornbeam stands Grądy	Coniferous stands Bory
Primaeval Pierwotny	1975	3.9 (2)	0.8 (5)	0.8 (2)
	1976	4.1 (3)	1.0 (5)	1.1 (2)
	1977	4.5 (3)	0.9 (6)	0.8 (3)
	1978	3.7 (2)	0.8 (6)	0.6 (3)
	1979	3.8 (2)	0.8 (6)	1.3 (3)
	1980	3.6 (2)	0.7 (3)	1.1 (2)
	1981	4.2 (2)	0.6 (3)	0.9 (2)
	1982	4.1 (2)	0.5 (3)	0.8 (2)
	\bar{x} (s)	4.0 (0.28)	0.8 (0.16)	0.9 (0.23)
Managed Zagospodarowany	1979	—	2.1	1.9
	1980	—	2.1	1.9
	1981	—	2.2	2.1
	1982	—	1.8	1.8
		\bar{x} (s)	—	2.0 (0.20)

partially resulted from very low densities there (settlement of even one additional bird had a relatively stronger effect on number variation than in areas populated more densely), the higher coefficients of variation in this case need not necessarily mean much lower stability.

Behaviour

Spring arrival, settlement pattern

In Białowieża the chiffchaff is completely migratory. The birds winter somewhere in the Mediterranean Basin and Africa, north of the Equator (MOREAU 1972, ZINK 1973). The earliest birds were returning to the Forest in the first days of April. The first singing males were recorded on April 3–9 in different years, *i. e.* about a month later than in Switzerland (GLUTZ 1964), at about the same time as in the neighbouring Masurian Lakeland (TISCHLER 1941) and two weeks earlier than in the vicinity of Leningrad (MALTSCHEVSKIY and PUKINSKIY 1983).

Table 4. Densities (territories/10 ha) of *Phylloscopus collybita* in different types of woodland habitats in Poland, outside the Białowieża Forest

Tabela 4. Zagęszczenie (terytoria/10 ha) pierwiosnka w różnych typach lasów w Polsce, poza Puszcza Białowieżską

Habitat type Typ lasu	Density Zagęszczenie	Plot size (ha) Wielkość powierzchni (ha)	Reference Źródło
Alder and riverine forests Łęgi i olsy	3.8–9.5	12.0–20.6	TOMIAŁOJC and PROFUS (1977)
	6.4–8.5	11.0–17.1	MRUGASIEWICZ (1974)
	4.0	9.9	TOMIAŁOJC (1974)
	4.0	18.5	WOLK and LEWARTOWSKI (pers. comm.)
	0.8(!)	23.0	GÓRSKI (1976)
Oak-hornbeam and beech forests Grądy i buczyny	2.3	37.3	GOC (1977)
	2.1	23.5	RANGSEK (1969)
	0.8	10.0	GRADZIEL (1977)
	0.4–0.6	35.5–37.0	GŁOWACIŃSKI (1975)
	0.2	45.7	MRUGASIEWICZ (1974)
Coniferous forests Bory	2.2–3.2	10.0	GRADZIEL (1977)
	2.2	68.0	KANIA (1968)
	0.5	20.3	TOMIAŁOJC (1974)

At the time of the first males arrival the ground vegetation was not developing yet and, in the late springs, patches of snow were still covering ground (in the very late spring of 1979 about 20% of the ground in the coniferous forest was snow-covered as late as April 20). Deciduous trees were completely leafless at that time, only on some of them buds began to swell.

In the ash-alder plot — K — all males settled within 10–13 days and in the managed plots 13–24 days following the first ones. These figures, however, are only crude approximates, as the plots were not checked daily and in order to calculate these figures, the last males were assumed to be settled at a date intermediate between the day on which all of them were recorded within the plot and the date of the preceding visit.

No differences in the timing of the settlement of different plots by the males were recorded in our material. However, because of the crudeness of our measurements, the existence of subtle delays, *e. g.* of the order of one or two days could not be detected even if they existed.

Females were arriving about three weeks later than males. The first ones were usually observed on 23–27 April, only in 1981 and 1982 were they first recorded on May 3 and 1, respectively. The delay of the female arrival in 1981–82 was probably related to low temperatures occurring during the period of their settlement. Mean minimum daily temperatures in the last ten-day period of April were -1.6° in 1981 and 0.7°C in 1982, whereas mean values for the other years ranged from 1.4° to 6.5°C .

Females started to settle in all the habitats at about the same time. In comparison with the males their settlement was much more synchronous. In the ash-alder plot the last females settled within only 5–8 days following the first ones. In the managed stands all females settled within 9–15 days in 1979 and 1980 and in less than a week in the late springs of 1981 and 1982. The actual settlement rates could even be more rapid than these figures suggest. In the managed oak-hornbeam plot in 1982 only one female was present on 5 May, but on the next day already nine of 11 males were observed with females.

Site tenacity

Every spring in intensively studied plots birds were checked for the presence of individuals ringed in previous seasons. However none of 529 birds marked as nestlings, nor any of 22 ringed females, were resighted (Table 5). Only males were site-tenacious, about a third of them come back in the following years. Apart from

Table 5. Return rates of different age and sex classes of *Phylloscopus collybita* to the Białowieża Forest

The males were significantly more site-tenacious than the females or young birds were ($p \leq 0.01$, chi-square test)

Tabla 5. Powracalność białowieskich pierwiosnków do miejsc gnieźdzenia lub urodzenia w zależności od płci i wieku

Powracalność samców była istotnie wyższa niż samic czy ptaków młodocianych (test chi-kwadrat, $p \leq 0,01$)

Birds ringed as: Ptaki obrączkowane jako:	Adults – Dorosłe				Nestlings Pisklęta	
	Territorial males Samce terytorialne		Nesting females Samice lęgowe			
Habitat type Typ siedliska	Number of birds in year one Liczba pta- ków w pier- wszym roku	Percentage returning in year two Procent po- wracających w roku na- stępnym	Number of birds in year one Liczba pta- ków w pier- wszym roku	Percentage returning in year two Procent po- wracających w roku na- stępnym	Number of birds in year one Liczba pta- ków w pier- wszym roku	Percentage returning in year two Procent po- wracających w roku na- stępnym
Primaeval forest (birds ringed in 1976–78) Las pierwotny (ptaki obrączko- wane w 1976–78)	15*	33	10	0	244	0
Managed forest (birds ringed in 1978–81) Las zagospodarowa- ny (ptaki obrącz- kowane 1978–81)	47*	30	12	0	285	0
Total – Łącznie	62	31	22	0	529	0

* Newly ringed and returning individuals pooled.

Łączna liczba ptaków obrączkowanych i wracających.

territorial birds, one male ringed as a nonterritorial bird came back the following spring and occupied a territory within plot K. Three males returned in two consecutive springs, and the third one, ringed in 1978, was back in 1979, absent in 1980, reappeared in 1981.

SCHÖNFELD (1978) obtained similar results in the GDR, though in his study area females were site-tenacious as well.

As a rule, the returning birds occupied territories in the same places as in previous years. In about 74% of cases the males settled in exactly the same territory, in about 16% of cases in a neighbouring territory, and only twice (10.5%) two average-sized territories apart.

Site-tenacity of the coming-back males was quite strongly manifested, as shown by one case observed in the managed stands, where the habitat structure of one territory underwent dramatic changes between two seasons. A mature tree-stand constituting the main part of the territory was cut down. All tall trees, having served as singing-posts, were removed. The tallest spruce left within a patch of young trees was only 5–7 m high. This patch was surrounded by young-tree plantation and clear-cut areas (Photo 2). In spite of all these changes the returning male re-settled in this place.

The philopatric males were settling earlier than the new males, as suggested by data collected in the managed plots. On 13 April 1981 there were already three colour-ringed males (out of four returning) present and four unringed ones (out of 26). This difference was significant: $p = 0.031$, FISHER exact probability test.

Territorial and other behaviour of males

The distribution pattern of the chiffchaff territories within the primaeval study plots in the early spring of 1979 is shown in Figs 5 and 6. Their distribution in other years of study was very similar to that in 1979. Every year in both plots almost the whole area was occupied by territories. Only an oak-hornbeam island in the northern-central part of plot K (*cf* Fig. 2 and Fig. 5) remained unoccupied during the whole study period.

In the managed stands the situation was different (Figs 7 and 8); the territories were patchily distributed, with large areas left unoccupied. The same places were occupied from year to year. Utilized and non-utilized places differed in their habitat structure (*cf* Fig. 7 with 3 and Fig. 8 with 4). Areas in which the chiffchaff established territories were characterized by the following features: they had at least some tall trees (which served as song-posts), as well as a dense undergrowth in the vicinity of open places (which served as foraging and breeding places of females). Lack of any of those habitat elements rendered an area unsuitable for settlement (however, *cf* p. 44). This was most clearly visible in the coniferous plot (Fig. 7): birds, having a choice of two sides of elongate blocks of mature tree-stands (one adjoining clear-cut areas, the other – dense, several meters high undergrowth) invariably settled along the latter.

Territory size was measured only in the primaeval stands. It varied between 0.41

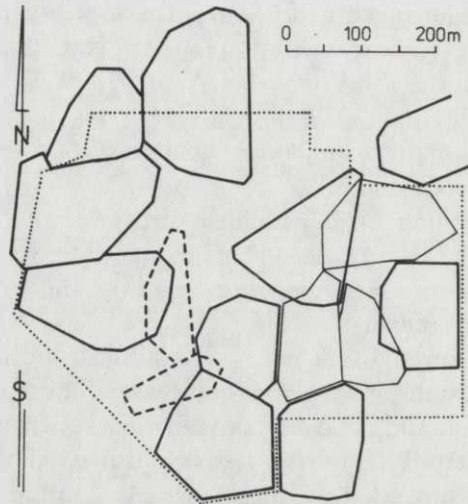


Fig. 5. Distribution of *Phylloscopus collybita* territories within the ash-alder stand (plot K) in 1979. Boundaries of the plot are marked with dotted line; maximum size of territories occupied permanently during the period April 23 – May 21 with thin and thick solid lines; approximate size of territories of males which were present only in April – with dashed lines. Overlapping parts of territories were occupied consecutively by different owners. Sizes and shapes of presented here territories cannot be compared with those presented at Figs 7 and 8 (see methods)

Ryc. 5. Rozmieszczenie terytoriów pierwiosnka w łęgu (pow. K) w r. 1979

Kropkowaną linią zaznaczono granice powierzchni, cienką i grubą ciągłą linią zaznaczono maksymalną wielkość terytoriów zajętych w okresie 23 kwietnia – 21 maja, przerywaną linią przybliżone rozmiary terytoriów samców obecnych tylko w kwietniu. Zachodzące na siebie części terytoriów były użytkowane kolejno przez różne samce. Rozmiary i kształty terytoriów tu przedstawionych nie mogą być bezpośrednio porównywane z przedstawionymi na ryc. 7 i 8 (por. metody)

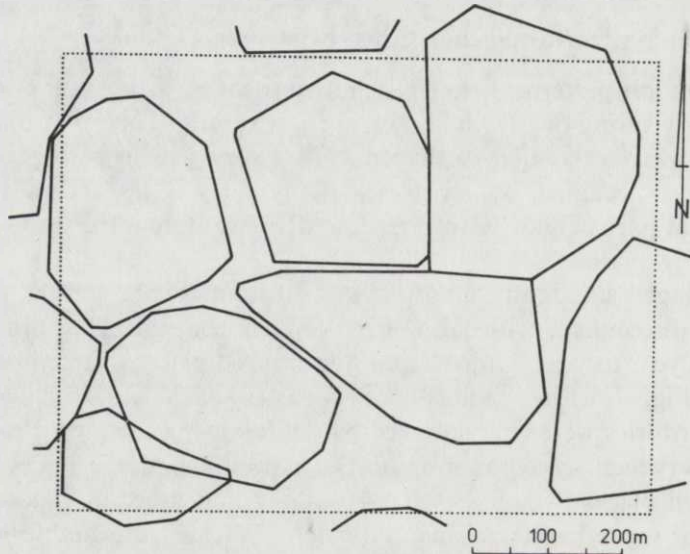


Fig. 6. Distribution of *Phylloscopus collybita* territories in the oak-hornbeam primeval stand (plot C) in 1979

For explanations see Fig. 5

Ryc. 6. Rozmieszczenie terytoriów pierwiosnka w pierwotnym łądzie (pow. C) w r. 1979

Objaśnienia patrz ryc. 5

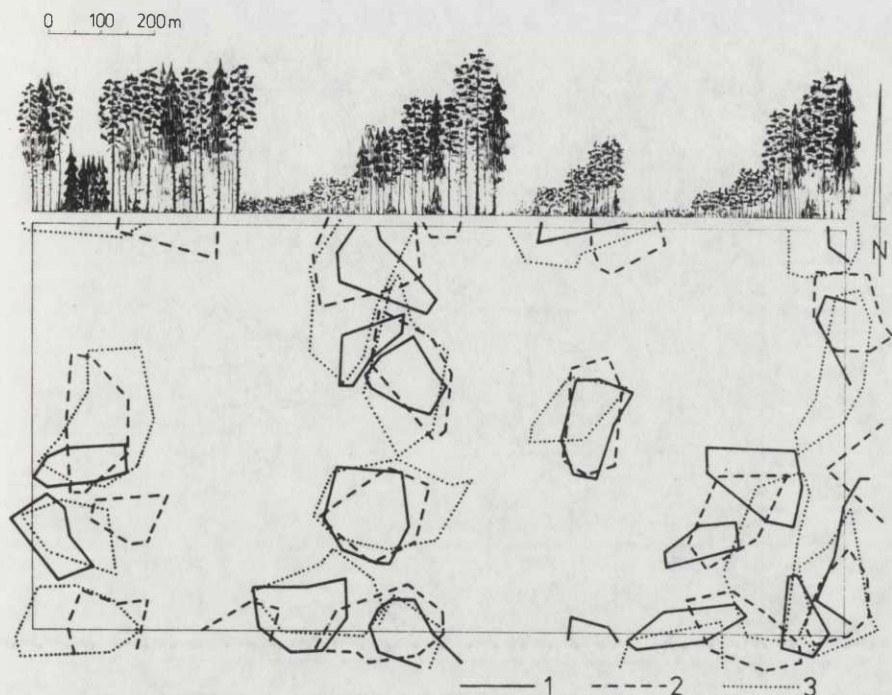


Fig. 7. Distribution of *Phylloscopus collybita* territories within a fragment of the managed coniferous plot in different years

1 — 1979, 2 — 1980, 3 — 1981. A schematic cross-section through the plot (above) indicates habitat structure of patches occupied and avoided by the birds

Other explanations see Fig. 5. Sizes and shapes of presented here territories cannot be compared with those presented at Figs 5 and 6 (see methods)

Ryc. 7. Rozmieszczenie terytoriów pierwiosnka na fragmencie powierzchni borowej zagospodarowanej części Puszczy w różnych latach

1 — 1979, 2 — 1980, 3 — 1981. Schematyczny przekrój przez drzewostan (u góry) pokazuje strukturę siedliska na fragmentach zajmowanych i omijanych przez ptaki. Inne objaśnienia — patrz ryc. 5. Wielkości i kształtu pokazanych tu terytoriów nie można porównywać z prezentowanymi na ryc. 5 i 6 (por. metody)

and 8.27 ha. The latter figure is really amazing if one takes into account that the chiffchaff weighs only about 8 g. There was a great within-habitat variation in the territory size, the difference between the smallest and the largest being over sevenfold in the ash-alder, and over fourfold in the oak-hornbeam stands (Table 6). Nevertheless, there was a significant between-habitat difference in the average territory size. The average territory in the ash-alder habitat was three and half times smaller than that in the oak-hornbeam habitat.

The territory size of the returning males varied between the seasons. The changes were as follows: male 33 — 2.95 ha in 1976, 1.32 ha in 1977; male 5 — 2.50 ha in 1976, 0.80 ha in 1977, 2.08 ha in 1978; male 52 — 0.75 ha in 1977, 2.18 ha in 1978, 2.24 ha in 1979 (all data from plot K).

The following changes in territory ownership within the period of first broods were recorded:

— only one colour-ringed male disappeared (it was caught during a cold spell and was not seen any more).

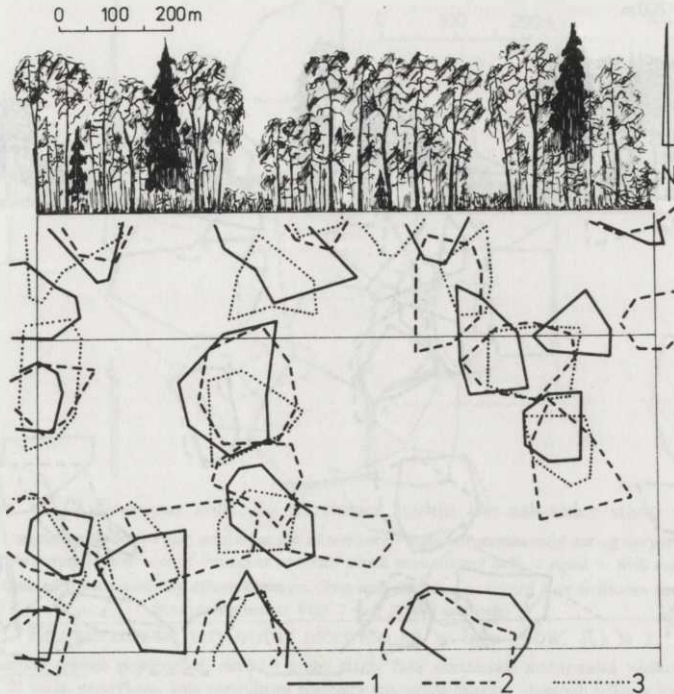


Fig. 8. Distribution of *Phylloscopus collybita* territories within a fragment of the managed oak-hornbeam plot in different years

A schematic cross-section through the plot (above) indicates habitat structure of patches occupied and avoided by the birds
Other explanations — see Fig. 7

Ryc. 8. Rozmieszczenie terytoriów pierwiosnka na fragmencie powierzchni łąkowej w zagospodarowanej części Puszczy

Schematyczny przekrój przez drzewostan (u góry) pokazuje strukturę siedliska fragmentów zajmowanych i omijanych przez ptaki.
Pozostałe objaśnienia — patrz ryc. 7

— one ringed male was expelled from his territory by a ringed neighbour, the expelled male established a new territory 200 m away from the old one.

— three males, present in April, disappeared in May; parts of their territories were occupied later by their former neighbours; two of these males (Fig. 5) were already mated but their mates did not begin to build nests yet (the females were probably taken over by the neighbours as well, as later on nests appeared in the very areas in which the females had been observed with the former owners).

— two males enlarged their territories after their mates had chosen nest-sites outside the borders of their original domains (*cf* Fig. 5, right-hand part).

The impact of all these changes, on numbers and distribution of territories was, however, rather slight.

The males stayed in the same territories throughout the whole breeding period, but the number of territories occupied during the period of second broods (end of June — July) was smaller than earlier in the season. In those years, when

Table 6. Sizes of *Phylloscopus collybita* territories (in ha) in relation to year and habitat in the Białowieża National Park

The difference between mean territory sizes in the two habitats were highly significant ($p < 0.001$, t test)

Tabela 6. Wielkość terytoriów (w ha) pierwiosnka w Białowieżskim Parku Narodowym w różnych latach i siedliskach

Różnica przeciętnej wielkości terytoriów między łągiem a grądem była wysoce istotna (test t, $p < 0,001$)

Year Rok	Ash-alder stand (plot K) Łęg (pow. K)			Oak-hornbeam stand (plot C) Grąd (pow. C)		
	\bar{x}	<i>N</i>	Range Zakres	\bar{x}	<i>N</i>	Range Zakres
1976	1.93	7	1.31–3.01	—	—	—
1977	1.35	12	0.41–2.72	4.82	2	4.31–5.32
1978	1.76	10	0.69–2.26	4.64	4	3.71–5.34
1979	1.41	10	0.73–2.24	5.69	6	1.95–8.27
Total Łącznie	1.50	39	0.41–3.01	5.19	12	1.95–8.27

observations were continued throughout the whole of July, the number of occupied territories at the time of second broods was lower by 14% (primaeval habitats, 1978) and 35% (managed habitats, 1980). Data from the managed stands from other years, though less detailed (some males could have been overlooked), suggest that 40–50% of the males were absent in July.

Before the arrival of females the males spent most of their time foraging and singing within their territories. Only during cold spells (often with snow storms), quite often early in spring, did the birds almost cease singing. The majority of them did not react then to play-backs of songs, even if they were played from the distance of a few meters. In such periods the males were foraging intensively, most frequently low above the ground or even in the ground – in litter and among roots at the bases of trees. In those periods some birds deserted their territories altogether and were observed up to several hundred meters outside their territories. However, such spells being over, the males resumed territorial behaviour in the previously occupied places.

The appearance of females in territories led to a conspicuous change in the behaviour of their owners. Paired birds sang much less frequently and uttered shorter songs than the unpaired ones. Though this aspect of their behaviour was not quantified in our study, the difference was so striking (*cf* also HOMAN 1960) that it was used by us as a main cue in looking for the presence of nest building females. Newly paired males usually closely followed females; because of that they sang from much lower posts than before. Also during nest building the males accompanied the females and usually sang from trees a dozen or so meters above the places in which females were building their nests.

Shortly before the arrival of females and during their arrival the territory owners

were often engaging in high-intensity conflicts with intruders. All observed chases and fights ($N=25$) took place between April 18–May 19 but 76% of them occurred between April 24–May 3, when most of the females were arriving (*cf* p. 44). These changes were not infrequently very prolonged, they could last several hours, with a dozen or so bouts of chases an hour. The chased birds could be in some cases females (GEISSBÜHLER 1954, HOMAN 1960) but in several cases they were singing, *i.e.* they were males. The intruding males could possess territories somewhere in the vicinity, as demonstrated by the localization of their netting places in 1976–77. Then the males had a chance to fall into one of some score of nets distributed within the study plots irrespective of territory boundaries (*cf* p. 44). All but two males were caught in territories other than their own. The same was also true of females.

The reaction of males to play-back of species-specific song was very strong at the time of female settlement. The majority of them flew in the direction of the tape-recorder looking for a rival. They usually fluttered down and some even landed on the tape-recorder. The birds, however, habituated rather quickly and if they failed to spot a “rival” in 15–30 min, their reaction weakened and they flew away. If a stuffed bird was placed near the tape-recorder (as we habitually did while attempting to catch birds) the territory owners usually attacked it vigorously, trying to dislodge the “rival” from its perch, often pecking it at the head. In an extreme case a male was so engaged in fight with its “rival” that it was caught by an observer by hand.

Some birds, however, did not respond to play-backs. In several cases it appeared that these were birds which had returned to their breeding places of previous year. As we used the same records every year, there can be the interesting possibility that they remembered the records to which they had already habituated the previous year and did not treat them as a serious threat.

During incubation the males paid almost no attention to their nests. They sang intensively during the whole day, often far away from the nests.

The males usually did not feed their young, or fed them only very rarely. During 29 hours of observations carried out in managed stands from June 7 to 14, 1982, at nests containing 3–10 days old nestlings, the males brought food only four times, which constituted only 1.0% of all feedings observed. Additionally, feeding by a male of freshly fledged young was observed twice. Also in other areas the male share in feeding their nestlings was almost negligible (data compiled by SCHÖNFELD 1978).

The males which remained in their territories sang until mid-July, but the last ones were heard singing as late as July 24, 1978. Some of the males seemed to spend also their moult period in their previous territories as colour-ringed birds were still observed in the territories in the first decade of August. After moulting the chiffchaff commenced singing once again. This took place in the Białowieża Forest at the end of August-September.

Male pairing success, sex ratios

As follows from Table 7 the males usually mated monogamously, though five cases of bigamy and one case of trigamy were recorded as well. Also two further cases of bigamy were recorded in the period of second broods in plot K in 1978. Taking into account the fact that in all published data on this species only five other

Table 7. Pairing success of *Phylloscopus collybita* males and sex ratios in different habitats of the Białowieża Forest

The success is expressed as the number of females nesting simultaneously in territories during the period of first broods. Because in the managed stands some — destroyed early — breeding attempts may have been overlooked, two values are given for them, the lower representing the number of territories in which breeding was confirmed and the higher one, the total number of territories where females were recorded (even if once). The difference between the proportion of polygynous males in plots K and C was not significant but there were significantly more polygynous males in plot K than in the combined sample from the managed stands ($p=0.0001$, FISHER exact probability test). Proportion of bachelor males in plot C was significantly higher than in plot K ($p=0.033$, FISHER exact probability test) or in the pooled data from managed stands ($p<0.01$, if maximum values for females were used, but not significant if minimum values were used).

Tabela 7. Udatność kojarzenia samców pierwszorka i proporcje płci w różnych siedliskach Puszczy Białowieżskiej

Udatność wyrażono liczbą samic gnieźdzących się jednocześnie w terytorium w okresie pierwszych lęgów. Niektóre (wcześnie zniszczone) legi w lesie zagospodarowanym mogły być przeoczone, dlatego też podano dla tego siedliska dwie wartości: mniejsza reprezentuje liczbę terytoriów, w których stwierdzono gnieźdzenie, a wyższa — łączną liczbę terytoriów, w których obserwowano samice (choćby tylko raz). Różnice udziału poligynicznych samców na powierzchniach K i C nie były istotne, lecz ich udział na powierzchni K był istotnie wyższy niż na obu (łącznie) powierzchniach w lesie zagospodarowanym (test dokładny FISHERA, $p=0,0001$). Udział samotnych samców na powierzchni C był istotnie wyższy niż na powierzchni K (test dokładny FISHERA, $p=0,033$) czy na obu powierzchniach (łącznie) w lesie zagospodarowanym (test chi-kwadrat, $p<0,01$), jeżeli użyć maksymalnych liczebności samic, lub nieistotnie — gdy użyć wartości minimalnych)

Habitat type and plot (years of study Typ siedliska i powierzchnia (lata obserwacji))		Number of territories with: Liczba terytoriów z:				Total number of females Łączna liczba samic	Total number of territories = males Łączna liczba terytoriów = samców	Sex ratio (males: females) Stosunek płci (samców: samic)
		0 females	1 female	2 females	3 females			
Primaeval forest Las pierwotny	Ash-alder, plot K (1976–79) Łęg—pow. K	4	31	4	1	42	40	1:1.05
	Oak-hornbeam, plot C (1977–79) (Grąd—pow. C)	5	11	—	—	11	16	1:0.69
Managed forest Las zagospodarowany	Oak-hornbeam plot C (1979–82) Pow. grądowa	5-14	47-56	1	—	49–58	61	1:0.80–0.95
	Coniferous plot (1979–82) Pow. borowa	4-13	49-58	—	—	49–58	62	1:0.79–0.93

cases (both those proved and those conjectured) of bigamy were detected (data compiled in SCHÖNFELD 1978), one can state that in the Białowieża Forest polygyny was unusually frequent (WESOŁOWSKI 1987).

Despite the cases of polygyny, sex ratios among sedentary birds were as a rule male-biased (Table 7).

The pairing success of males was the highest in ash-alder stands, as there all but one cases of polygyny occurred, and the proportion of bachelors was the lowest. The success of males in the managed stands was intermediate, and the success of males in the primaeval oak-hornbeam stands was the lowest. These interhabitat differences were also visible when data from individual years, were compared separately and when data from the period of second broods were compared.

Behaviour of females

Weather conditions permitting, the females commenced nest building just after their settlement. The period of time passing between the first observations of females and the beginning of building of the earliest nests ranged from 0 to 3 days in different years. The building females usually uttered characteristic "fiet" calls and, as a result, they were especially easy to detect at that time. Some females commenced egg-laying immediately after finishing the construction of their nests, but gaps (up to 12 days) not infrequently occurred. Such breaks were recorded most often during cold spells. However, not all the females delayed egg-laying during adverse weather. For example, in 1980 when temperatures dropped on 12–16 May to a minimum -3.1°C , in the managed stands five females with ready nests did not commence laying, but ten others started to lay precisely during that period. The females which began laying before such cold spells did not interrupt it and were laying at the normal rate of one egg a day.

Only females incubated. The incubation period lasted 3×14 days, 5×15 days and 6×16 days, 14.8 days on the average. During this period the females were very silent, and it was difficult to find their nests. All brooding and almost all feeding (*cf* p. 44) was done by the females as well. During the nestling period the females were frequently calling when collecting food and approaching nests, which made them easily detectable again.

After destruction of broods or fledgling of young, some females re-nested in the same territories. Six out of 12 females observed in 1978 and 1980 (the years in which observations were carried out throughout July) built their second nests within the same territories but the remaining ones did not nest again within our plots. They could breed somewhere outside the plots, as demonstrated by a case observed in 1981, when a female resettled several hundred meters away after the destruction of her first brood.

In the second nests egg-laying commenced 5–15 days after the destruction of young or their fledgling from the first ones.

Breeding ecology

Nests, nest sites

The chiffchaff built domed nests with entrances oriented slightly obliquely upwards. Only exceptionally (four cases) was the nest entrance directly upwards-directed. Three of these nests were situated in very shaded places under a close tree canopy.

Nest entrances were rather uniformly directed toward different quarters of the world, though entrances oriented to the East could be encountered twice as often as would be expected by chance (Fig. 9). Preference towards one geographic direction, if there existed any, was confounded by a very strong tendency to orient the nest entrance towards the nearest well lit and open space. As many as 47.6% of 130 nests in the managed forest had their entrances directed that way ($p < 0.02$, chi-square test).

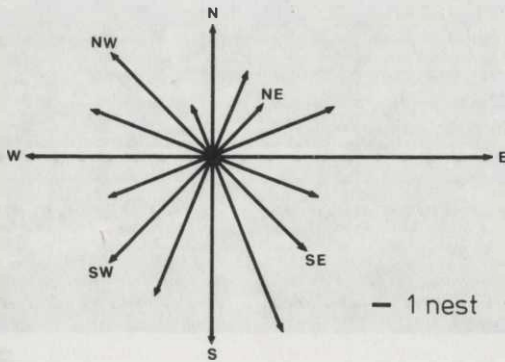


Fig. 9. Orientation of entrances of *Phylloscopus collybita* nests in relation to geographical direction. Data from managed stands. $N = 125$. The length of an arrow is proportional to number of nests with entrances oriented in direction shown by the arrow.

Ryc. 9. Położenie otworów wlotowych gniazd pierwiosnka w stosunku do stron świata

Dane z zagospodarowanej części Puszczy. $N = 125$. Długość strzałek jest proporcjonalna do liczby gniazd, których otwór był skierowany w daną stronę

The nests, especially those not covered by vegetation, were usually well camouflaged. Their external layer was, depending on local conditions, built from different materials (dry grasses, mosses, dry leaves, flakes of bark) so as to make nests blend with their surroundings. Few of the nests, however, were not disguised and contrasted sharply with their background (e. g. a nest made of dry oak leaves in a pile of branches, or another one made of pale dry grasses situated in dark litter).

The nests were additionally masked by being concealed among herb vegetation. Though at the time of building the first nests (beginning of May) herbs were not yet developed enough to cover them, later on, during nestling time the majority of them, especially in the oak-hornbeam stands, were surrounded by luxuriant herb vegetation (Table 8).

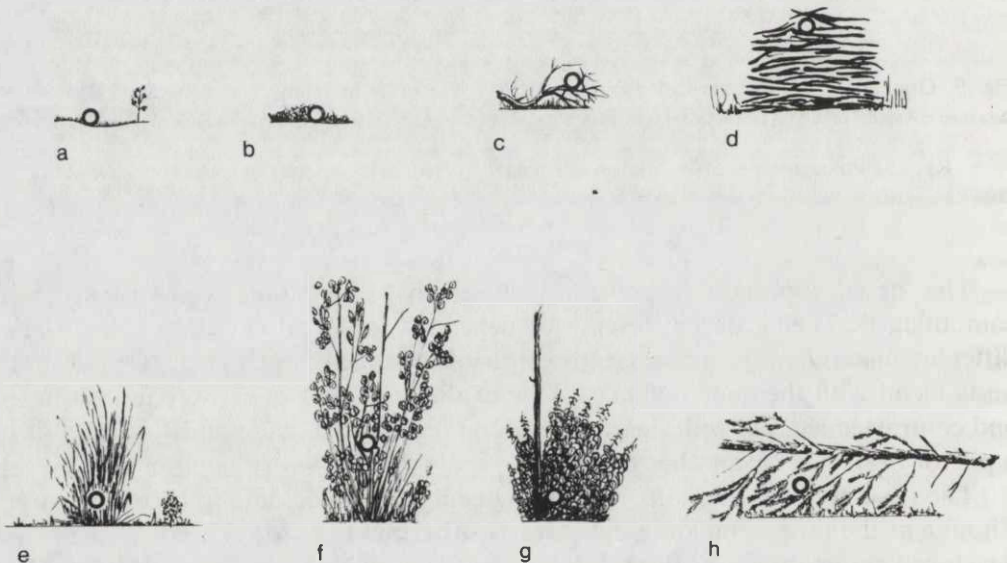
Table 8. *Phylloscopus collybita*, types of nest-cover in the managed Białowieża stands

Measurements of vegetation height were taken during the first half of June (nestling period of first broods). There were significantly more noncovered nests ($p < 0.01$, chi-square test) and significantly fewer nests surrounded by tall vegetation ($p < 0.001$, chi-square test) in the coniferous than in the oak-hornbeam stands

Tabela 8. Sposób osłony gniazd pierwiosnka w zagospodarowanych borach i grądach Puszczy Białowiejskiej

Pomiarów wysokości roślinności w otoczeniu gniazda dokonywano w pierwszej połowie czerwca (w okresie pobytu piskląt z pierwszych legów w gniazdach) W porównaniu z grądem w borze stwierdzono istotnie więcej gniazd nie osłoniętych roślinnością (test chi-kwadrat, $p < 0.01$) oraz istotnie mniej gniazd ukrytych wśród roślinności wyższej od 25 cm (test chi-kwadrat, $p < 0.001$)

Nest-cover Osłona gniazda	Habitat – Siedlisko			
	Coniferous Bór		Oak-hornbeam Grąd	
	N	i	N	i
Noncovered by vegetation Nie osłonięte roślinnością	21	28.4	5	8.8
Concealed by 20–25 cm high vegetation Osłonięte roślinnością o wysokości 20–25 cm	27	36.5	8	14.0
Concealed by herbs over 25 cm high Osłonięte przez bujną roślinność zielną, wyższą niż 25 cm	26	35.1	44	77.2
Total – Łącznie	74	100	57	100

Fig. 10. Typical nest-sites of *Phylloscopus collybita* in the Białowieża Forest

Ryc. 10. Typowe miejsca zakładania gniazd przez pierwiosnka w Puszczy Białowiejskiej



Photo L. WILCZEK

Photo 5. Typical placement of *Phylloscopus collybita* nest (encircled) in coniferous forest
 Fot. 5. Typowy sposób umieszczenia gniazda pierwiosnka (obwiedzione kółkiem) w borze

The nests were usually placed closely to some open area — a gap formed by fallen trees in the primaeval forest, or in the managed forest, near forest roads, paths and the like. At the same time there were usually some thickets (luxuriant herbs or shrubs) in close proximity of the nests (*cf* Photos 1–4) as well.

The substrates on which nests of the chiffchaff were built were rather variable. Their most frequently recorded types are shown in Fig. 10 and Photos 3–6. These were branches of fallen spruces still covered with needles, single branches (mostly coniferous) of varying size lying on the ground, small deciduous and coniferous bushes, clumps of herbaceous vegetation or piles of dry twigs. The nests were also found in several other places, such as: at the base of small trees, on slopes of ditches, on the bottom of small pits, or on fallen logs over a stretch of water.

It is true that the majority of the chiffchaff nests in the Białowieża Forest were placed in branches lying on the ground. Nevertheless, the utilization of other nest substrates varied between the habitats (Table 9). This differentiation followed the variation in the structural properties of the habitats. In swampy habitats in which



Photo L. WILCZEK

Photo 6. Oak-hornbeam habitat. *Phylloscopus collybita* nest (marked with the arrow) in clump of *Calamagrostis* sp.

Fot. 6. Grąd – gniazdo pierwiosnka (zaznaczone strzałką) w kępie trzcinnika

clump forming perennials (sedges, ferns, nettles, reeds) were most abundant, the birds placed almost 37% of their nests among plant stems on tops of such clumps. In the primaeval oak-hornbeam stands, in which the bush layer was underdeveloped, only a single “bush” nest was found (Table 9), whereas in the managed oak-hornbeam habitat, where bushes and thickets of young trees were plentiful, almost 44% of nest were situated in bushes.

In Białowieża the chiffchaffs as a rule situated their nests on the ground or up to 40 cm above it (Fig. 11) though several nests were placed over 1 m (1.3, 1.7, 1.8, 2.7 and 7.5 m). The highest nest, found in the managed coniferous forest in 1982, was situated in low branches of a tall spruce.

The proportion of ground nests was the lowest (less than 4%, Fig. 11) in the ash-alder stands, in which swampy soil made such placement of nests very difficult. Ground nests were significantly more frequent in the drier oak-hornbeam and coniferous habitats, being the most frequent in the managed coniferous stands in

Table 9. Nest-sites of *Phylloscopus collybita* in the Białowieża Forest in relation to the habitat

The proportion of nests situated in clumps of herbs in the ash-alder stands was significantly higher than in the primaeval oak-hornbeam ($p < 0.05$, chi-square test) or in coniferous stands ($p < 0.05$, chi-square test). The proportion of nests "in bushes" in the managed oak-hornbeam stands was significantly higher ($p < 0.01$, chi-square test) than that in the primaeval oak-hornbeam stands

Tabela 9. Miejsca umieszczenia gniazd pierwiosnka w zależności od siedliska

Udział gniazd usytuowanych w kępach roślinności zielonej w łęgu był istotnie wyższy niż w pierwotnym grądzie (test chi-kwadrat, $p < 0,05$) czy borze (test chi-kwadrat, $p < 0,05$). Udział gniazd umieszczonych „w krzewach” w grądzie zagospodarowanym był istotnie wyższy niż w grądzie pierwotnym (test chi-kwadrat, $p < 0,01$)

Nest-site Położenie gniazda		Habitat Siedlisko				
		Ash-alder Łęg Primaeval Pierwotny	Oak-hornbeam Grąd		Coniferous Bór	
			Primaeval Pierwotny	Managed Zagospoda- rowany	Primaeval Pierwotny	Managed Zagospoda- rowany
On the ground Na ziemi	In lying branches W leżących gałę- ziach	3 (100.0)	5 (83.3)	1 (6.2)	3 (60.0)	14 (31.8)
	Other place Inne miejsce	— —	1 (16.7)	15 (93.8)	2 (40.0)	30 (68.2)
Above the ground Nad ziemią	In lying branches W leżących gałę- ziach	38 (45.2)	20 (74.1)	15 (36.6)	7 (70.0)	19 (63.3)
	In "bush" W „krzaku”	14 (16.7)	1 (3.7)	18 (43.9)	2 (20.0)	8 (26.7)
	In clump of her- baceous vegeta- tion W kępie roślin- ności zielonej	31 (36.9)	5 (18.6)	— —	— —	— —
	Other place Inne miejsce	1 (1.2)	1 (3.7)	8 (19.5)	1 (10.0)	3 (10.0)

which they prevailed. This habitat had a very poorly developed herb layer and only very few fallen spruces in which to hide nests.

Early nests of the chiffchaff, built when plants were still not developed, were placed lower than the later ones, which were constructed after a full development of the vegetation (Table 10). Lower placement of early nests was further confirmed by a comparison of the localization of successive nests of the same females (Fig. 12), in every case the second nest of the female was situated higher than the first.

Białowieża chiffchaffs placed their nests at a height similar to that recorded elsewhere, though the nest substrates chosen by the Białowieża birds differed in details from those found elsewhere (STEINFATT 1938, TREUNFELS 1938, MILDEN-

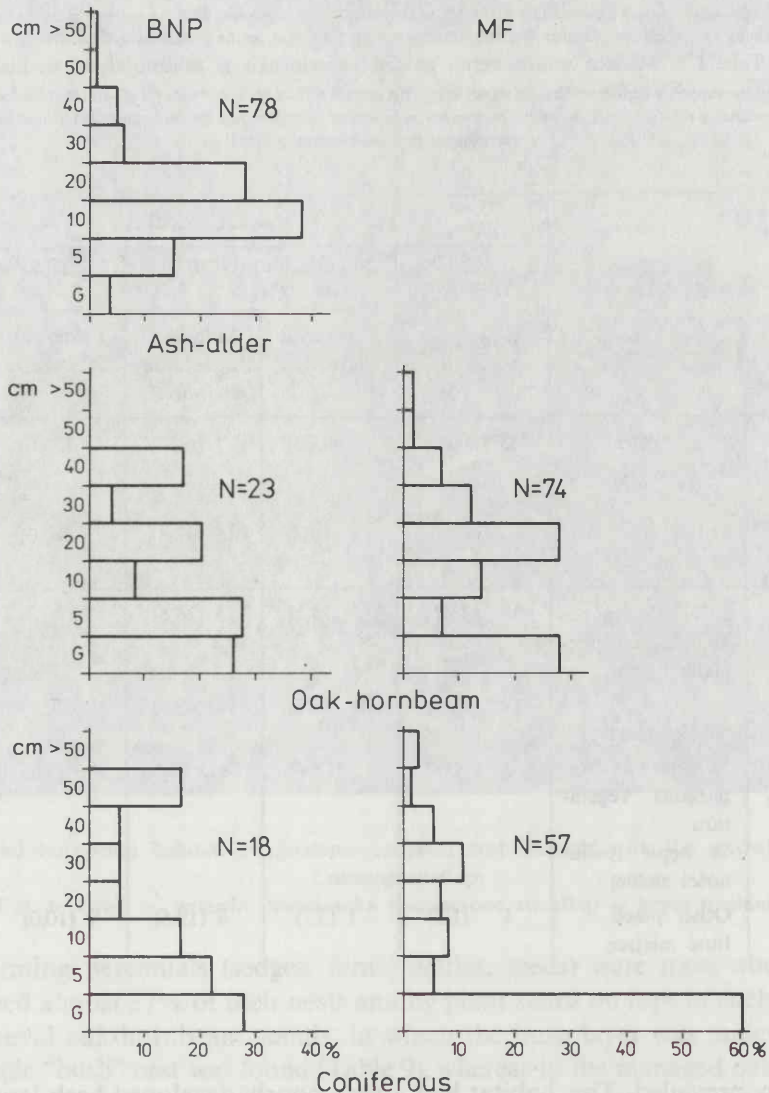


Fig. 11. Percentage distribution of *Phylloscopus collybita* nest-heights in different habitats of the Białowieża Forest

Pooled data from all years. BNP – primaeval stands, MF – managed stands, G – nests on the ground. Proportion of ground nests varied significantly between different habitats: in managed stands – oak-hornbeam vs. coniferous ($p < 0.001$), in primaeval stands – ash-alder vs. coniferous ($p < 0.01$), ash-alder vs. oak-hornbeam ($p < 0.01$), as well as between primaeval and managed coniferous stands ($p < 0.02$).

Probabilities shown refer to chi-square test. The other differences were not significant

Ryc. 11. Wysokość umieszczenia gniazd pierwiosnka w różnych siedliskach Puszczy

Zsumowano dane ze wszystkich lat. BNP las pierwotny, MF – las zagospodarowany, G – gniazda na ziemi. Udział gniazd zakładanych na ziemi różnił się istotnie między siedliskami: w lesie zagospodarowanym grądy-bory ($p < 0.001$), w lesie pierwotnym łęgi-bory ($p < 0.01$), łęgi-grądy ($p < 0.01$), jak również borami pierwotnymi i zagospodarowanymi ($p < 0.02$). Pozostałe różnice były nieistotne. Wszystkie prawdopodobieństwa odnoszą się do testu chi-kwadrat

Table 10. Percentage of *Phylloscopus collybita* nests in the Białowieża Forest built on, the ground in relation to the period of egg-laying and the habitat

In the case of the ash-alder habitat the percentage of nests situated up to 10 cm high is shown in parentheses. The difference between nest-height of first and later nests was significant in the managed coniferous stands ($p < 0.02$, chi-square test) and in the ash-alder stands ($p < 0.01$, chi-square test, calculated for data in parentheses)

Tabela 10. Udział procentowy gniazd zakładanych przez białowieskie pierwiosnki na ziemi, w zależności od pory składania jaj i siedliska

W przypadku łęgów przedstawiono również udział gniazd zakładanych do wysokości 10 cm (wartości w nawiasach). Różnica między udziałem gniazd naziemnych wśród wczesnych i późnych łęgów była istotna w borze zagospodarowanym (test chi-kwadrat, $p < 0,02$) i w łęgu (test chi-kwadrat, $p < 0,01$, dla wartości w nawiasach)

Habitat Siedlisko		First clutches (commencement of egg-laying up to 25 V) Pierwsze łęgi (składanie jaj roz- poczęło się od 25 V)		Replacement and second clutches (commencement of egg-laying af- ter 25 V) Powtarzane i drugie łęgi (składa- nie jaj rozpoczęło się po 25 V)	
		N	i	N	i
Coniferous Bór	Primaeval Pierwotny	16	31.2	2	0.0
	Managed Zagospoda- rowany	55	67.3	19	36.8
Oak-hornbeam Grąd	Primaeval Pierwotny	19	31.6	4	0.0
	Managed Zagospoda- rowany	42	33.3	15	13.3
Ash-alder Łęg	Primaeval Pierwotny	65	4.6 (64.6)	13	0.0 (23.1)

BERGER 1940, GEISSBÜHLER 1954, GLUTZ 1964, von HAARTMAN 1969, SCHÖNFELD 1978, HAVLIN 1983, MALTČEVSKIY and PUKINSKIY 1983). The tendency towards a higher localization of nests in wetter habitats and later in the season recorded in our material fits well the findings of GEISSBÜHLER (1954) and SCHÖNFELD (1978). Data of the former confirm also our finding that the chiffchaff prefers to orient nest entrances in the direction of the nearest open space.

Timing of egg-laying, length of breeding season

The start of egg-laying was recorded directly only in a small number of nests. For the remaining nests first egg dates were estimated by "counting-back". The calculations were based on the following assumptions (GEISSBÜHLER 1954, HOMAN 1960, SCHÖNFELD 1978): females lay one egg a day, incubation starts after the

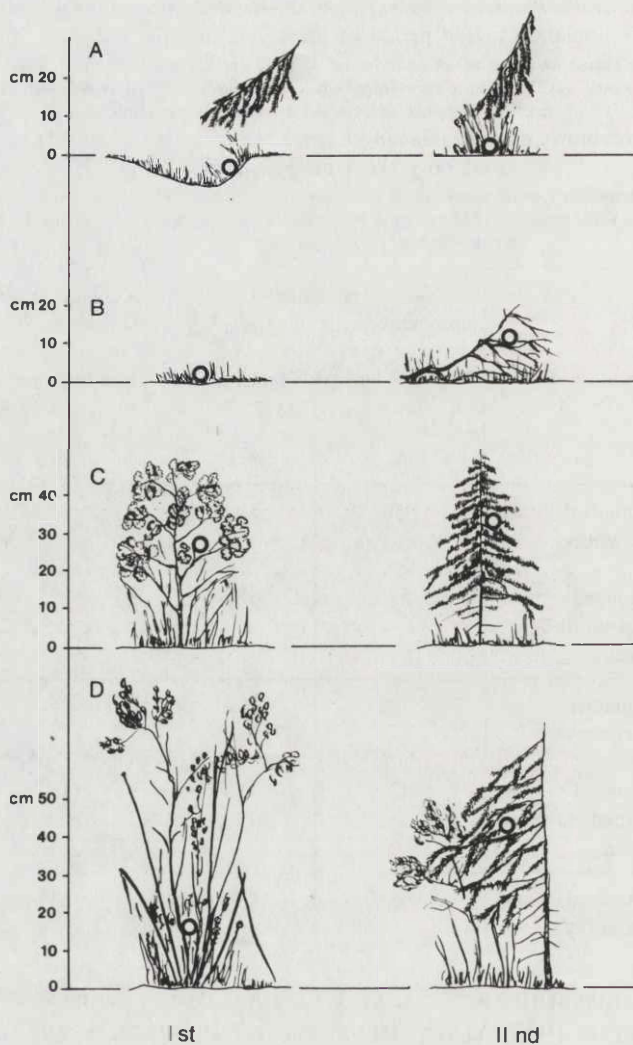


Fig. 12. Nest-sites chosen by the colour-ringed *Phylloscopus collybita* females during their first and second breeding attempts

The second nests were places structurally similar to those of first nests, but in every case they were placed slightly higher than the first ones. A – female “14”, B – female “20”, C – female “40”. Data from managed forest: A, B – coniferous stands 1980, C – oak-hornbeam stands 1980, D – oak-hornbeam stands 1981

Ryc. 12. Położenie pierwszych i drugich gniazd kolorowo obrączkowanych samic pierwiosnka

W okresie drugich lęgów gniazda były umieszczane w miejscach o podobnej strukturze do miejsc, w których znajdowały się pierwsze gniazda, lecz w każdym przypadku były one umieszczone nieco wyżej. A – samica “14”, B – samica “20”, C – samica “22”, D – samica “40”.

Dane z zagospodarowanej części Puszczy: A, B – bór w r. 1980, C – grąd w r. 1980, D – grąd w r. 1981

laying of the last egg and lasts for 15 days (*cf* p. 44), the nestling period lasting 15 days.

Egg-laying commenced between May 2 (1983) and July 6–7 (1979), thus the egg laying period at the Białowieża Forest lasted slightly more than two months. The

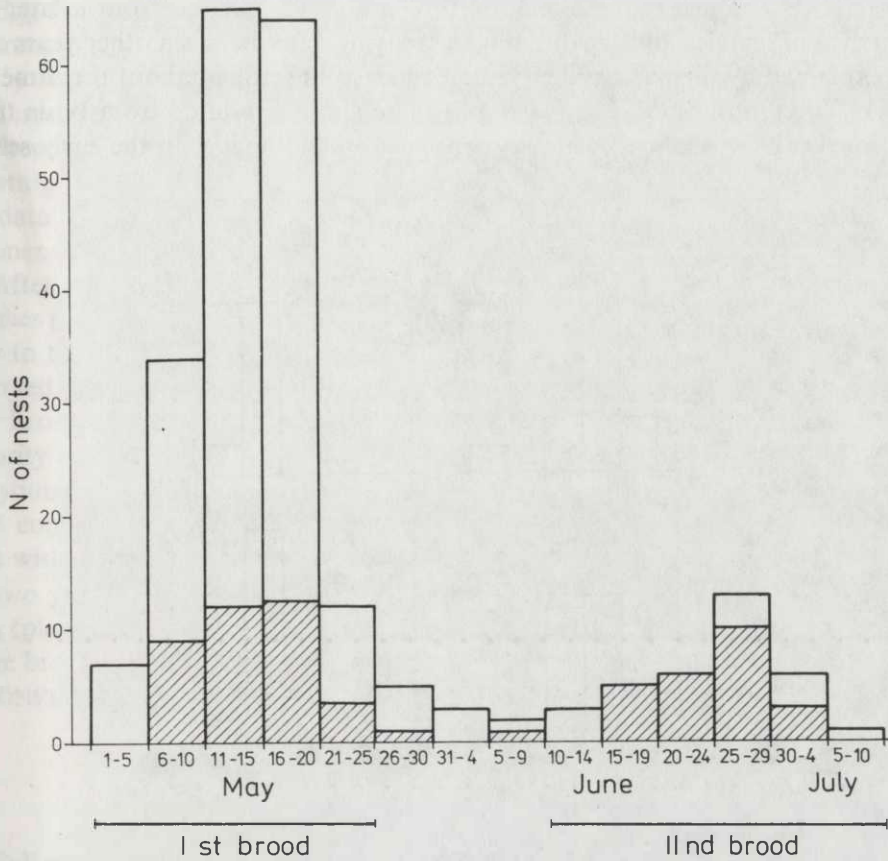


Fig. 13. Distribution of dates of egg-laying commencement by *Phylloscopus collybita* at the Białowieża Forest expressed as number of clutches commenced in consecutive five-days periods

White bars — all data, dashed bars — data from years and plots in which observations were carried out during the whole breeding season (plot K and C, 1978; managed plots, 1980). As young from the earliest nests did not fledge before June 3, only clutches commenced after ca June 10 could be the real second clutches, laid after successful rearing of the first ones

Ryc. 13. Rozpoczynanie składania jaj przez pierwiosnka w Puszczy Białowieżskiej w kolejnych pentadach Białe słupki — całość materiału, słupki kreskowane — dane z tych lat i powierzchni na których obserwacje prowadzono przez cały sezon lęgowy (pow. K i C, 1978, powierzchnie w lesie zagospodarowanym, 1980). Ponieważ młode z najwcześniejszych gniazd nie opuszczały ich wcześniej niż 3 czerwca, tak więc dopiero lęgi rozpoczynane po 10 czerwca mogły być rzeczywistymi drugimi lęgami — rozpoczynanymi przez samice po pomyślnym wylocie młodych z ich pierwszych gniazd

majority of females started their first clutches between May 6 and 20 (Fig. 13). In comparison with other areas the peak of egg-laying at the Forest was 10–20 days later than in Switzerland or in the GDR (GEISSBÜHLER 1954, SCHÖNFELD 1978) and 10–20 days earlier than in the Leningrad area and in Finland (MALTCEVSKIY and PUKINSKIY 1983, von HAARTMAN 1969).

Dates of commencement of egg-laying in first clutches varied greatly between seasons. In early springs (1977, 1983) — 67% of females began to lay eggs before May 11, whereas in late springs (1981, 1982) none of the females started before that

date (Fig. 14). The delayed breeding of 1981 and 1982 resulted from a later than usual arrival of females, but the differences in laying dates between other years could not be explained by this factor: then females started to settle at about the same time (*cf* p. 44). The retardation of egg-laying in these springs resulted from birds taking breaks longer than usual between nest construction and laying. In the early seasons

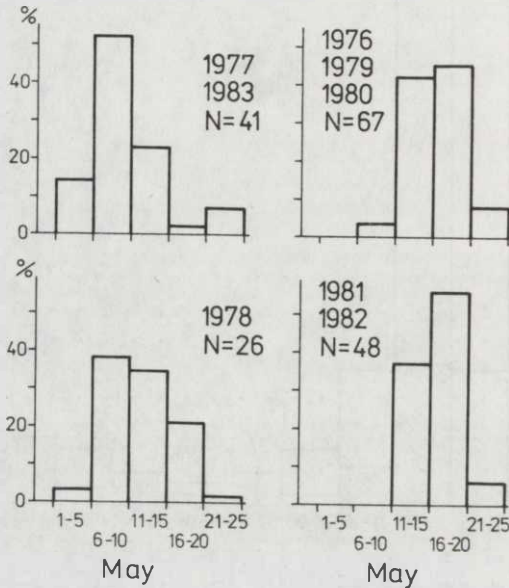


Fig. 14. Percentage distribution of dates of laying commencement in first clutches (= clutches commenced before 25 May) of *Phylloscopus collybita* in different years at the Białowieża Forest

Proportion of clutches begun before May 11 in 1977, 1983 was significantly higher than in other years ($p < 0.05$), the same was true in comparison of 1978 with 1976, 1979, 1980 as well as with 1981 and 1982 ($p < 0.01$). The differences between proportion of early clutches (commenced before May 16) in 1976, 1979, 1980 and 1981, 1982 was not significant. Probabilities shown refer to chi-square test

Ryc. 14. Rozpoczązanie składania jaj w pierwszych lęgach (rozpoczęzanych przed 25 maja) u pierwiosnka w różnych latach w Puszczy Białowieżskiej

Proporcja lęgów rozpoczęzanych przed 11 maja w latach 1977 i 1983 była istotnie wyższa niż w innych latach ($p < 0,05$). Podobny wynik uzyskano porównując rok 1978 z latami 1976, 1979, 1980 oraz z 1981 i 1982 ($p < 0,01$). Różnice udziału lęgów wczesnych (rozpoczęzanych przed 16 maja) między latami 1976, 1979, 1980 a 1981 i 1982 nie były istotne. Prawdopodobieństwa odnoszą się do testu chi-kwadrat

(1977, 1978, 1983), the time that elapsed between the beginning of nest construction by the earliest birds and the start of egg-laying in the earliest clutches was 6–7 days, but in 1976, 1979 and 1980 it was 11, 15 and 9 days, respectively. These longer intervals resulted probably from low temperatures which then prevailed at the beginning of May. The mean minimum daily temperatures during the first ten days of May in 1976, 1979 and 1980 ranged from 1.7 to 2.9°C, whereas in the other years they varied between 4.9 and 9.1°C.

Egg-laying commenced at the same time in all the habitats, despite the differences in the timing of vegetation development which, according to FALIŃSKA (1975) was delayed five days in the ash-alder stands and fourteen days in the coniferous stands, when compared with the oak-hornbeam habitat.

Breeding was well synchronised, the majority of females laid their clutches within a fortnight of the first one (Fig. 13). This period was even shorter when we look at the data from single seasons separately, the majority of females within the plots commence then egg-laying during just 7–10 days.

After the period of intensive egg-laying, which lasted until about 25 May, new clutches (most probably replacements) appeared with low frequency from the end of May to the first half of June. In the second half of June another peak of laying was observed (Fig. 13). This was due partly to the females re-laying after destruction of their broods and partially to the females starting their second clutches (*cf* p. 44). The majority of the young from these late nests fledged between 25 July–1 August, and the young from the latest one on 6 August (1979).

A comparison of the number of females which laid their first clutches within the plots with that of females breeding in them at the end of June–July was carried out for two years in which the observations lasted long enough and revealed that only 64% (plots K and C, 1978) and 73% (managed plots, 1980) of females participated in the breeding at that time. These figures are in good agreement with the results of SCHÖNFELD (1978) from the GDR.

Clutch size

Full clutches of the chiffchaff in the Białowieża Forest contained 4–7 eggs. Over 80% of first clutches comprised six eggs, while replacement and second clutches were smaller, usually with five eggs (Table 11). As follows from the Table there were no significant differences between the size of the first clutches laid in the primaeval and that in the managed stands of the same habitat type. Inter-habitat comparisons revealed, however, that clutches laid in densely populated swampy stands were significantly larger than those laid in low-density coniferous stands (*cf* Tables 3 and 11).

The mean size of clutches changed over a season. It was lower at the very beginning of the laying period, reached its peak after five (coniferous) or 10–15 (deciduous stands) days to decline later on (Table 12). A similar seasonal decline of the chiffchaff clutch size was observed also elsewhere (GEISSBÜHLER 1954, GLUTZ 1964, ALEKNONIS 1976, SCHÖNFELD 1978, HAVLIN 1983, MALTCHEVSKIY and PUKINSKIY 1983).

The mean clutch size of Białowieża birds was slightly higher than that in the regions further to the South, but similar to that found in places situated farther to the North (Table 13).

Table 11. Distribution of clutch sizes of *Phylloscopus collybita* in Białowieża Forest in relation to the habitat and the period of egg-laying

The differences between the sizes of first clutches in the ash-alder and coniferous ($p < 0.05$, t test) and between the size of first and later clutches in all habitats ($p < 0.05$, t test) were significant

Tabela 11. Wielkość zniesienia pierwszaka w Puszczy Białowieżskiej w zależności od siedliska i pory składania jaj

Różnice między wielkością pierwszych zniesień w łęgu i borze były istotne (test t , $p < 0,05$), podobnie jak między wielkością pierwszych i późniejszych zniesień we wszystkich siedliskach (test t , $p < 0,05$)

	Habitat Siedlisko	Clutch size Wielkość zniesienia				Number of nests Liczba gniazd	Mean clutch size Przeciętna wiel- kość zniesienia	
		4	5	6	7 eggs jaj		\bar{x}	(S.D.)
First clutches (commenced up to 25 V)	Managed Zagospoda- rowany	1	3	22	1	27	5.85	(0.53)
	Oak- hornbeam Grąd Primaeval Pierwotny	—	2	15	1	18	5.94	(0.42)
	Total – Łącznie	1	5	37	2	45	5.89	(0.49)
Pierwsze zniesienie (rozpoczynane do 25 V włą- cznie)	Managed Zagospoda- rowany	1	8	19	2	30	5.73	(0.64)
	Coniferous Bór Primaeval Pierwotny	1	—	4	—	5	5.60	—
	Total – Łącznie	2	8	23	2	35	5.71	(0.67)
	Ash-alder Łęg Primaeval Pierwotny	—	4	48	2	54	5.96	(0.33)
	All habitats Wszystkie siedliska	3	17	108	6	134	5.87	(0.50)
Repeated and se- cond clutches (commenced after 25 V)								
Powtarzane i dru- gie zniesienia (rozpoczynane po 25 V)	All habitats Wszystkie siedliska	2	5	3	1	11	5.27	(0.90)
All clutches Wszystkie znie- sienia		5	22	111	7	145	5.83	(0.56)

Table 12. Clutch size of *Phylloscopus collybita* in relation to the date of egg-laying commencement (Pooled data from all types of stands)

In order to compensate for inter-year differences in the onset of laying, the date of commencement of egg-laying in the earliest nest of the season has been treated as the starting point, thus in 1977, 1978 and 1983 clutches commenced 1-5 May; in 1976, 1979 and 1980 clutches commenced 6-10 May; and in 1981 and 1982 clutches commenced 11-15 May were included into the first five-day period. There were significant differences between the size of clutches commenced in the second and third five-day periods in the coniferous habitat ($p < 0.02$, t test) and, in the deciduous habitats, between the size of clutches commenced during first and second five day periods ($p = 0.01$, t test)

Tabela 12. Wielkość zniesienia pierwiosnka w zależności od pory składania jaj (Dane połączone dla siedlisk pierwotnych i zagospodarowanych)

Dla skompensowania różnic między latami w porze rozpoczęcia zniesienia datę złożenia pierwszego jaja w najwcześniejszym w danym sezonie gnieździe traktowano jako punkt wyjściowy. I tak do zniesień rozpoczynanych w pierwszej pentadzie włączono zniesienia, w których składanie jaj rozpoczęło się 1-5 V (1977, 1978 i 1983), 6-10 V (1976, 1979, 1980) lub 11-15 V (1981, 1982). Stwierdzono istotne różnice między przeciętną wielkością zniesień rozpoczynanych w borach w drugiej i trzeciej pentadzie (test t , $p < 0,02$), a w siedliskach liściastych między przeciętną wielkością zniesień rozpoczynanych w pierwszej i drugiej pentadzie okresu składania jaj (test t , $p = 0,01$)

Habitat Siedlisko	Consecutive five-days of lay- ing period Kolejne pentady okresu składania jaj	Clutch size Wielkość zniesienia				Number of nests Liczba gniazd	Mean clutch size Przeciętna wielkość zniesienia	
		4	5	6	7 eggs jaj		\bar{x}	(S.D.)
Coniferous Bór	I	—	3	7	1	11	5.82	(0.60)
	II	—	1	10	1	12	6.0	(0.43)
	III	2	3	4	—	9	5.22	(0.83)
	IV-V	—	1	1	—	2	5.5	—
	After 25 V Po 25 V	1	1	—	—	2	4.5	—
Oak- -hornbeam + Ash- -alder	I	—	1	10	—	11	5.91	(0.30)
	II	1	6	48	1	56	5.89	(0.43)
	III	—	—	17	1	18	6.06	(0.26)
	IV	—	—	6	1	7	6.14	(0.38)
	V	—	1	2	—	3	5.71	—
Grąd + łęg	After 25 V Po 25 V	1	4	3	1	9	5.44	(0.88)

Breeding losses

Partial nesting failures

As follows from Table 14, the number of eggs hatched was on the average smaller by 0.44 egg (7.5%) than the number of eggs laid. Partial egg losses were higher in bigger clutches, but in spite of this, the number of eggs hatched in nests with 6–7 eggs was higher than their number in nests with fewer eggs. The most important reason for hatching failure was some physiological defects, as unfertilized eggs or eggs containing dead embryos were found in 64.6% of the nests in which not all eggs hatched. In two cases single eggs were found in the vicinity of nests, they were probably incidentally evicted by birds leaving nests. Only about 35% of partial

Table. 13. Geographical variation of mean clutch size in *Phylloscopus collybita*
 Tabela 13. Zmienność geograficzna przeciętnej wielkości zniesienia u pierwiosnka

Author Autor	Region	First clutches Pierwsze zniesienia		All season data Dane z całego sezonu	
		N	\bar{x}	N	\bar{x}
GEISSBÜHLER (1954)	Switzerland Szwajcaria	34	5.7	49	5.4
GLUTZ (1964)	Switzerland Szwajcaria	151	5.6*	166	5.6
MILDENBERGER (1940)	Rheinland, FRG Nadrenia, RFN	—	—	191	5.5
HAVLIN (1983)	Czechoslovakia Czechosłowacja	92	5.5*	117	5.4
SHÖNFELD (1978)	Halle region, GDR okolice Halle, NRD	170	5.8	244	5.4
This study— — niniejsza praca	Białowieża Forest Puszcza Białowiecka	134	5.9	145	5.8
ALEKNONIS (1976)	Lithuania Litwa	—	—	45	5.8
VON HAARTMAN (1969) +	S Finland	—	—	31	6.0
TIAINEN <i>et al.</i> (1983)	Pd Finlandia	—	—	—	—

* Clutches commenced in April and May.
 Zniesienia składane w kwietniu i maju.

egg losses could be attributed to predators. In a few cases gradual disappearance of single eggs and nestlings on consecutive days was observed. This could be due to predation by small mammals.

Partial losses of nestlings were quite negligible. Only two nests were partially robbed just before fledging, and in two other ones single young disappeared. No case of nestling starvation was recorded.

Total nesting failures

All nests from which at least one young fledged were treated as successful, while those from which whole clutches or broods < 11 days old disappeared — as predated. In many instances predation was confirmed by the appearance of the nest and/or by the presence of egg-shell fragments or feathers of young near it.

The most important single factor responsible for total nesting failures was predation. It caused almost all the losses of broods and almost 40% of losses in clutches. In general it was responsible for almost 70% of losses (Table 15). The predators which could be responsible for the loss of the chiffchaff nests were: various species of insectivores and small rodents, *Sciurus vulgaris*, *Martes martes*, *Mustela*

Table 14. Relationship between clutch size and number of eggs hatched in *Phylloscopus collybita* in the Białowieża Forest

Partial losses of eggs in clutches containing 6-7 eggs were significantly higher ($p < 0.05$, chi-square test) than in clutches containing 3-5 eggs

Tabela 14. Zależność między wielkością zniesienia a liczbą wykłutych piskląt u pierwiosnków w Puszczy Białowiejskiej

Straty częściowe w zniesieniach zawierających 6-7 jaj były istotnie wyższe niż w zniesieniach zawierających 3-5 jaj (test chi-kwadrat, $p < 0,05$)

		Number of eggs laid Liczba złożonych jaj			Total Łącznie
		3-4	5	6-7	
Number of eggs hatched	The same Taka sama	76.2%	80.0%	61.9%	67.6%
Liczba wykłutych piskląt	Smaller by: 1 Mniejsza o:	19.0	13.3	28.9	24.3
	Smaller by: 2-3 Mniejsza o:	4.8	6.7	9.3	8.1
Total number of nests Łączna liczba gniazd		21	30	97	148
Mean difference between clutch and brood size Przeciętna różnica między wielkością zniesienia a liczbą wykłutych piskląt		0.29	0.27	0.53	0.44

putorius, *Vulpes vulpes*, *Nyctereutes procyonoides*, *Meles meles*, *Sus scrofa*, *Strix aluco*, *Glaucidium passerinum*, *Buteo buteo*, *Garrulus glandarius*, *Natrix natrix* and *Vipera berus*. The majority of these species were recorded both in the primaeval and the managed stands.

Nest desertion during egg-laying and incubation constituted about 15% (25% if we include also nests from the category deserted/predated) of losses (Table 15). Nineteen cases of desertion of unfinished nests were also observed. These cases, however, are not included in the Table. Desertion was an especially important factor of clutch mortality in the managed stands, where it caused 44% of losses, whereas in the primaeval stands the proportion of deserted clutches (23%) was significantly lower – Table 15.

Other mortality factors had negligible effect, they jointly caused about 5% of the loss.

The amount of losses was calculated separately for two periods of the nesting cycle: pre-hatching (egg-laying and incubation) and post-hatching. In order to avoid an underestimation of losses, only the nests found during building, egg-laying and first days of incubation were used in the calculation of pre-hatching losses. For the

Table 15. Causes of nesting failures in *Phylloscopus collybita* in relation to the type of stands and the stage of nestling cycle

Cases when nest construction was finished but eggs not found on later visits, are included into the desertion/predation category, as it is not known whether these nests had been deserted before egg-laying or whether they were predated at the egg-laying stage. Five cases of nest destruction that occurred roughly at the hatching time, recorded in the primaeval stands, are included in the nests with young category. Predation was a more important cause of brood failures than the clutch failures ($p < 0.001$, chi-square test). Primaeval and managed stands differed significantly in the frequency of predated and deserted clutches ($p < 0.02$, chi-square test)

Tabela 15. Przyczyny strat w lęgach pierwiosnka w zależności od siedliska i stadium cyklu gniazdowego
Przypadki, w których budowa gniazda została zakończona, a nie stwierdzono w nim jaj w czasie kolejnych kontroli, zaliczono do kategorii „porzucenie/drapieżnictwo”, gdyż nie ma tu pewności, czy gniazdo zostało porzucone przed złożeniem jaj, czy też jaja zostały zrabowane w trakcie ich składania. Stwierdzone w lesie pierwotnym pięć przypadków zniszczeń gniazd w okresie klucia wliczono do kategorii „gniazda z pisklętami”. Drapieżnictwo było ważniejszą przyczyną strat w gniazdach z pisklętami niż w gniazdach z jajami (test chi-kwadrat, $p < 0,001$). Między lasem pierwotnym a zagospodarowanym stwierdzono istotne różnice we względnym znaczeniu drapieżnictwa i porzucenia jako przyczyn strat gniazd z jajami (test chi-kwadrat, $p < 0,02$)

Cause of failure Przyczyna zniszczenia	Nests with eggs Gniazda z jajami			Nests with young Gniazda z pisklętami			Overall Ogółem
	Primaeval forest Las pierwotny %	Managed forest Las zagospodarowany	Total Łącznie	Primaeval forest Las pierwotny %	Managed forest Las zagospodarowany	Total Łącznie	
Desertion Porzucenie	22.9	44.0	31.7	—	—	—	15.2
Desertion/predation Porzucenie/drapieżnictwo	17.1	28.0	21.7	—	—	—	10.4
Predation Drapieżnictwo	51.4	20.0	38.3	90.0	100.0	95.4	68.0
Trampling by animals Zdeptanie przez zwierzyne	2.9	4.0	3.3	3.3	—	1.5	2.4
Hailstorm Gradobicie	2.9	—	1.7	6.7	—	3.1	2.4
Parasitism by <i>Cuculus canorus</i> Pasożytnictwo kukułki	—	4.0	1.7	—	—	—	0.8
Dead female on nest Martwa samica na gnieździe	2.9	—	1.7	—	—	—	0.8
Number of nests destroyed (100%) Liczba zniszczonych gniazd	35	25	60	30	35	65	125

calculation of post-hatching losses only those nests that were found before hatching were used. The few nests which were destroyed at hatching were treated as destroyed in the post-hatching period.

The amount of pre-hatching losses varied only slightly between years, therefore data from all seasons have been pooled (Table 16). Losses in the ash-alder stands and in the managed habitats — about 30% (parenthesed data) were lower than in

Table 16. Total pre-hatching losses of *Phylloscopus collybita* nests in different habitats

Non-parenthesed values refer to nests in which egg-laying was recorded. Parenthesed values include also nests in which eggs were never found, though their construction had been finished (cf Table 15, category predation/desertion). They may have been predated at the egg-laying stage. The amount of losses caused by predation in the managed stands was significantly lower than in the equivalent primaeval stands (non-parenthesed data - $p < 0.01$, parenthesed data - $p < 0.02$, chi-square test)

Tabela 16. Całkowite zniszczenia lęgów pierwiosnka w okresie do wyklucia piskląt, w różnych siedliskach

Wartości bez nawiasów odnoszą się do gniazd, w których stwierdzono składanie jaj. Wartości w nawiasach obejmują również gniazda, w których jaj nigdy nie stwierdzono, chociaż ich budowa została ukończona. Jaja w tych gniazdach mogły zostać zrabowane w czasie składania (por. tab. 15, kategoria „porzucenie/drapieżnictwo”). Wielkość strat powodowanych przez drapieżniki w lesie zagospodarowanym była istotnie niższa niż w odpowiednich siedliskach lasu pierwotnego (test chi-kwadrat, $p < 0.01$ dla danych bez nawiasów i $p < 0.02$ dla danych w nawiasach)

Forest type Typ lasu	Habitat Siedlisko	Number of nests Liczba gniazd	% of losses caused by predation % strat spo- wodowanych przez drapie- znictwo	% of losses caused by other factors % strat spo- wodowa- nych innymi czynnikami	Total losses % Ogółem straty
Managed Zagospodarowany	Oak-hornbeam Grąd	30 (35)	6.7 (20.0)	13.3	20.0 (31.4)
	Coniferous Bór	36 (40)	2.8 (12.5)	22.2	25.0 (32.5)
	Total - Łącznie	66 (75)	4.5 (16.0)	18.2	22.7 (32.0)
Primaeval Pierwotny	Oak-hornbeam Grąd	22 (25)	18.2 (32.0)	9.1	27.3 (40.0)
	Coniferous Bór	11 -	36.4 -	9.1	45.4 -
	Total - Łącznie	33 (36)	24.2 (33.3)	9.1	33.3 (41.7)
	Ash-alder Łęg	67 (68)	13.4 (14.7)	14.9	28.3 (29.4)

the primaeval oak-hornbeam and coniferous stands, where about 40% of nests were lost. This difference, however, was not significant. The proportion of nests destroyed by predators in the managed stands was significantly, two-three times lower than in the equivalent primaeval stands.

Post-hatching losses varied significantly between years. Losses in the managed stands were significantly lower in 1982 than in the remaining years. This was also visible in the ash-alder habitat, though the difference was not significant (Table 17). The very low breeding losses in 1982 resulted probably from the switching of predators to foraging on leaf-eating caterpillars. Foraging of potentially important predators such as *Garrulus glandarius* and *Sciurus vulgaris* on caterpillars was frequently observed in the years when they were abundant, and 1982 was the season of the highest abundance of caterpillars ever recorded (TOMIAŁOJĆ *et al.* 1984 and

Table 17. Total post-hatching failures of *Phylloscopus collybita* nests in relation to year and habitat
 Almost all losses at this stage were due to predation (cf Table 15). Significant differences: managed stands, 1982 vs. other years – $p < 0.01$,
 oak-hornbeam primaeval stands vs. ash-alder stands (other years) – $p < 0.05$, chi-square test

Tabela 17. Całkowite zniszczenia lęgów pierwiosnka zawierających pisklęta, w różnych latach i siedliskach
 Niemal wszystkie straty w tym stadium były wynikiem drapieżnictwa (por. tab. 15). Istotne różnice: las zagospodarowany, 1982. w stosunku
 do innych lat – $p < 0.01$, pierwotny grąd w stosunku do łęgu (pozostałe lata) – $p < 0.05$, test chi-kwadrat

Forest Las	Habitat Siedlisko	Year Rok	Number of nests Liczba gniazd	% of nests lost % zniszczonych gniazd
Managed Zagospodarowany	Oak-hornbeam Grąd	1982	8	—
		Other years	16	43.7
		Pozostałe lata		
		All Wszystkie	24	29.2
	Coniferous Bór	1982	10	10.0
		Other years	17	41.2
Pozostałe lata				
All Wszystkie		27	29.6	
Primaeval Pierwotny	Ash-alder Łęg	1979	9	55.6
		1982	4	—
		Other years	33	27.3
		Pozostałe lata		
		All Wszystkie	46	30.4
	Oak-hornbeam Grąd	All Wszystkie	15	60.0
		Coniferous Bór	All Wszystkie	5

unpubl.). On the other hand, in the very dry spring of 1979, when in the ash-alder stands, the usually swampy ground dessicated and predators had easy access to nests, the losses were twice as high as normally.

By excluding these “unusual” years from comparisons one would find that the post-hatching losses were the lowest in the coniferous stands (though this could be by chance due to the small sample) and in the ash-alder forest (20–27%), intermediate in both types of managed stands (41–43%), and the highest in the oak-hornbeam primaeval forest – 60%.

Nests with young were two-three times more frequently predated than nests with eggs (cf. Table 16 and 17). If we take into account the fact that the pre-hatching period was about twice as long as the post-hatching stage (20 and 10 days

respectively), then it can be concluded that the risk of a nest with young being predated was four-six times higher than the risk of nest with eggs. This result is in variance with the findings of other students (GEISSBÜHLER 1954, HOMAN 1960, SCHÖNFELD 1978), who found that the pre-hatching losses were higher (in absolute values) than the post-hatching ones.

Since sample sizes were not constant for different periods of the nesting cycle, the overall rate of nest losses was estimated using the following formula:

$$\text{total nesting losses} = (1 - a \times b) \times 100\%,$$

where a – fraction of nests with clutches from which at least one egg hatched, and b – fraction of nests with nestlings from which at least one young fledged. Calculations were carried out by substituting both parenthesized and non-parenthesized data (*cf* Table 16) for a and by substituting data from “normal” years for b . The overall loss rate estimated that way was the lowest in the ash-alder habitat (47.9–48.7%), intermediate in the managed oak-hornbeam (55–61.4%) and coniferous (59.9–60.3%) stands and in the primaeval coniferous stands (56.3%), and the highest in the primaeval oak-hornbeam stands (70.9–76.0%). Nesting losses in other areas were usually lower than in the Białowieża Forest, they ranged from 40 to 48% (von TREUNFELS 1938, GEISSBÜHLER 1954, HOMAN 1960, SCHÖNFELD 1978).

Production of young

Due to the usually slightly male-biased sex ratio (*cf* Table 7), the number of fledglings produced in the first broods per a territorial male was usually slightly lower than the number of young per a breeding female (Table 18). The differences in the production of young in various habitats paralleled those of nesting success; production was the highest in the ash-alder stands (3.3 young/male), intermediate in both the types of managed stands (2.1–2.4 young/male) and the lowest in the primaeval oak-hornbeam stands (1.05 young/male). Due to the inter-year variation in nest loss rate, the production varied between seasons. It ranged 1.5–5.0 fledglings/male in the ash-alder stands, 1.1–3.0 in the managed oak-hornbeam stands and 2.0–3.0 in the managed coniferous stands.

In order to estimate the yearly production rate one should add to the figures above also the production of young from the second broods. Assuming that about 70% of females participated in the second broods (*cf* p. 44), that the nest loss rate in them was similar to that of the first broods, and taking into account the smaller size of the second clutches (*cf* Table 11), one would arrive at estimates of the second brood production, and, by adding them to the values for the first broods – at the values of yearly production. They are as follows (expressed as fledglings/male): primaeval ash-alder stands – 5.5, managed coniferous stands – 3.9, managed oak-hornbeam stands – 3.3, and primaeval oak-hornbeam stands – 1.7.

Table 18. Mean nestling success and production of *Phylloscopus collybita* young within the plots studied. Data for the first broods. Values of success for males and females were calculated by dividing the number of successful nests respectively by the number of territorial males and females nesting within the plots (cf Table 7). Production (p) was estimated according to the following formula: $p = a \times (b - c)$; where a – nesting success of males or females, b – clutch size in first breeding attempts (cf Table 11) and c – mean partial losses of eggs (cf Table 14). Nesting success of males in the ash-alder habitat was significantly higher than in the primaeval ($p < 0.02$, chi-square test) or managed ($p < 0.05$, chi-square test) oak-hornbeam stands. The success of males in the managed coniferous stands was higher ($p < 0.02$, chi-square test) than in the primaeval oak-hornbeam stands.

Tabela 18. Przeciętna udatność lęgów i produkcja młodych pierwiosnka na szczegółowo badanych powierzchniach

Dane dla pierwszych lęgów. Wartości dla samców i samic obliczono dzieląc liczby zakończonych pomyślnie gniazd przez – odpowiednio – liczbę terytorialnych samców i samic gnieźdzących się na powierzchniach (por. tab. 7). Produkcję (p) obliczono według następującego wzoru: $p = a \times (b - c)$; gdzie a – udatność lęgów samców lub samic, b – wielkość zniesienia w pierwszym lęgu (por. tab. 11) i c – przeciętne częściowe straty jaj (por. tab. 14). Udatność lęgów samców w lęgu była istotnie wyższa niż w grądzie zarówno pierwotnym (test chi-kwadrat, $p < 0,02$), jak i zagospodarowanym (test chi-kwadrat, $p < 0,05$). Udatność lęgów samców w borze zagospodarowanym była istotnie wyższa niż w pierwotnym grądzie (test chi-kwadrat, $p < 0,02$)

Habitat type and plot Typ siedliska i powierzchnia (years of study) (lata obserwacji)		Number of successful nests Liczba pomyślnie zakończonych lęgów	Mean nestling success Przeciętna udatność lęgów		Mean production Przeciętna produkcja	
			Nests/male Gniazd/samca	Nests/female Gniazd/samicę	Fledglings/male Podlotów/samca	Fledglings/female Podlotów/samicę
Primaeval forest	Ash-alder plot K (1976–79)	24	0.60	0.57	3.31	3.15
Las pierwotny	Łęg pow. K Oak-hornbeam plot C (1977–79) Grąd pow. C	3	0.19	0.27	1.05	1.49
Managed	Oak-hornbeam plot (1979–82)	23	0.38	0.40–0.47	2.06	2.16–2.54
Las zagospodarowany	Pow. grądowa Coniferous plot (1979–82) Pow. borowa	28	0.45	0.48–0.57	2.38	2.53–3.01

DISCUSSION

Habitat distribution of the chiffchaff

Habitat distribution of a species is brought about mostly by a process of habitat selection (HILDEN 1965, PARTRIDGE 1978, MORSE 1980), though in the case of birds returning in consecutive seasons (cf p. 44) it is difficult to decide whether they really choose habitats every time they arrive or perhaps they select a habitat only when first settling and in the consecutive years they just return to the same geographical point. Available observations (cf p. 44) are consistent with both possibilities.

The chiffchaff can satisfy its requirements in a wide array of habitats, as demonstrated by its very ubiquitous distribution in the Białowieża Forest, and in other woodlands of Central Europe (SCHÖNFELD 1978). However, not all forest habitats are suitable for it, as only places characterized by the presence of tall trees in the vicinity of bushes and open places were utilized in the Forest. Habitat patches lacking any of the above structural elements were not occupied by the birds (*cf* p. 44).

The difference in the number of structurally suitable patches among various habitats explains to a large extent the inter-habitat differences in densities (*cf* p. 44) and territory sizes (*cf* p. 44). The densities were the highest in the primaeval ash-alder habitat in which there was a fine-grained mosaic of tall trees, dense undergrowth and open spaces, which made almost the whole area suitable for the chiffchaff. On the other hand, in the oak-hornbeam and coniferous primaeval stands such conditions were met only locally, where gaps in the canopy after fallen trees were present. Accordingly, densities in these habitats were much lower than in swampy stands (*cf* p. 44). The territories in the oak-hornbeam plot were far bigger than in the ash-alder forest (*cf* p. 44) because of the incorporation of several such gaps separated by large patches of continuous canopy. It seems, that, similarly to what suggested for *Troglodytes troglodytes* (WESOŁOWSKI 1983), in a low-density habitat chiffchaff males try to compensate for lower density of suitable patches by defending bigger territories.

A direct result of forest management in the oak-hornbeam and coniferous stands is segmentation of their almost continuous canopy and creation of numerous new gaps. Thus, forestry practices increased the number of patches structurally suitable for the chiffchaff and made possible the settlement of a greater number of birds, which in turn resulted in densities over twice higher in the managed forest than in the equivalent primaeval stands (*cf* p. 44).

In the Białowieża Forest the chiffchaff prefers swampy deciduous habitats. Also birds breeding in other parts of Central Europe demonstrate such predilections (*cf* p. 44). This occurs even though they belong to different subspecies: nominate *Phylloscopus collybita collybita* in the western and *P. c. abietinus* in the eastern part of this area (TISCHLER 1941, TOMIAŁOJC 1972). On the other hand, birds from the vicinity of Leningrad and Finland, though they belong, like (probably) the Białowieża ones, *P. c. abietinus*, prefer quite different habitats, *i. e.* spruce-dominated coniferous stands (MALTSCHEVSKIY and PUKINSKIY 1983, TIAINEN *et al.* 1983b). If this difference in the habitat requirements is real, we would have to deal with an interesting situation in which morphological variation (recognized by taxonomists) and ecological characteristics change to a large extent independently. However, these differences in habitat preferences might be more apparent than real. It could happen that, though birds in both areas prefer the same, and they use the same proximate cues (HILDÉN 1965) when selecting habitats, but due to the geographical variation in structural properties of different types of tree-stands, they settle in "different", but only from human point of view, habitats. The lack of differences in numbers and breeding performance of the chiffchaff between the oak-hornbeam and coniferous

managed stands recorded in the Białowieża Forest is very instructive here. This clearly demonstrates that these were two different habitats mostly for humans, but not so much for the chiffchaff. It is impossible to solve the problem of these geographical differences with the data at hand. An undertaking of special comparative study of it would be worthwhile.

Optimal habitat of the chiffchaff

If the mechanism of habitat selection has evolved by the process of natural selection one would expect that birds should preferentially settle in optimal habitats, *i. e.* in places in which, on average, they would achieve the highest fitness. Moreover, one would also expect that birds should possess some adaptations for breeding exactly in the preferred type of habitat.

As it was shown, the chiffchaff males in the Białowieża Forest clearly prefer swampy stands. This preference is still more pronounced in the females, as the ash-alder stands were the only habitat type in which the females (slightly) outnumbered males (*cf.* p. 44).

The question is then whether birds settling in the ash-alder stands could expect to achieve highest fitness. As the nesting success and production of young per breeding bird was much higher in the swampy forest than in other types of primaeval stands (*cf.* p. 44), the answer is: yes, they could. The main factor which made the production of young different among habitats was the varying nest predation rate. Predation induced losses were the lowest in the ash-alder stands (*cf.* p. 44), though these were the most densely populated by the chiffchaff. This low predation rate probably reflects difficulties which mammalian predators face when in search of nests in this swampy, densely overgrown habitat. Observations from the dry spring of 1979 (*cf.* p. 44) are in accordance with this suggestion, because the whole area of the plot then dried out, the losses being much higher than in any other year.

After showing that the swampy forest constitutes the optimal, the chiffchaff habitat one can ask if the chiffchaff has any special features (adaptations) for breeding in it.

The way of nest location may be such an adaptive feature in this species. The swampy forest with "islands" of vegetation surrounded by mud or water can be a very good place for breeding, provided some trick to protect nests against dampening and flooding is "invented". A closely related *Phylloscopus sibilatrix* has not solved this problem; it nests only on the ground and avoids breeding in swampy stands (ASCHENBRENNER 1966, FOUARGE 1968, WESOŁOWSKI 1980, 1985). Similarly, *Phylloscopus trochilus* places its nests above the ground only quite exceptionally (LAPSHIN 1976, SCHÖNFELD 1982, MALTCHESKIY and PUKINSKIY 1983). The chiffchaff, on the other hand, places its nests routinely in a variety of slightly elevated places (*cf.* p. 44), which safeguards its nests against raising water level. There is yet another important difference between these species. The entrances in *P. sibilatrix* and *P. trochilus* nests are oriented horizontally, whereas in the chiffchaff

they are directed slightly obliquely upwards. Such an orientation of the entrance allows the birds to easily escape from nests without getting entangled with dense stems in which nests are usually hidden in swampy stands. This would be impossible with the entrance directed horizontally.

These two details of nest placement have clear adaptive value only in the swampy stands, and it is hard to imagine how they could have emerged in coniferous or dry deciduous habitats.

It was already mentioned that a feature of the chiffchaff habitat was the presence of open spaces within its home ranges. Yet such areas serve the chiffchaff neither for nesting nor for singing or foraging. What could be their role, then? As nests, though themselves hidden in vegetation, had openings usually directed to open, well-lit patches (*cf* p 44), it can be suggested that they served incubating and/or brooding females as a kind of screen. The birds, sitting in dark nests, had their field of vision unobstructed and could easily spot the appearance and movement of any potential enemies against such light back-ground, without being visible themselves.

Summing up this part of discussion it can be said that swampy forest is the optimal chiffchaff habitat, and that this species seems to be evolutionarily adapted to nesting in it.

Managed versus primaeval habitats

An increase in the numbers of settling males, which follows the changes in habitat structure (a result of forestry practices) has been considered previously (*cf* p. 44). In what other respects do birds breeding in the managed stands differ from those which breed in the equivalent primaeval ones? The number of females in the managed stands was higher, too. It was more on the increase than the number of males, as shown by better pairing success of males in the managed oak-hornbeam habitats (*cf* p. 44). The timing of bird settlement, onset of breeding and clutch size did not differ between the two types of stands. In the coniferous habitat also nesting success in the two types of stands is similar. In the oak-hornbeam habitat, however, the nestling success of birds from primaeval stands (24–29%) was poorer than that in the managed ones (39–45%), in spite of much lower densities in the former. This difference was almost entirely due to differing predation rates (*cf* p. 44). The lower predation rate in the managed stands could not result from lack of an important predatory species in this type of habitat, the qualitative composition of potential predators assemblage was identical in the primaeval and managed stands. However, we have no information about differences in numbers and activity of predators or in their searching patterns, which could account for differences in nesting success. Nests in the managed oak-hornbeam stands are more often hidden in dense vegetation (bushes, *cf* p. 44), and this could decrease their visibility to predators. Moreover, dense thickets of young trees, in which nests are frequently hidden, could impede movements of predators and preclude their surprise attacks. Another factor which might differ between these two types of stands could be the availability of

alternative prey. Data from 1982 illustrate a potential importance of this factor; that year an outbreak of leaf-eating caterpillars was recorded and it is known that during the outbreak years several potential nest predators such as small rodents, *Sciurus vulgaris* or *Garrulus glandarius* switch to foraging on caterpillars (PUCEK 1978, TOMIAŁOJĆ *et al.* 1984 and unpubl.). In accordance with this, predation rates in 1982 were unusually low (*cf* p. 44).

Returning to our managed-primaeval comparisons, one can conclude that the differences found between birds breeding in undisturbed and in transformed stands are rather small, besides numbers. In other words, breeding in the managed stands demands from birds only slight adjustments. Probably conditions in the managed forest do not exceed the range of conditions met with normally by the chiffchaff in its primaeval habitats.

Much higher densities of birds in the managed forest result from an increase in the number of suitable habitat patches created inadvertently by forestry practices.

Generally, it can be said that man-made changes in the Białowieża Forest have been advantageous for the chiffchaff. They made a great increase in its numbers possible there, and, at the same time, did not depress and sometimes even enhanced the production of young.

Life-history tactics

Though the breeding of the chiffchaff in the Białowieża Forest does not begin before the start of May, first singing males already appear in the Forest before April 10 and often have to face adverse weather conditions (not infrequently snow-storms and freezing temperatures). Why do they arrive so early if the breeding starts so much later? It seems that similarly to what was suggested for *Phylloscopus sibilatrix* (WESOŁOWSKI 1980) this could have arisen as a result of strong inter-male competition for territories. Under such circumstances an earlier arrival gives the males a better choice and allows them to claim the best territories. The birds cannot, however, arrive earlier than are permitted by food and/or weather conditions along the migration route and on the breeding grounds. Thus, the actual timing of bird arrival may be seen as an evolutionary compromise between two opposing selection forces: intermale competition (favouring early arrivals) and food/weather conditions (selecting against early arrivals).

Hypotheses dealing with the timing of breeding seasons in birds (LACK 1950, PERRINS 1970, IMMELMANN 1971) refer to the situation occurring on breeding grounds. However, as our observations demonstrate, the onset of nesting may be determined not only by the conditions prevailing on the breeding grounds, but also by circumstances faced by birds outside them. In some years breeding in the Forest was delayed because of the late arrival of females (*cf* p. 44). Thus, in the case of migratory birds, the current explanatory framework seems to be too narrow. Hence, in order to achieve a better understanding of the factors influencing the breeding seasons of migratory birds, additional factors, which act outside breeding areas, should be considered as well.

In the chiffchaff a SW-NE geographical trend towards an increasing clutch size

occurs, but the latitudinal increase is rather small (*cf.* p. 44). Swiss birds clutches smaller by less than an egg than do the birds breeding close to the northern limit of the species range. However, though laying slightly smaller clutches, Swiss birds, have a possibility to go through two full breeding cycles, similarly to the birds from other Central European populations, Białowieża ones including. In birds breeding far in the North this is hardly possible because the breeding season is short. If one took the number of clutches a year into account, it would appear that the chiffchaff in northern parts of its range had a chance to produce fewer offspring, even though it lays bigger clutches. Their lower fecundity there could be offset, at least to some extent, by lower nesting mortality in these areas. Though there are no data supporting this possibility in the chiffchaff, in the closely related *Phylloscopus trochilus* in Karelia (NE of Leningrad) nesting losses were found unusually low: only 22% of all eggs laid failed to give fledglings (LAPSHIN 1976).

The clutch size in the chiffchaff is only slightly smaller than in its sympatric congeners: *Phylloscopus sibilatrix* and *P. trochilus* (GLUTZ 1964, von HAARTMAN 1969, LAPSHIN 1976, SCHÖNFELD 1978, 1982, TIAINEN *et al.* 1983a, WESOŁOWSKI 1985), though males in the latter species share extensively in the feeding of young (ASCHENBRENNER 1966, FOUARGE 1968, LAPSHIN 1976, WESOŁOWSKI 1980, SCHÖNFELD 1982), while those of the chiffchaff do not (*cf.* p. 44). As a result of this the work-load of the chiffchaff females caring for nestlings is much heavier than in two other species. Females of the chiffchaff, however, seem to possess some ways to alleviate this problem. Firstly – the growth of the chiffchaff nestlings is slowed down in relation to the other species (TIAINEN 1978) and, secondly – nests of this species are relatively thicker and better insulated than the nests of the other two species (LAPSHIN 1976, SCHÖNFELD 1978, TIAINEN *et al.* 1983a). This might to some extent decrease the energy demand of growing nestlings.

The pattern of nesting mortality recorded in the Białowieża Forest, with losses concentrated in the nestling period (*cf.* p. 44), is very costly (in terms of invested time and energy) for the birds. Loss of brood on the last days before fledging practically denotes the loss of the whole breeding cycle. As a result of such timing of losses, in spite of the long nesting seasons, the mean yearly production of young does not exceed the size of a single clutch even in the most productive habitats. However, the production of young by the chiffchaff in the Forest is still much higher than in the Białowieża *Phylloscopus sibilatrix* (WESOŁOWSKI 1985), which has a considerably shorter breeding season.

ACKNOWLEDGEMENTS

For various forms of help and encouragement we wish to thank the following: Przemysław BUSSE, Simona KOSSAK, Eugeniusz PUGACEWICZ, Zdzisław PUCEK, Aleksander W. SOKOŁOWSKI, Stefan STRAWIŃSKI, Arkadiusz SZYMURA, Ludwik TOMIAŁOJCZAK, Wiesław WALANKIEWICZ and Mirosław WASZKIEWICZ. Field work of T. W. was supported by a grant from Ecological Committee and Zoological Institute, Polish Academy of Sciences. While collecting field data and analysing them M. P. was employed in the Department of Nature Protection, Forestry Research Institute, Białowieża.

REFERENCES

- ALEKNONIS A. 1976. Clutch size of woodland birds of Lithuania. In: *Ekologiya ptits Litovskoy SSR*: 107–113. (in Russian).
- ASCHENBRENNER L. 1966. *Der Waldlaubsänger*. Wittenberg.
- FALIŃSKA K. 1975. Phenological studies as a method of ecological analysis of ecosystems. *Wiad. ekol.* **21**: 211–232. (in Polish with English summary).
- FALIŃSKI J. B. 1977. Białowieża Primateval Forest. *Phytocoenosis* **6**: 133–148.
- FOUARGE J. G. 1968. Le Pouillot siffleur *Phylloscopus sibilatrix* Bechstein. *Gerfaut* **58**: 1–368.
- GEISSBÜHLER W. 1954. Beitrag zur Biologie des Zilpzalps, *Phylloscopus collybita*. *Orn. Beob.* **51**: 71–99.
- GLUTZ VON BLOTZHEIM U. N. 1964. Die Brutvögel der Schweiz. Aarau.
- GŁOWACIŃSKI Z. 1975. Ptaki Puszczy Niepołomickiej (studium faunistyczno-ekologiczne). *Acta zool. crac.* **20**: 1–87.
- GOC M. 1977. Ilościowe badania awifauny rezerwatu „Las Piwnicki” koło Torunia. *Acta Univ. Nicolai Copernici. Biologia* **19**: 193–216.
- GÓRSKI W. 1976. Ptaki lęgowe Pobrzeża Bałtyku między Mielnem a Ustką w latach 1965–1975. *Not. orn.* **17**: 1–34.
- GRĄDZIEL T. 1977. Jakościowe i ilościowe badania awifauny Roztoczańskiego Parku Narodowego. Unpubl. Ph. D. thesis. UMCS Lublin.
- HAVLIN J. 1983. *Phylloscopus collybita* (Vieillot, 1817) – Hnízdění. In: HUDEC K. (Ed.) *Fauna ČSSR Ptáci*. Vol. 3/1. 684–685, Praha.
- HILDÉN O. 1965. Habitat selection in birds: A. review. *Ann zool. fenn.* **2**: 53–75.
- HOMAN P. 1960. Beitrag zur Verhaltensbiologie des Weidenlaubsängers (*Phylloscopus collybita*). *J. Orn.* **101**: 195–224.
- IMMELMANN K. 1971. Ecological aspects of periodic reproduction. In: FARNER D. S., KING J. R. (Eds.) *Avian Biology*. Vol. 1. New York: 341–389.
- KANIA W. 1968. Ptaki południowo-wschodniej części Puszczy Niepołomickiej. *Acta orn.* **11**: 61–86.
- LACK D. 1950. The breeding seasons of European birds. *Ibis* **92**: 288–316.
- LAPSHIN N. V. 1976. Nesting biology of Willow Warbler in South Karelia. In: *Ekologiya ptits i mlekopitayushchikh severozapada SSR*. Petrozavodsk. (in Russian).
- MALTCHEVSKIY A. S., PUKINSKIY Yu. B. 1983. Birds of the Leningrad region and neighbouring areas. Vol. 2. Leningrad. (in Russian).
- MILDENBERGER H. 1940. Beobachtungen über Fitis-, Weiden- und Waldlaubsänger im Rheinland. *J. Orn.* **88**: 537–549.
- MOREAU R. E. 1972. *The Palearctic-African bird migration system*. London.
- MORSE D. H. 1980. *Behaviour mechanisms in ecology*. Cambridge, Mass.
- MRUGASIEWICZ A. 1974. Badania ilościowe awifauny lasów w powiecie milickim. *Acta Univ. Wratisl.* **6**: 15–35.
- PARTRIDGE L. 1978. Habitat selection. In: KREBS J. R., DAVIES N. B. (Eds.) *Behavioural ecology*. 351–376. Oxford.
- PERRINS C. M. 1970. The timing of birds' breeding seasons. *Ibis* **112**: 242–255.
- PIOTROWSKA M., WOLK K. 1983. Breeding awifauna in coniferous forests of the Białowieża Primateval Forest. *Acta orn.* **19**: 81–95.
- PUCEK Z. 1978. Ssaki drapieżne jako szkodniki roślin. In: BOCZEK J., LIPA J. J. (Eds.) *Biologiczne metody walki ze szkodnikami roślin*, 387–401. Warszawa.
- RANOSZEK E. 1969. Ilościowe obserwacje ptaków w grądzie nadodrzańskim. *Not. orn.* **10**: 10–14.
- SCHÖNFELD M. 1978. Der Weidenlaubsänger *Phylloscopus collybita*. Wittenberg.
- SCHÖNFELD M. 1982. Der Fitislaubsänger *Phylloscopus trochilus*. Wittenberg.
- STEINFATT O. 1938. Das Brutleben des Weidenlaubsängers. *Ber. Ver. Schles. Orn.* **23**: 20–27.
- STEINFATT O. 1939. Beobachtungen über die Laubsänger in der Rominter Heide. *Ber. Ver. Schles. Orn.* **24**: 41–50.

- TIAINEN J. 1981. Habitat preferences by breeding forest passerines in an area in S Finland. Proc. Second Nordic Congr. Ornithol. 1979: 38–42.
- TIAINEN J., HANSKI I. K., MEHTÄLÄ J. 1983a. Insulation of nests and the northern limits of three *Phylloscopus* warblers in Finland. Ornis Scand. 14: 149–153.
- TIAINEN J., VICKHOLM M., PAKKALA T., PIIRONEN J., VIROLAINEN E. 1983b. The habitat and spatial relations of breeding *Phylloscopus* warblers and the Goldcrest *Regulus regulus* in southern Finland. Ann. zool. fenn. 20: 1–12.
- TISCHLER F. 1941. Die Vögel Ostpreussens und seiner Nachbargebiete. Vol. 1. Königsberg.
- TOMIAŁOJĆ L. 1972. Ptaki Polski — wykaz gatunków i rozmieszczenie. Warszawa.
- TOMIAŁOJĆ L. 1974. Charakterystyka ilościowa lęgowej i zimowej awifauny lasów okolic Legnicy (Śląsk Dolny). Acta orn. 14: 59–97.
- TOMIAŁOJĆ L. 1980. The combined version of the mapping method. Proc. VI Intern. Conf. on Bird Census Work, Göttingen: 92–106.
- TOMIAŁOJĆ L., PROFUS P. 1977. Comparative analysis of breeding bird communities in two parks of Wrocław and in adjacent *Quercus-Carpinetum* forest. Acta orn. 16: 117–177.
- TOMIAŁOJĆ L., WESOŁOWSKI T., WALANKIEWICZ W. 1984. Breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland). Acta orn. 20: 241–310.
- TREUNFELS H. 1938. Beobachtungen am Weidenlaubvögel (*Phylloscopus c. collybita*). Beitr. Fortpflanzungsbiol. Vögel 14: 124–129, 185–188.
- VON HAARTMAN L. 1969. The nesting habits of Finish birds. I. Passeriformes. Coment. Biol. 32: 1–187.
- WESOŁOWSKI T. 1980. Territorial behaviour and population ecology of Wood Warbler (*Phylloscopus sibilatrix*) in Białowieża National Park. Unpubl. Ph D. thesis. Wrocław Univ. (in Polish).
- WESOŁOWSKI T. 1981. Population restoration after removal of Wrens (*Troglodytes troglodytes*) breeding in primaeval forest. J. Anim. Ecol. 50: 809–814.
- WESOŁOWSKI T. 1982. Aims and methods of bird ringing in the breeding period. Not. orn. 22: 49–54. (in Polish, with English summary).
- WESOŁOWSKI T. 1983. The breeding ecology and behaviour of Wrens (*Troglodytes troglodytes*) under primaeval and secondary conditions. Ibis 125: 499–515.
- WESOŁOWSKI T. 1985. The breeding ecology of the Wood Warbler *Phylloscopus sibilatrix* in primaeval forest. Ornis Scand. 16: 49–60.
- WESOŁOWSKI T. 1987. Polygyny in three temperate forest Passerines (with a critical reevaluation of hypotheses for the evolution of polygyny). Acta orn. 23: 273–302.
- WESOŁOWSKI T., TOMIAŁOJĆ L. 1986. The breeding ecology of woodpeckers in a temperate primaeval forest — preliminary data. Acta orn. 22: 1–21.
- WŁOCZEWSKI T., ILMURZYŃSKI E. 1957. Hodowla lasu. Warszawa.
- ZINK G. 1973. Der Zug europäischer Singvögel. Ein Atlas der Widerfunde beringter Vögel. Vol. 1. Stuttgart.

STRESZCZENIE

[Ekologia rozrodu i zachowanie pierwiosnka w pierwotnych i wtórnych drzewostanach Puszczy Białowieskiej]

Obserwacje prowadzone równolegle w Białowieskim Parku Narodowym (T. WESOŁOWSKI) i zagospodarowanej części Puszczy (M. PIOTROWSKA) miały, poza opisem biologii rozrodu lokalnej populacji, dać również odpowiedź na następujące pytania:

- co decyduje o rozmieszczeniu siedliskowym pierwiosnka?
- jakie siedlisko jest optymalne dla tego gatunku?
- czy pierwiosnek posiada adaptacje do gniazdowania w siedlisku optymalnym?
- jaki jest wpływ gospodarki leśnej na liczebność i sposób zachowania tego gatunku?

W Białowieskim Parku Narodowym obserwacje prowadzono w trzech typach siedlisk – łągu, grądzie i borze (tab. 1), natomiast w zagospodarowanej części Puszczy – w grądzie i w borze (ryc. 1). Wiek drzewostanu, jego struktura i skład gatunkowy analogicznych zespołów roślinnych w obu częściach Puszczy były podobne. Różnice dotyczyły głównie znacznego udziału drzewostanów młodych, młodników i upraw w części zagospodarowanej (ryc. 3 i 4).

Obserwacje w pierwotnej części Puszczy (BPN) prowadzono w latach 1975–83, a intensywne badania objęły obszar 12 ha w 1976 r. i 73 ha w latach 1977–79. W lesie zagospodarowanym badaniami objęto 40 ha boru w 1978 r., a w latach 1979–82 intensywne obserwacje prowadzono na 82,8 ha boru i 82,9 ha grądu.

W obu przypadkach (BPN i las zagospodarowany) stosowano zbliżoną metodologię badań. Obserwacje prowadzono od przylotu samców (początek kwietnia) do końca czerwca, przedłużając je do końca lipca (w 1978 r. w BPN i w 1980 r. w części zagospodarowanej). Dorosłym ptakom zakładano kolorowe obrączki – samce łapano wkrótce po przylocie, natomiast samice łapano w pobliżu gniazd, już po wykluciu młodych. Liczbę zaobrączkowanych ptaków i znalezionych gniazd przedstawiono w tabeli 2.

Najwyższe zagęszczenie pierwiosnka stwierdzono w łągu (około 4 par/10 ha), niższe w zagospodarowanym grądzie i borze (2 pary/10 ha), a najniższe w pierwotnym grądzie i borze (0,8 pary/10 ha). Otrzymane różnice zagęszczeń były istotne statystycznie (tab. 3).

W Białowieży samce pierwiosnków powracają z zimowisk w pierwszych dniach kwietnia, a samice około 3 tygodni później. Nie obserwowano różnic w terminach zasiedlania przez ptaki różnych siedlisk. Stwierdzono, że około 30% dorosłych samców powracało do miejsc odbywania poprzednich łągów, nie odnotowano natomiast przypadku powracania samic i młodych ptaków (tab. 5). Z reguły (74%) samce zajmowały w kolejnych latach te same terytoria. Filopatryczne samce przylatywały nieco wcześniej niż pozostałe.

Miejsca zajmowane przez pierwiosniki charakteryzowały się obecnością wysokich drzew, gęstej roślinności krzewiastej, a także otwartej prześwietlonej przestrzeni, w pobliżu której samica budowała gniazdo. Wielkość terytoriów mierzono tylko w pierwotnej części Puszczy – terytoria w łągu były znacznie mniejsze niż w grądzie (tab. 6). Samce zajmowały te same terytoria również w okresie drugich łągów, chociaż liczba samców terytorialnych była wtedy mniejsza niż w okresie pierwszych łągów. Samce aktywnie broniły terytoriów od momentu przylotu mniej więcej do połowy lipca. Wyjątkiem były okresy ze znacznym spadkiem temperatury, z opadami śniegu czy z silnym wiatrem.

W łągu samce miały najwyższą udatność kojarzenia, odnotowano tu kilka przypadków poligynii (tab. 7).

Gniazdo budują wyłącznie samice. W czasie zbierania materiału i budowy odzywają się charakterystycznym „fiet”, co ułatwiało wyszukiwanie gniazd. Podobnie odzywają się samice w czasie karmienia młodych.

Gniazda były budowane w pobliżu nie zarośniętej przestrzeni (np. dróg leśnych, polanek, leżących drzew) i umieszczane najczęściej w leżących gałązkach, powalonych świerkach, kępach traw, a gniazda nie osłonięte roślinnością były dobrze maskowane (ryc. 10, fot. 3–6). Najczęściej gniazda były budowane na ziemi i do 40 cm nad nią (ryc. 11), wyjątkowo wyżej. Gniazda zakładane w późniejszym okresie (powtarzane i drugie łągi) umieszczane były nieco wyżej niż przy pierwszych łągach (ryc. 12). Wysiadywały tylko samice, okres ten trwał około 15 dni. W przypadku zniszczenia łągu, część samic ponownie budowała gniazdo i rozpoczynała składanie jaj w ciągu 5–15 dni.

W Białowieży pierwszorki rozpoczynają składanie jaj w tym samym czasie w różnych siedliskach, między 1 a 25 maja. W okresie drugich łągów stwierdzono gniazdowanie od 64% do 73% samic uczestniczących w pierwszych łągach.

Pełne zniesienie wynosiło 4–7 jaj (tab. 11), największe zniesienie stwierdzono w łągu, najmniejsze w borze. Wielkość zniesienia malała z upływem czasu (tab. 12).

Straty częściowe w łągach były spowodowane obecnością nie załęczonych jaj, zamarych zarodków i drapieżnictwem – wynosiły przeciętnie 0,44 jaja/łąg (tab. 14). Najważniejszą przyczyną strat całkowitych było drapieżnictwo, inną ważną przyczyną było porzucanie gniazd. Do potencjalnych drapieżników należały drobne gryzonie, wiewiórka, kuna, lis, jenot, borsuk, dzik, puszczyk, myszołów, sójka, zaskroniec i żmija. W okresie składania jaj i wysiadywania straty powodowane przez drapieżniki były istotnie niższe niż w okresie pobytu młodych w gnieździe. Wielkość strat powodowanych przez drapieżniki w lesie zagospodarowanym była istotnie niższa niż w odpowiednich siedliskach lasu pierwotnego. Straty w łągach w okresie przebywania piskląt w gniazdach były niemal wyłącznie powodowane przez drapieżniki (tab. 15). Wyjątkowo niskie straty w łągach w 1982 r. były prawdopodobnie rezultatem występowania niezwyklej obfitości (w stosunku do lat poprzednich) gąsienic motyli, stanowiących pokarm zarówno pierwszorka, jak i jego potencjalnych wrogów, np. sójki czy wiewiórki.

Śmiertelność łągów była najniższa w łągach (około 48%), pośrednia w zagospodarowanych grądach i borach oraz pierwotnych borach (55–61%), a najwyższa w naturalnych grądach (71–76%). Produkcja podlotów w przeliczeniu na samca i samicę była najwyższa w łągu (tab. 18).

Pierwszorek może gnieździć się w różnych typach lasu pod warunkiem, że występują w nich w pobliżu siebie następujące elementy: wysokie drzewa, bujny podszyt, otwarte przestrzenie. Brak któregośkolwiek z tych elementów czyni teren nieatrakcyjnym dla tego gatunku. Różnice zagęszczenia i wielkości terytoriów między poszczególnymi typami lasów zależały w dużym stopniu od różnic ilości odpowiednich strukturalnie fragmentów siedliska. łąg obfitujący w takie fragmenty

był siedliskiem preferowanym. Podobne upodobania obserwuje się również w innych częściach Europy środkowej. Natomiast pierwiosniki gnieźdzące się w okolicach Leningradu i w Finlandii zasiedlają głównie bory świerkowe.

Zmiany wywołane gospodarką leśną (rozluźnienie i prześwietlenie drzewostanów) stworzyły korzystną sytuację dla pierwiosnika, umożliwiły wzrost jego zagęszczenia w lesie zagospodarowanym w stosunku do siedlisk pierwotnych. Poza różnicami zagęszczenia nie wykryto większych różnic między gnieźdzeniem pierwiosników w lasach zagospodarowanych i naturalnych. Jedynie udatność lęgów w grądach zagospodarowanych była istotnie wyższa niż w grądach naturalnych.

Najwyższe zagęszczenie pierwiosnika i najwyższą produkcję młodych obserwowano w łęgu. Tak więc łęg jest siedliskiem optymalnym dla tego gatunku. Przystosowaniem pierwiosnika do gnieźdzenia się w tym siedlisku są zdolności do zakładania gniazd nad ziemią i skośne ustawienie otworów gniazdowych. Takie położenie gniazda umożliwi pierwiosnikowi jego zabezpieczenie przed zalaniem wodą, jego ukrycie na otoczonych wodą kępach gęstej roślinności, a w razie ataku drapieżnika swobodne opuszczenie gniazda.