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PHENOLOGY AND BREEDING SUCCESS IN A POPULATION OF COLLARED FLYCATCHER, *FICEDULA ALBICOLLIS* (TEMM.), IN THE NIEPOŁOMICE FOREST (SOUTHERN POLAND)

(Ekol. Pol. 21:219–228). The Collared Flycatcher, *Ficedula albicollis* (Temm.) arrives in the Niepołomice Forest during the period from April 10th-20th, depending on the early spring temperature. The start of clutches is affected by the temperature prevailing not more than 10 days before the first egg is laid. The average size of 120 complete hatches was 6.1 eggs (min. 3, max. 8 eggs), clutches containing 6 eggs being most frequently observed (55.8%). In 1970 losses from the time the first eggs were laid up to the advanced fledgling stage was 28.2%. In 1968 and 1969 losses were far higher (49.2% and 71.6%), which is explained as primarily due to working methods. In 1970 population increase was 4.7 nestlings per breeding pair.

The Collared Flycatcher, *Ficedula albicollis* (Temm.), is a rare south-eastern European bird. It occurs in large numbers only in certain places, for instance in the Tellerman Forest in the Voronež district (Dementev, Gladkov 1954), the Białowieża Forest (Sokołowski 1958), in trees-tands of the *Carpinion betuli* alliance on the Oder near Wrocław (Tomiałojć 1972) and in the Stuttgart area (Löhrl 1957), hence there are few data available on the biology of this species. In the stands of the Niepołomice Forest it reaches a density of up to 13 pairs per 10 ha. It builds in natural holes in trees, and also in nesting boxes A, A1 and B. The greatest amount of informa-

tion on the Collared Flycatchers' breeding habits is contained in studies by Löhrl (1957) and Balat (1971).

The purpose of this study was to define the phenology of this species in the Niepołomice Forest, and also to assess the size and effectiveness of breeding in the study population. The data available on other populations of the Collared Flycatcher make comparison of results possible.

MATERIAL AND METHODS

Studies were made on the basis of inspection of nesting boxes in 1968–1970, every 2–4 days during the breeding period. In 1968 and 1969 measurements were made of the eggs at the same time and in 1969 of nests also. A total of 134 clutches were inspected, 120 of which were used to determine the number of eggs laid, and 85 to calculate reproduction.

In order to estimate effectiveness of breeding the product of the average number of eggs in a clutch and the number of clutches under observation in a given season was taken as the starting value (100%). Clutches just started (when at least 1 egg had been laid), but which were either destroyed or interrupted in some other way during the egg-laying period, were also taken into consideration. Losses during egg-laying were defined by referring the maximum, factual number of eggs laid and allowed to develop in the sample to the corresponding starting value of this same sample.

Data on the state of the weather were obtained from readings made in the local meteorological station.

RESULTS

The first individuals appear in the Niepołomice Forest from the 10th to about the 20th of April (1968, April 10th; 1969, April 21st; 1970, April 20th). Dates are similar in Slovakia (Matoušek 1963) and in Württemberg (Löhrl 1957). Eastern populations arrive slightly later: in the Lvov area about April 22nd (Miczyński 1962), near Kiev from April 17–26th, but at Charkov not until April 25th-May 11th (Dementev, Gladkov 1954). Males from the vanguard of the spring migration, arriving a few days earlier than females, the absence of which is evident in the Niepołomice Forest up to the end of the first 10-day period in May, and probably lasts even longer. The earliest clutches were found on May 4th 1969, and on May 7th in 1968 and 1970. The full period of the Collared Flycatcher's stay in the Niepołomice Forest is given, using 1968 as an example (Fig. 1). The prolonged period during which migration of this species takes place is remarkable. The area is gradually

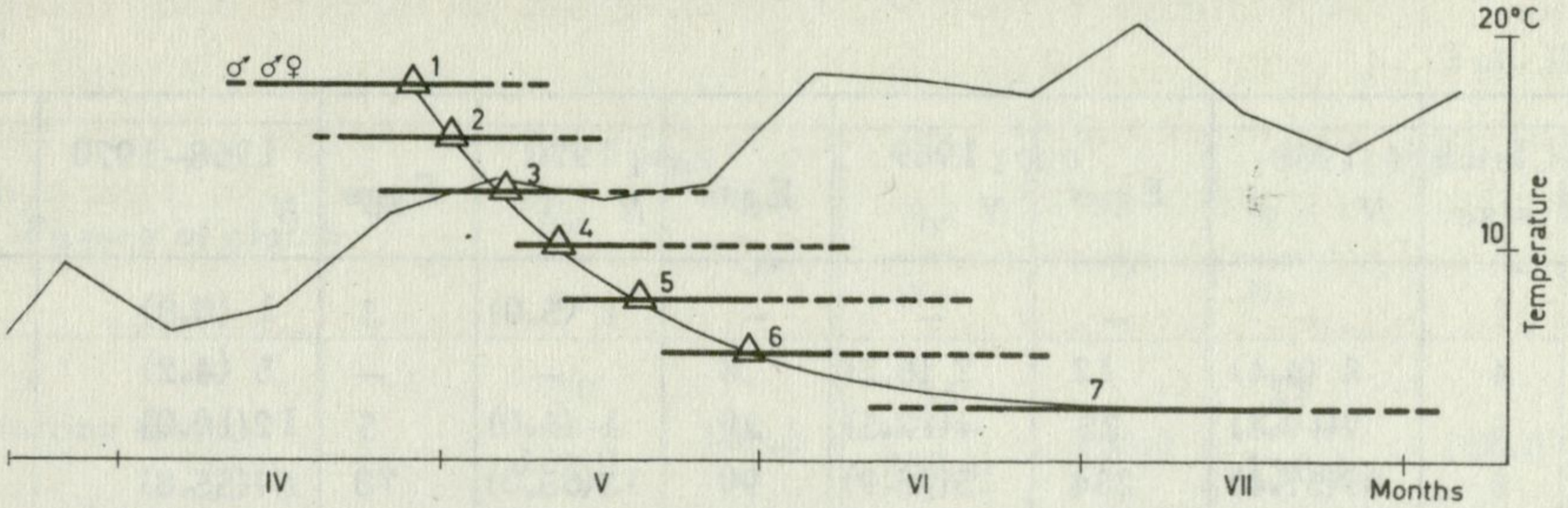

Fig. 1. Breeding phenology of the Collared Flycatcher, taking 1968 as an example
1 – arrival, *2* – occupation of territory and courtship *3* – building nests *4* – egg-laying, *5* – sitting the eggs, *6* – hatching young, *7* – departure. Dotted line indicates state not exceeding 5% of whole population, triangle – culmination of process

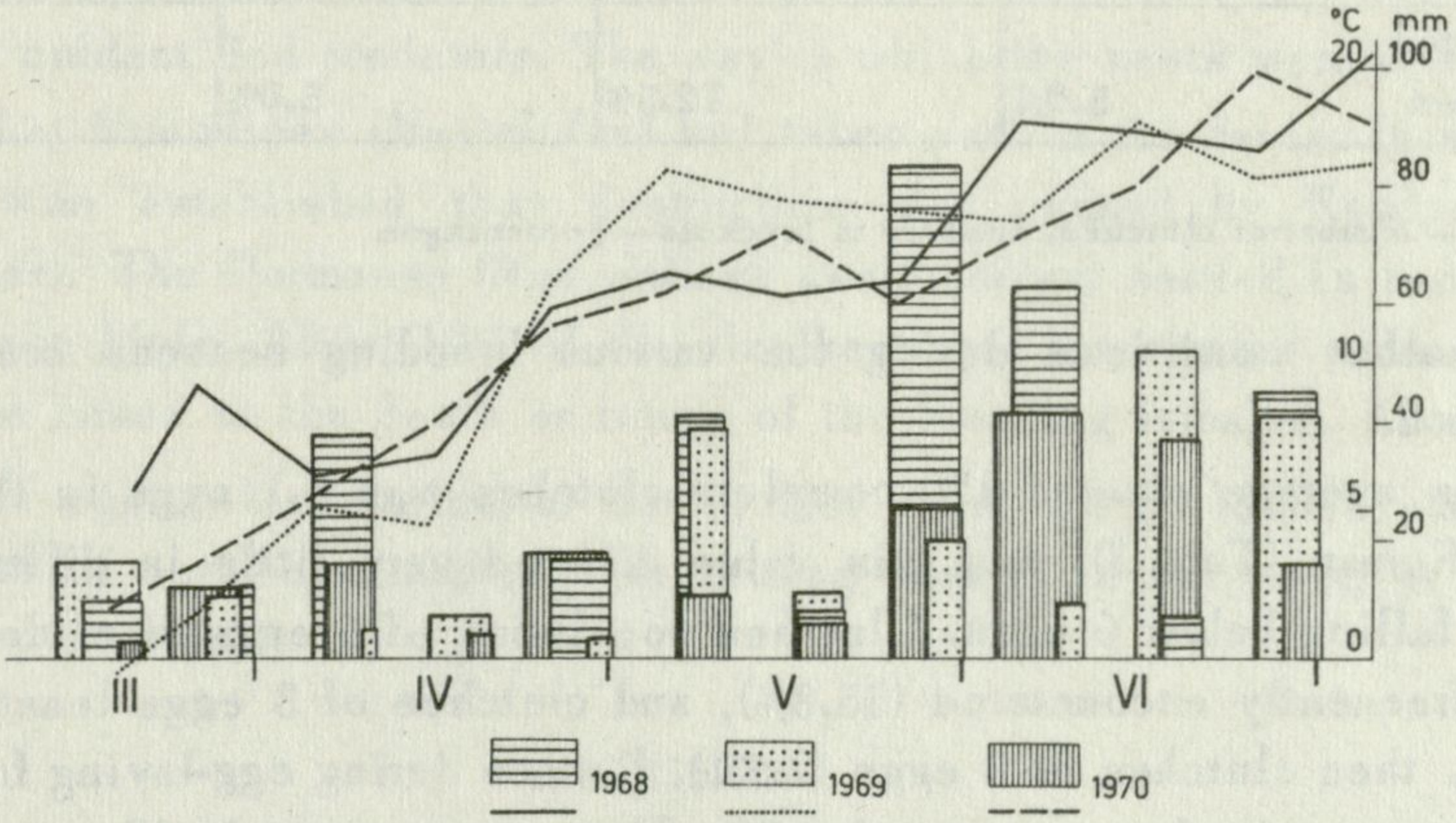

Fig. 2. Average daily temperatures (lines) and rainfall in 10-day periods (columns) in breeding seasons 1968–1970

left by the population as breeding ends, i.e. in the third 10-day period of June. At the end of June and beginning of July only about 50% of the total number of individuals was observed in Niepołomice Forest. It is chiefly birds taking part in repeat breeding which remain longer. In all the study years observations of this species ended approximately in mid-August, after which time this species is only sporadically encountered, e.g., August 15th 1968, Sept. 19th 1971. It is, however, possible that these were birds from another population in transit flight. The population from the Voronež region flies away in August, and the Charkov population remains until approximately mid-September (Dementev, Gladkov 1954). Collared Flycatchers have been observed as late as September in Czechoslovakia also (Matoušek 1963).

Clutch size of Collared Flycatcher in the Niepołomice Forest

Tab. I

Clutch size	1968 *N*	Eggs	1969 *N*	Egss	1970 *N*	Eggs	1968–1970 *N*	Eggs
3	–	–	–	–	1 (5.0)	3	1 (0.8)	3
4	3 (4.4)	12	2 (6.2)	8	–	–	5 (4.2)	20
5	7(10.3)	35	4(12.5)	20	1 (5.0)	5	12(10.0)	60
6	39(57.4)	234	15(46.9)	90	13(65.0)	78	67(55.8)	402
7	17(25.0)	119	10(31.3)	70	5(25.0)	35	32(26.7)	224
8	2 (2.9)	16	1 (3.1)	8	–	–	3 (2.5)	24
Total	68	416	32	196	20	121	120	733
$\bar{x}$	6.118		6.125		6.050		6.108 ≈ 6.11	
Repeated clutches		5.0%		12.5%		5.0%		7.6%

N – number of clutches, numbers in brackets – percentages.

Weather conditions during the various breeding seasons are shown in Figure 2.

The average size of 120 complete clutches was 6.1 eggs in the Niepołomice Forest (Tab. I), and this value differed very little in different years, never falling below 6 eggs. Clutches consisting of 6 eggs were decidedly the most frequently encountered (55.8%), and clutches of 3 eggs least frequently (0.8%), then clutches of 8 eggs (2.5%). Losses during egg-laying for the three seasons examined were not quite 5%. There were very significant differences between the different years in respect of the number of nestlings hatching out, and losses at this stage increased by a further 4.8–52.1%. Losses during the development of young birds until they left the nest were found to be very similar for all three study seasons, and in relation to the preceding stage were 15.0–19.5% (Tab. II). The Collared Flycatcher nests once a year, but in the event of the first attempt proving unsuccessful may immediately start breeding a second time. It was never found, however, that this attempt at compensating for losses ever occurred after loss of nestlings. The greater the losses which occurred in nests after the first attempt at producing young, the larger the number of pairs which start breeding again. In 1969 the number of eggs lost to reproduction was very high, hence the number of repeat breedings was over twice greater it that season than in 1968 and 1970.

Losses from the time the eggs are laid until the young leave the nest were due in about 75% of the cases to total or almost total destruction of the

Effectiveness of clutches of the Collared Flycatcher in the Niepołomice Forest

Tab. II

Phases of clutch	1968 Nc/Ne	1968 %	1969 Nc/Ne	1969 %	1970 Nc/Ne	1970 %
I. Starting state	30/183.0	100.0	34/207.4	100.0	21/128.1	100.0
II. Eggs laid	176	96.2	198	95.1	122	95.2
III. Hatched nestlings	126	69.9	90	43.2	117	91.3
IV. Youngs before leaving the nest	93	50.8	59	28.4	92	71.8

Nc – number of clutches, *Ne* – number of individuals (eggs, youngs).

clutches by unidentified predators. The way in which the nests were destroyed indicated that Mustelines (*Mwstelidae*) had taken part in the raids. In several cases it was established that destruction was caused by Woodpeckers (*Dendrocopos*). The Dormouse (*Muscardinus avellanarius*) settled in two nests built by these birds. About 10% of the clutches were interrupted or deserted, due in some cases to the death or injury of the brooding females. About 10% consisted of eggs which failed to hatch, and about 5% of losses was due to the death of nestlings, either from getting soaked in the nest, or being invaded by parasites.

DISCUSSION

The very similar time at which Collared Flycatchers migrate to the Niepołomice Forest, areas in Czechoslovakia and Germany, is due to the proximity of the geographical location of these populations. Their later appearance in the Ukraine is undoubtedly due to the populations migrating there having to cover a longer migration route from their wintering places. It must be assumed that the return of different populations. from their wintering places in tropical Africa (Mauersberger, Portenko 1960) begins at a similar time, hence differences in their time of arrival at their breeding places are due to the longer or shorter distances they have to cover.

The earlier arrival of males is understandable from the evolutional aspect, since the role of males and females are clearly separated in the case of the Collared Flycatcher. It is the duty of the male to choose a suitable hole in a tree, to occupy it and to defend the territory near it. The female builds the nest and after laying her eggs sits on them. Occupation of the hole and

defence of the territory is a necessary condition for entering upon breeding activity, and thus the greater haste of the male is understandable, as it has to contend with competition both within and between species. The earlier it arrives, the greater the chances of obtaining a hole in a tree and occupying the adjacent territory, with consequently better opportunities for reproduction.

The dates of arrival of the first Collared Flycatchers, and the course taken by their breeding, is directly connected with weather conditions (Fig. 2). In 1968 the first individuals arrived on April 10th; the early spring was then relatively warm, with average 24-hour temperature of 10°C. In 1969 and 1970 the birds did not arrive until April 21st and 20th, when the early spring temperature was only just above zero, and in March 1969 was even below freezing point. This shows that the time at which the birds arrive depends on the temperature in the area. As both amount and frequency of rainfall between mid-March and April were fairly similar in all three of the study seasons, this factor may be disregarded here. The time of the birds' arrival did not, however, have any noticeable effect on the time at which egg-laying started. Although the Collared Flycatcher arrived relatively late in the Niepołomice Forest in 1969, the earliest clutches were found as early as May 4th, and in 1968 and 1970 on May 7th. The diagram of temperatures explains this phenomenon. In 1968 and 1970, at the end of April and beginning of May, the average air temperatures were very similar, hence the similarity in the time at which breeding started in these two seasons. During the same period in 1969 the temperature was several degrees higher, and this must be considered responsible for the earlier start of breeding during this season. It is possible to gather from the dates at which the first clutches appear and the temperature chart that the temperature not more than 10 days preceding the first egg-laying has a significant effect on the start of breeding. Löhrl (1957) drew attention earlier on to the considerable influence of ambient temperature on the start of breeding, and in that author's opinion temperatures below 10°C reduce the Collared Flycatchers' activity to such an extent that two competitive males can sit quietly side by side under such conditions. Studies on the House Sparrow, *Passer domesticus* L., and Tree Sparrow, *P. montanus* L. (Mackowicz, Pinowski, Wieloch 1970), showed that the start of the breeding period in the case of these birds depends primarily on air temperature during the week before the first egg is laid. The role of rainfall is of secondary importance in this case also.

The average clutch size of the Collared Flycatcher in the Niepołomice Forest is the highest value in comparison with cultches in several other populations situated further to the south and southwest (Tab. III). As in the case of other species (Lack 1954), these values differ slightly in different geographical latitudes. Generally speaking there is decrease in a direction

Size of Collared Flycatcher clutches in different parts of Europe

Tab. III

Area	Number of clutches	Size of clutches	
		range	$\bar{x}$
Niepołomice Forest	120	3–8	6.11
Saxony (Creutz 1970)	5	5–7	6.02
Stuttgart district (Löhrl 1957)	645	(2) 3–8	5.8
Moravia (Balat 1971)	198	1–8	5.67
USSR (Dementev, Gładkov 1954)	?	4–7	?
Hungary (A. Keve, J. Györy, L. Mate, F. Varga – personal communic.)	22	4–6	5.55
Gotland (Durango, Kahlström – after Löhrl 1957)	33	?	5.5 (?)

from north to south – Poland, East Germany – 6.1–6.0; West Germany, Czechoslovakia – 5.8–5.7; Hungary – 5.6[1]. This fact is clearly explained by contemporary interpretation of natural selection and adaptation of species (MacArthur, Connel 1966), but in relation to this the finding of a relatively small number of eggs in clutches of the population of Gotland is puzzling since clutches should be expected to be largest in this most northerly habitat of the Collared Flycatchers. The list of fecundity presented is deficient in that the values for some populations (e.g. from West Germany) are based on too small an amount of material and are consequently not sufficiently reliable. The clutches taken into consideration originate from different study years, which to a great extent ensures that results are not distorted by the effect of the size of clutches depending on weather conditions. In relation to the Collared Flycatcher, a species related to it and inhabiting more northerly stations – the Pied Flycatcher, *Ficedula hypoleuca* Pall., has larger clutches, for instance Campbell (1949, 1950 – after Löhrl 1957) found the average size of a clutch of the Pied Flycatcher in England, out of a total of 133 clutches, was 7.3 eggs, Creutz (1955) for 629 clutches in Central Germany – 6.3 eggs, Enemar (1946 – after Löhrl 1957) fot 64 clutches in Sweden – 6.3 eggs, and Haartman (1951) for 275 clutches in Finland – 6.4 eggs.

The period spent by the female sitting the eggs is the main factor responsible for differences in reproduction between the different years (Fig. 3, Tab. II). The high losses during the phase of breeding found for the first two

[1] I am very grateful to Dr. Andrew Keve of Budapest and his Hungarian colleagues for enabling me to have access to unpublished material relating to Hungary.

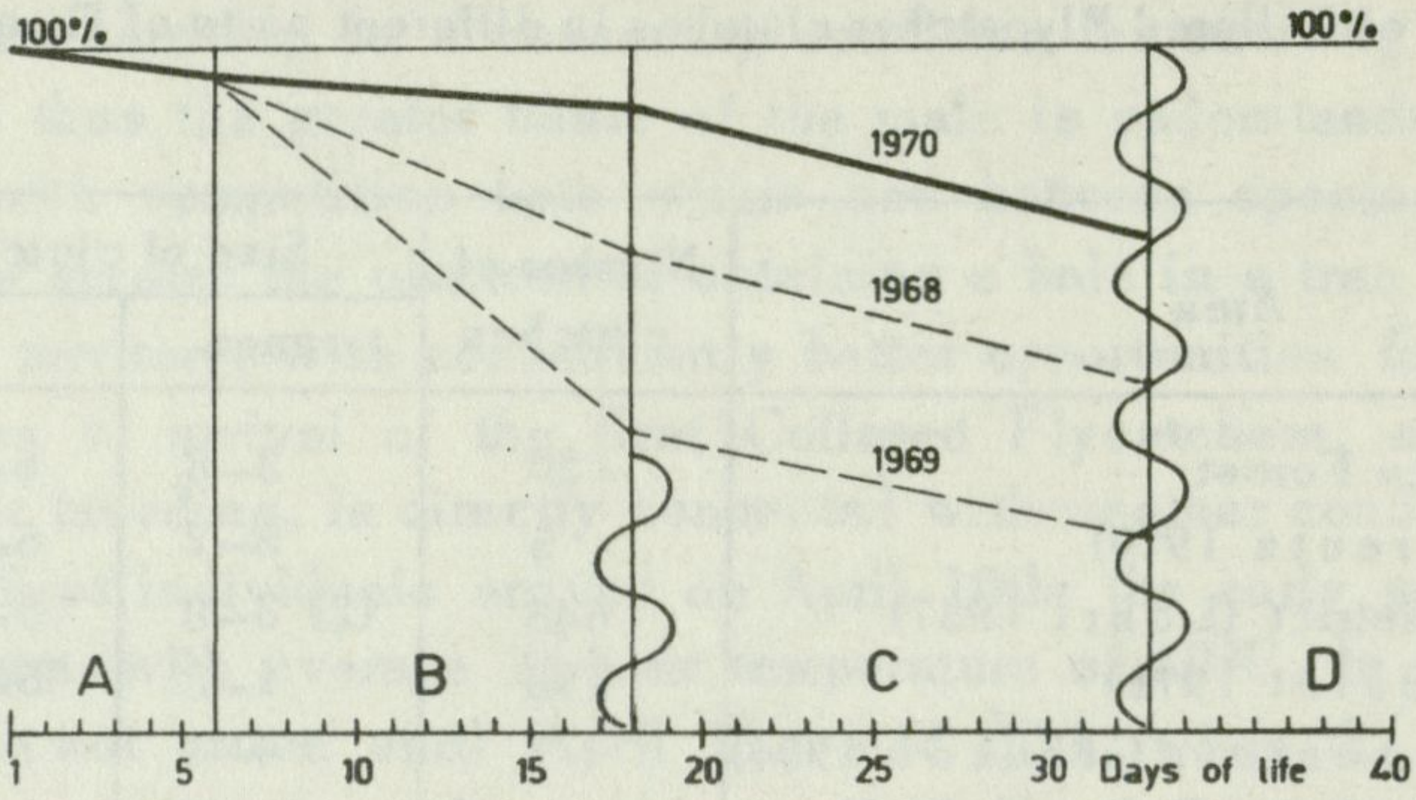

Fig. 3. Survival rate of the Collared Flycatcher at the egg-fledgling stages
A – egg-laying, *B* – sitting the eggs *C* – development of nestlings, *D* – young leaving the nest

study years, particularly 1969, cannot be explained by natural external factors only (weather conditions, activities of predators and other birds etc.). The chief cause of these losses was probably the study method. In 1968 and 1969, in addition to the normal inspection of clutches, measurements were made of eggs, and in 1969 also of nests. It is a well known fact that if birds are disturbed during the period they are laying eggs and sitting them, they tend to desert the clutches, and therefore results may have been distorted. During the year which proved most disastrous for breeding, 1969, out of 16 totally destroyed or deserted clutches (i.e. 66% of cases of death in the sample) 9 were deserted (or often scattered) soon after the measurements of eggs and nests had been made. In the other 7 cases the clutches were deserted or destroyed before, or a few days after, the measurements, 3 of these 7 clutches being destroyed by other animals. It may be assumed that the habitat pressure on the population might have been greater in 1968 and 1969 than in 1970, but it is difficult to accept that these differences were in fact as great. There are even less grounds for holding that weather conditions were responsible, since although the egg-laying and sitting period was slightly less favourable in 1968 than in 1970, as there was higher rainfall, weather conditions were clearly the best in 1969. Even if it were assumed that the results obtained for all three years were correct, it must be expected that there would be significant fluctuations in population numbers in successive seasons, whereas in 1967–1970 the Collared Flycatcher was the most stabilized species of forest birds in the Niepołomice Forest (Głowaciński)[2]. If we assume that over 50% breeding success is necessary in order to maintain a population

[2] Birds of the Niepołomice Forest (typescript).

on a relatively stable level (Löhrl 1957), the results obtained in 1969 and possibly in 1968 also, must be considered as markedly under-estimated. More realistic values, on the other hand, were obtained in 1970. This is confirmed by studies in Moravia (Balat 1971), showing that morality is not greater than 30% in this species. In the population living near Stuttgart breeding losses were estimated as 77%, but the author of this study (Löhrl 1957) omitted deserted or completely destroyed clutches from his calculations, taking into consideration only the so-called "positive clutches" ("erfolgreiche Gelege"). In the Niepołomice Forest in 1970 population increase (allowing for compensation due to repeat breeding) was 4.7 nestlings per actively reproducing pair of birds. In the samples as to which there are doubts, obtained in 1968 and 1969, population increase was 3.4 and 2.2 nestlings per breeding pair.

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FENOLOGIA I POWODZENIE LĘGÓW U POPULACJI MUCHOŁÓWKI BIAŁOSZYJEJ, *FICEDULA ALBICOLLIS* (TEMM.), W PUSZCZY NIEPOŁOMICKIEJ (POŁUDNIOWA POLSKA)

Streszczenie

Badania przeprowadzono w oparciu o kontrolę skrzynek lęgowych co 2–4 dni w latach 1968–1970. W 1968 i w 1969 r. dokonano przy okazji pomiarów jaj, a w 1969 r. także gniazd. Uwzględniono 134 lęgi, z tego 120 pełnych lęgów wykorzystano do opisu wielkości zniesień, 85 lęgów do obliczenia reprodukcji. Dla oceny efektywności lęgów za wartość wyjściową (100%) przyjęto iloczyn średniej ilości jaj w lęgu i liczby lęgów objętych obserwacją w danym sezonie. Uwzględniono też lęgi zapoczątkowane (zniesienie co najmniej 1 jaja), lecz w okresie składania jaj zniszczone lub z jakichś względów przerwane. Straty podczas składania jaj określono poprzez odniesienie maksymalnej faktycznej ilości jaj złożonych i dopuszczonych do dalszego rozwoju w próbie do odpowiedniej wartości wyjściowej tej samej próby.

Przylot muchołówki białoszyjej do Puszczy Niepołomickiej przypada na około II dekadę kwietnia 1968 – 10 IV, 1969 – 21 IV, 1970 – 20 IV. W podobnym czasie pojawia się ten gatunek w Słowacji i Wirtembergii, na Ukrainie natomiast o kilka lub kilkanaście dni później. Pełny okres pobytu muchołówki białoszyjej w Puszczy Niepołomickiej podano na przykładzie roku 1968 (fig. 1). Terminy przylotu na miejsce rozrodu zależą od temperatur przedwiośnia (fig. 2). Wcześniejszy przylot samców jest wytłumaczalny z ewolucyjnego punktu widzenia, ponieważ wybierają one dziuple oraz zajmują i bronią terytorium. Na rozpoczęcie lęgów ma wpływ temperatura nie więcej niż 10 dni przed zniesieniem pierwszego jaja.

Średnia wielkość 120 kompletnych zniesień wynosiła 6,1 jaj (min. 3, maks. 8 jaj; tab. I). Największą frekwencją odznaczały się lęgi z 6 jajami (55,8%). Średnia wielkość zniesień muchołówki białoszyjej z Puszczy Niepołomickiej tworzy największą wartość w porównaniu ze zniesieniami u kilku populacji położonych bardziej na południe i południowy zachód (tab. III). W zestawieniu wielkości te maleją postępując od wyższych ku niższym szerokościom geograficznym, co wyjaśnia współczesna interpretacja doboru naturalnego i adaptacji gatunków. W świetle tego niejasne jest natomiast stwierdzenie stosunkowo małej płodności u populacji z Gotlandii.

Różnice w reprodukcji między poszczególnymi latami nastąpiły przede wszystkim w okresie wysiadywania jaj (fig. 3, tab. II). Wielkie straty w tej fazie lęgów w dwóch pierwszych latach badań, zwłaszcza w 1969, nie dadzą się uzasadnić tylko naturalnymi czynnikami zewnętrznymi (warunki pogodowe, działalność innych ptaków i drapieżców). Prawdopodobnie zadecydowały o tym przeprowadzone dodatkowo pomiary jaj i gniazd. Przeciwko uznaniu za miarodajne wyników uzyskanych w latach 1968 i 1969 przemawia ponadto wielka stabilność badanej populacji w kolejnych sezonach 1967–1970. W roku 1970 przyrost populacji, uwzględniając rekompensatę wynikającą z powtórzeń lęgów, wynosił 4,7 piskląt na parę ptaków przystępujących do rozrodu. W kwestionowanych próbach z lat 1968 i 1969 przyrost ten wynosił 3,4 i 2,2 pisklęta na parę lęgową.

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