ACTA ZOOL. CRACOV.	31	3	115—166	KRAKÓW, 30. VI. 1988

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The breeding biology of the Dunnock *Prunella modularis modularis* (Linnaeus, 1758) in the Ojców National Park (South Poland)

[with Plates V—VII and 6 text-figs]

Biologia okresu lęgowego płochacza pokrzywnicy *Prunella modularis modularis* (Linnaeus, 1758) w Ojcowskim Parku Narodowym

Abstract. In 1974—1986 the Dunnocks of ONP started breeding towards the end of Apri or at the beginning of May. The average clutch — size was 5.14 eggs. The eggs were incubated by the female, the share of male in incubation being small. The incubation period was 12—13 days. The female cared for the chicks almost to the end of the nestling period. Both parents fed the chicks, providing food to 1, 2 or 3 chicks at one visit to the nest; the frequency of feeding increased with the age of the nestlings. The diet of young consisted of invertebrates, on the average 35 specimens making up a portion (the *Diptera*, *Arachnidae*, *Homoptera* and *Collembola* were the most frequent components). The nestling period lasted 11 days. The data concerning the increase in body-weight and the developmental state of young on successive days of life are presented. On the average 1.21 chicks fly from one nest built in the Ojców National Park.

CONTENTS

I. INTRODUCTION

Last century the Dunnock *Prunella m. modularis* (LINNAEUS, 1758) nested only in the north-eastern and southorn parts of the present territory of Poland (TACZANOWSKI, 1882). In the first half of the present century its occurrence in the breeding season was observed in central Poland (Świętokrzyskie Mts. and Poznań region — SOKOŁOWSKI, 1958). From the fiftier onward, the reports of the nesting of Dunnocks increased in number (NOSKIEWICZ, 1959; OKO, 1961; POMARNACKI, 1962; KRZYWIŃSKI, 1965) and FERENS (1950) showed the necessity to study the biology of this species in Poland. The above-mentioned reports contain the results of observations of one or, at the most, a few nests. And so the need of a study of the biology of the Dunnock, especially that of its breeding period, was still an open matter and it has become still more essential because of a recent increase in its abundance. At present the Dunnock belongs to numerous or even very numerous birds in the south and north-east of Poland (DYRCZ, 1973; GŁOWACIŃSKI, 1969; BOCHEŃSKI, 1970; TOMIAŁOJĆ et al., 1984, author's own unpublished observations) and regularly met with in the remaining area (TOMIAŁOJĆ, 1963, 1972 and the data comprised in the Index Cards of Wrocław University concerning nests and breeding).

In addition to the above-mentioned studies, information about the biology of the Dunnock is included only in general works, mostly from before a few tens of years and not coming from the territory of Poland, e.g. those by NAUMANN (1905), HARTERT (1905), DEMENTEV et al. (1951—1954), BANNERMAN (1954), HEINROTH and HEINROTH (1966) or in works devoted to other problems, e.g. monographs of the avian fauna of particular regions (FERIANC, 1965; HAARTMAN, 1969; HUDEC et al., 1983) or the discussions of select problems of the biology of the breeding period (VERHAYEN, 1967; READE and HOSKING, 1974; HARRISON, 1975; MAKATSCH, 1976, KOVSHAR 1981).

A close investigation of the Dunnock seems to be the more important because its ethology differs in different places of occurrence: in western Europe and Great Britain it is a stationary parkgarden bird, whereas in eastern Europe and Scandinavia it flies away for winter (MAUERSBERGER et al., 1977) and nests chiefly in coniferous forests in higher mountainous areas.

Most information (derived from the above-mentioned general works or contained in detailed studies carried out on this species chiefly in Great Britain) collected in Handbuch der Vögel Mitteleuropas (GLUTZ and BAUER, 1985) concerns mainly the stationary population or is based on publications presenting the results of observations which cover a small number of nests of the migratory population. It seems therefore expedient to present the data collected for this last population so as to find whether there are any differences in reproduction season between the residents and the migrants and to get better acquainted with the biology of this not very well known species.

II. STUDY AREA

I carried out my study of the breeding season of the Dunnock in the Ojców National Park (further referred to by its initials ONP), situated in southern Poland, about 30 km north-west of Kraków. The part of ONP from which the bulk of information comes is a forest complex, about 800 ha in area, which was partly grown over by an about 80-year-old stand of trees of the *Pino-Quercetum* association (MEDWECKA-KORNAŚ and KORNAŚ, 1963), with two clearings, several tens of ares in area each, in which there were some buildings. In the seventies thick understorey occurred over about 60% of the area (in places even 100%) in this forest complex. Towards the end of the seventies and at the beginning of the eighties the coniferous trees began to wither rapidly owing to industrial air pollution. No new trees grew in the place of the dead young conifers. As a result, in 1986 scarcely several dozen young firs or spruces, to 2 m high, grew in an area of 10 ha, where 10 years earlier in addition to single small trees there were many dense clumps of young trees, occupying as large areas as several ares. This has naturally caused a decrease in the numbers of Dunnocks.

III. MATERIAL AND METHODS

In 1974—1986 I gathered information concerning the biology of the breeding season of the Dunnock, in the Ojców National Park. Most information comes from 1976—1978 later the number of Dunnocks in the study area dropped dramatically and has not recovered by now.

The material was collected during the breeding season, i.e. from the end of March till the beginning of August. In this period I searched out nests nad next inspected them every day or every several days. I have gathered information about 148 nests. At visits to the nests I took down the following data: behaviour of adult birds, contents of the nest, i.e. number of eggs and chicks, advancement of breeding, weight and size of eggs and weight of chicks. Pesola spring scales with ranges of 5 and 25 g were used to weigh eggs and chicks. The inspection of nests permitted me to obtain the date of the beginning of breeding, that of egg-laying, clutch-size, incubation period, nestling period, growth rate of young and breeding success. Breeding success expressed by the number of young leaving their nest was calculated in two ways: on the basis of the number of eggs laid — here were included all the repeatedly inspected nests, for which the number of eggs and chicks and their fate were known, and the other way, based on the number of nests, the history of which was known but the number of eggs and chicks not always known exactly (e.g. nests with shells of destroyed eggs, remains of chicks eaten up by a predacious animal, or scales and faeces left by the chicks, which had abandoned the nest recently). In order to establish the phenology and breeding success of these birds I availed myself — in addition to the materials from ONP — of the data concerning the whole territory of Poland, recorded in the Nest and Breeding Index Cards at Wrocław University (141 cards) and Nest Index Cards in the Institute of Systematic and Experimental Zoology, P. A. Sc. in Kraków (17 cards of nests outside ONP).

Detailed studies of the growth and development rate of the young included 13 nests with 52 chicks. During my visits to these nests I recorded the changes in the appearance of the young: the degree of opening of their eyelids, skin and bill pigmentation and the development of feathers.

Twelve nests were observed from concealment, 1—7 m away from them, for about 270 hrs all together. In several cases, when the observation tent was situated close to the nest, it was possible to distinguish the sex of adult birds. The difference lay in the shade of the head plumage: the male's head was cinereous in shade, while that of the female was more grey. The observation of birds from concealment provided the following data: the period of incubation and the length of breaks in incubation, the frequency of arrivals of the adults with food at the nest, the cleaning of the nest and removal of excreta, changes in the behaviour of the young during the nestling period and the part played by the male and female in the care of their offspring. Even though males and females were as a rule distinguishable from each other, it was sometimes impossible to determine the sex of a bird, e.g. when the visibility was not very good (twilight, rain), the bird turned its back on the observer or the observer was busy taking down a previous observation at the time of the arrival of a bird so that only its departure was seen. For this reason in the sections dealing with the share of adult birds in the care of their progeny I have distinguished the category "sex undetermined", in which I place also all the observations with the sex of adult birds unrecorded.

In order to examine the diet of chicks I furnished them with neck rings in 5 nests. In this way I obtained 136 portions of food brought by adult birds at their 99 visits to the nest. The food was analysed in respect of its specific composition and the frequency of particular animal groups in it. The food under study was brought to chicks 5—10 days old in 1978 (3 nests on 1 and 2 June, 15 portions; 11—14 July, 18 portions; 27—31 July, 38 portions), 1980

(1 nest, 17 portions on 24 and 25 July) and 1981 (1 nest, 12 portions on 3 and 4 July).

The above-mentioned materials collected in the field have been supplemented with observations of a pair of Dunnocks, which built their nest and incubated chicks in an aviary situated in one of the clearings of ONP. These observations mainly concerned the behaviour of the adult birds during the incubation period. They were fragmentary and interrupted on the day following the hatching of the chicks (the brood had been destroyed).

IV. RESULTS AND DISCUSSION

1. Occupation of territory and its size

The Dunnocks appear in ONP at the end of March and beginning of April. The number of birds captured then and ringed was greater than the number of pairs nesting later in the same area. The fact that the birds caught after their arrival were already those of the breeding population was evidenced by the observation of the ringed specimens made in the place of catches in May, June and July (Bocheński and Oleś, 1977; catches in nets carried out later). At the same time a fairly large number of birds caught in one place (i.e. in the place where the nets were stretched) would suggest that the Dunnocks did not occupy their territories at once but were wandering about in the forest in search of as good a territory as possible.

I determined the size of a territory on the basis of the number of singing males, the number of nests and the distance at which they were built from each other. And so in the years in which these birds abounded in ONP (1974—1978) 3—4 pairs nested in the study area of 4 ha (Tomek, 1979) and the density of Dunnocks in other places with a similar stand of trees resembled that found in it. The nests of Dunnocks in which the young had been raised were situated 60—90 m from each other. At the same time the total number of nests found in that area was 2—4 times as great as the number of pairs. This "surplus" consisted of destroyed and abandoned nests, which lay 30—60 m, on the average 40 m, from each other or from the nests left by the young. This shows that 40 m was an average distance at which the birds built their new nests after the destruction of the previous ones. Having taken into consideration the nests occupied at the same time and so such as could not belong to one pair of birds, I found that their number equalled the number of singing males. It may be assumed therefore that the number of singing males agreed with the numbers of nesting pairs and the breeding territory of one pair was approx. 1 ha. After a decrease in the number of birds in the following years (1979—1986) the density of Dunnocks was 3—4 pairs/10 ha (the author's own unpublished materials) and so 2.5—3 ha fell to one pair.

The density of Dunnocks in ONP in 1974—1978 was high, a higher one was observed only in Great Britain (Snow and Snow, 1982; Birkhead, 1981; de Prato, 1985), in the broom-heath association at Eifel in GFR (Wink, 1975), in the cultured landscape of Central and Western Europe (Glutz and Bayer, 1985), in higher situations in the mountains grown over by bushy vegetation like patches of dwarf mountain pines in the Karkonosze Mts. (Dyrcz, 1973), in the *Juniperetum* association in Rumania (Korodi-Gal, 1958) or in young woods in the Alps (Glutz, 1962 in Glutz and Bayer, 1985), i.e. in the bird communities in which the Dunnock was dominant. In next years, after the number of birds had decreased to less than its half, the density of pairs in ONP became fixed at more or less such a level as found in similar biotopes of Central Europe, i.e. in mixed forests or parks with thick understorey (Dürnberger, 1978; Scholz, 1972; Feriancová-Masárová and Ferianc, 1977), alder-swamps and ash-alder woods of the Białowieża Forest (Tomiałojć et al., 1984) or farmland in England (Williamson, 1971). At the same time it was considerably greater than that observed in the lowlands of Poland: in alder-swamps in the Bug valley (Jabłoński, 1984) or some forest associations in the Białowieża Forest, such as oak-hornbeam, mixed coniferous, deciduous and pine-bilberry forests (Tomiałojć et al., 1984). The relatively great abundance of Dunnocks in ONP suggests that those forest contituted the optimum biotope for this species. Besides ONP is situated more or less in the centre of the distribution of the Dunnock (Mauersberger et al., 1977; Voous, 1962, Glutz and Bauer, 1985) and so all the information derived from here should be representative of the nominative form *Prunella modularis modularis* inhabiting the nearly whole continental part of Europe and particularly of the birds flying away for winter and inhabiting wooded areas.

2. Nest

In ONP, as in the whole territory of Poland, some Dunnocks started to ouild nests in the second half of April and the remaining ones at the beginning bf May. The birds placed their nests not very high above the ground, i.e. from some dozen centimetres to 4 m, most of them being situated 0.5—2 m above the ground. They were well hidden amidst the twigs of a tree or shrub in which they were placed, rested on a horizontal branch screened by herbs, or were squeezed in among heaped-up dry branches. The most nests were built in coniferous trees: in young ones, among branches of newly felled old trees, or in the heaps of already dry needleless branches. Only a small number of nests were among the twigs of thick, mostly thorny deciduous shrubs. The nests were built of material of vegetable or animal origin, chiefly of sticks, moss and animal hair. The structure of nests was stratified; the layers differed in material and texture. The ready nest was a solid construction, well attached to the supporting branches and with walls up to several centimetres in thickness (for a detailed description of the nest structure see Tomek, 1980).

It took the birds several (3—4) days to build the nest. The female lay the first egg in the ready nest usually on the second or third day after its completion. Having raised a brood or when the eggs or chicks had been destroyed, the birds began to build another nest. They probably proceeded sooner to the second brood after they had raised the first than after the first brood had been destroyed. This would be evidenced by the interval between successive broods in a pair observed. This pair was caught on 6 May 1978 and placed in an aviary. On 9 May the birds began to build the nest and on 12 May, or 7 days after their being put in the aviary, the female laid the first egg. After the destruction of the brood and setting the birds at liberty they built another nest in an old spruce growing about 30 m away from the aviary and in this nest the female laid the first egg on 8 June, or on the 10th day after the destruction of the previous brood. The young left the nest on 3 July and on the fifth day, i.e. on 7 July the female laid the first egg in the next nest built by it in the same spruce. The distance of the successive nests from each other (about 30 m from the destroyed nest and about 4 m from the effective one) indicates that the breeding success may have been the factor influencing the distance of the site of the last nest. This opinion is also supported by the fact that some nests were found at a distance of several or somewhat more than ten metres from the nests in which the young had been raised in the preceding year or even in the very place of the last year's nest (Phot. 1).

3. Eggs

3.1. Date of egg-laying

The Dunnocks proceeded to egg-laying in the last days of April, but most of the females began to lay eggs in the first decade of May. The egg-laying period lasted from the end of April throughout the first decade of July. The beginning of the breeding period expressed by the number of pairs in which egg-laying was started in successive decades from the end of April to July is shown in Table I.

Table I

Times of egg-laying in Dunnocks in ONP and other parts of Poland

Region	Time of egg-laying (decade of month)										
	April	May			June			July			Total
	3	1	3	3	1	2	3	1	1	3	
ONP	7	7	12	4	5	10	3	3	—	—	51
outside ONP	19	47	29	7	15	15	5	10	—	1	148
Total	26	54	41	11	20	25	8	13	—	1	199

It can be seen from this table that the most females started to lay eggs in the third decade of April and the first and second decades of May. It may therefore be assumed that that was the egg-laying period of the first brood. The second period in which relatively many females started egg-laying included the first and second decades of June and so it may be assumed to be the egg--laying period of the second brood. Eggs laid in the remaining periods, i.e. in the third decade of May, third decade of June and in July would belong to the broods repeated after the loss of the preceding clutches.

The Dunnocks inhabiting the greater part of Europe began breeding at various dates. The birds living in Western Europe (England, Belgium) started egg-laying earliest, even in the third decade of March (PERCIVAL, 1946; VERHAYEN, 1967; GINN, 1975) and the first decade of April (SNOW and MAYER-GROSS, 1967); somewhat later in Central Europe and the farther towards the north-east the later the Dunnocks began to lay eggs: those living close to the north-eastern boundary of their distribution proceeded to breeding as late as the first decade of June (CURRY-LINDHAL, in MAUERSBERGER et al., 1977; MOLODOVSKIY, 1979). And so the time of laying of the first eggs was extended more than 2 months. The second half of April, or the time when the Dunnocks living in Poland began to lay eggs, was more or less in the middle of that period.

After juxtaposing the dates of the beginning of breeding all over the area and marking the isotherms in this area (acc. to The Climatic Atlas of Europe), I found that there is a correlation between the beginning of egg-laying and the +5 and +10°C isotherms (Fig. 1). In the regions between the March isotherms of +5 and +10°C the birds started the breeding season in March, whereas in April they begin to lay eggs in the area situated west-south of the +5°C isotherm or between the April isotherms of +5 and +10°C. In the region where the 5°C isotherm does not run before May the egg-laying period began in May and where the May isotherm was lower than 5°C the birds did not breed till June. A similar situation was observed in higher positions in the mountains, where the birds laid eggs later than they did in the lower-lying adjacent areas (the start of breeding also agreed with the isotherms of 5 and 10°C). I think therefore that the effect of such factors as" altitude, latitude, weather conditions, principally temperature", determining the start of the breeding season in Europe (DYER, PINOWSKI and PINOWSKA, 1977), can be presented in the form of a line in its course comes close to the above-mentioned istoherms.

3.2. Number of eggs

About half the number of the Dunnock's nests contained 5 eggs each, there were also full clutches of 4 or 6 (about 1/4 of the total of nests either), very few had 3 eggs (5% of the total) and only exceptional birds incubated a clutch of 2 (Table II).

The average clutch calculated as the mean from 151 clutches was 4.91 eggs/nest. The Dunnocks had the relatively greatest clutches in June and the

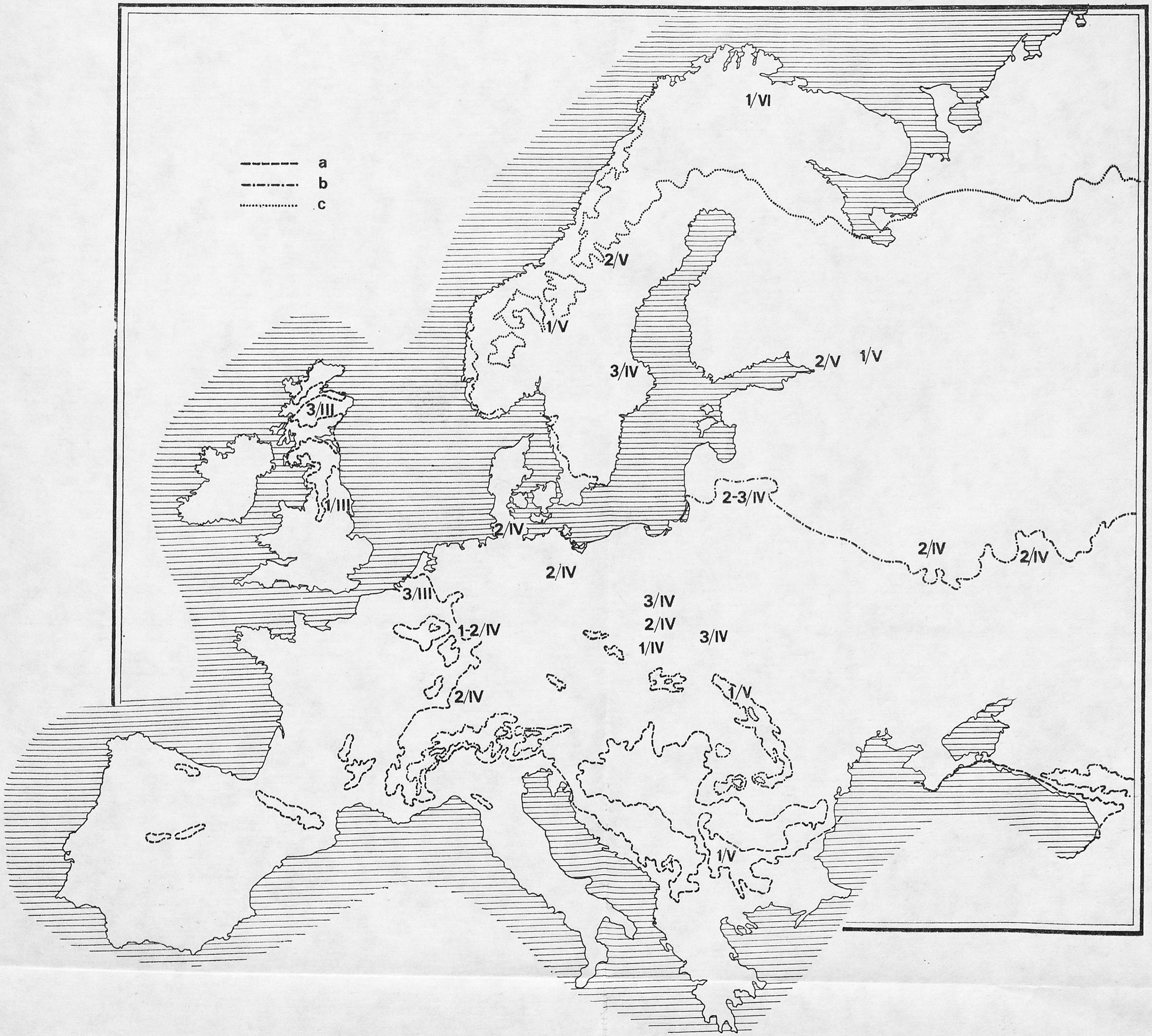

Fig. 1. A map showing the start of breeding in Dunnocks in Europe. a — +5°C isotherm for March, b — +5°C irotherm for April, c — +5°C isotherm for May (after Climatic Atlas of Europe, 1970) The Roman numerals represent the month and Arabic ones the successive decade of the month in which the Dunnocks started to breed in a given region. The dates of the start of breeding have been obtained from papers by: ALEKNONIS, 1977; BIRKHEAD, 1981; CAMPBELL, FERGUSON-LEES, 1972; DONCHEV, 1961; FERIANC, 1979; GLUTZ, BAUER, 1985; HAARTMAN, 1969; HUDEC, 1983; INOZEMTSEV, 1968; KALIVODOVA, BRTEK, 1977; KEIL, 1984; MAKATSCH, 1959; 1976; MAUERSBERGER et al., 1974, after CURRY-LINDHAL; MOLODOVSKIY, 1979; NANKINOV, 1978; SNOW, MAYER-GROSS, 1967; STRAUTMAN, 1963; VERHAYEN, 1967; YAKOVLEVA, 1983; present material

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last broods started in July consisted of the smallest number of eggs (Table III). These smallest clutches were probably repeated broods.

The above-presented data show that the mean clutch-size in ONP was higher than the mean from the whole territory of Poland. It was also high in comparison with other regions: similar clutches have been reported only from Scandinavia (HAÁRTMAN, 1969; ENEMAR and EDULA, LILLELEHT, in GLUTZ and BAUER, 1985) and slightly lower ones from Lithuania (ALEKNONIS, 1977a) and the region of Lake Ladoga (YAKOVLEVA, 1983). The mean clutch-size

Table II

Clutch-size in Dunnocks in ONP and other parts of Poland

Region	Nests with clutches consisting of the following number of eggs						
	2	3	4	5	6	Total	Mean clutch-size
ONP	—	1	3	21	10	35	5.14
outside ONP	1	6	29	54	26	116	4.84
Total	1	7	32	75	36	151	4.91

Table III

Variation in mean clutch-size relative to the time of egg-laying in Dunnocks in Poland (numbers of broods used to calculate means are given in brackets)

Region	Time of egg-laying			
	April	May	June	July
ONP	5.0 (5)	5.25 (15)	5.25 (12)	4.30 (3)
outside ONP	4.74 (19)	4.78 (60)	5.13 (29)	4.50 (8)
Total	4.79 (24)	4.88 (75)	5.17 (41)	4.45 (11)

(4.84) obtained from the territory of Poland exclusive of ONP resembled that given from Czechoslovakia — 4.76 (HUDEC et al., 1983) or Central Europe — 4.74 (MAKATSCH, 1976). The higher mean clutch-size found in ONP (5.14) than in the neighbouring regions (remaining areas of Poland, Czechoslovakia and Central Europe) and resembling that calculated for Dunnocks under more severe conditions, namely, those living much farther to the north (Scandinavian Peninsula), might indicate the reactions of the birds to counteract the danger threatening the population from the changing environment, for in HAUKIOJA'S (1970) opinion, the environmental factors influence the clutch-size and this "is low in areas when there are stable environmental conditions" (HAUKIOJA, 1970 after CODY). It may be supposed that the availability of food was not the cause of the larger clutches of the Dunnock in ONP, since it has no influence on the clutch-size (DAVIES and LUNDBERG, 1985). The fact that in spite of the relatively large clutches and the large number of Dunnocks in 1974—1978, instead of an increase in the size of the population there was a rapid decrease in following years, confirms the existence of this threat to the birds. I think that the changes in the environment resulting from heavy industrial air pollution, which in the region of ONP is considerably greater than in other regions of Poland (GRODZIŃSKA, 1985) were here one of the factors. On the one hand, it reduced the number of places suitable for nest-sites in consequence of the withering of trees, in particular young coniferous trees (GRESZTA, 1975; GRESZTA et al., 1979; CAPECKI and TUTEJA, 1977, 1979; ZĄBECKI, 1984), in which Dunnocks nest most readily (TOMEK, 1980). On the other hand, it may have caused a change in the food supplies, for as can be seen from KRAWCZYK'S (1985) experiments, sulphur dioxide, which is one of the main elements contributing to the environmental pollution in ONP (LASA, typescript), lowered the reproductive power of aphides, which in turn were one of the most frequent constituents of the diet of young Dunnocks (see Section 4.6. — Diet of young).

The low mortality rate of the young in the nestling period shows that the poor availability of food cannot exert an unfavourable influence upon the survival rate of the young before they leave the nest. The results of WINK'S (1977) study of many years confirm the hypothesis that the pollution of environment caused a decrease in the number of birds. He found that the weather conditions and severe winters did not cause changes in the number, among others, of Dunnocks, whereas the use of chemical compounds to reduce the abundance of invertebrates has a lasting effect upon the number of birds that feed on arthropods living in litter.

3.3. Size and weight of eggs

A total of 133 eggs of the Dunnock, derived from 28 clutches were used to determine the size of the eggs laid by the birds nesting in ONP. The length of eggs ranged from 17.4 to 21.0 mm ($\bar{x}$ — 19.56 mm, SD — 0.79) and their width from 13.8 to 15.5 mm ($\bar{x}$ — 14.71 mm, SD — 0.36). The dimensions of the smallest eggs were 17.9 × 14.0 and 17.4 × 14.6 mm and those of the largest egg 21.0 × 15.3 mm. The eggs belonging to one clutch differed in size from each other and the differences in their length within a clutch fluctuated between 0.2 mm (clutch of 5 eggs) and 1.7 mm (clutch of 6). The differences in the width of eggs ranged from 0.2 mm (clutch of 5) to 1 mm (clutch of 6). In three cases recorded, in which the order in which the eggs had been laid was known, I found that the size of the eggs increased with the order of laying (Table IV). In the next four clutches the last egg was found to be heavier than the eggs preceding it.

The weight of the eggs was dependent on their size and the duration of incubation. The weight of newly laid eggs ranged between 1.78 and 2.60 g; the mean weight of an egg calculated from the weights of 73 eggs obtained from 14 clutches was 2.17 g (SD — 0.19). It was about 10.6% of the weight of adult birds (the mean body weight from 7 adult birds was 20.7 g). The difference in weight between the eggs belonging to one clutch was 0.11—0.45 g. The repeated weighing of 29 eggs obtained from 7 clutches showed that they

Table IV

Variation in size and weight of eggs within a clutch in Dunnocks

Eggs in order of laying	Clutch 1		Clutch 2		Clutch 3	
	Dimensions in mm	Weight in g	Dimensions in mm	Weight in g	Dimensions in mm	Weight in g
1	19.0×14.3	2.05	19.6×14.0 *	1.65	18.6×14.7	2.10
2	19.3×14.2	2.15	19.7×17.0 *	1,75	18.7×15.0	2.20
3	19.2×14.4	2.18	19.7×14.4 *	1.88	19.0×14.9	2.20
4	19.7×14.7	2.25	19.2×14.6	2.00	19.7×15.0	2.30
5	19.7×14.9	2.50	20.4×14.8	2.10		

* Order of laying uncertain.

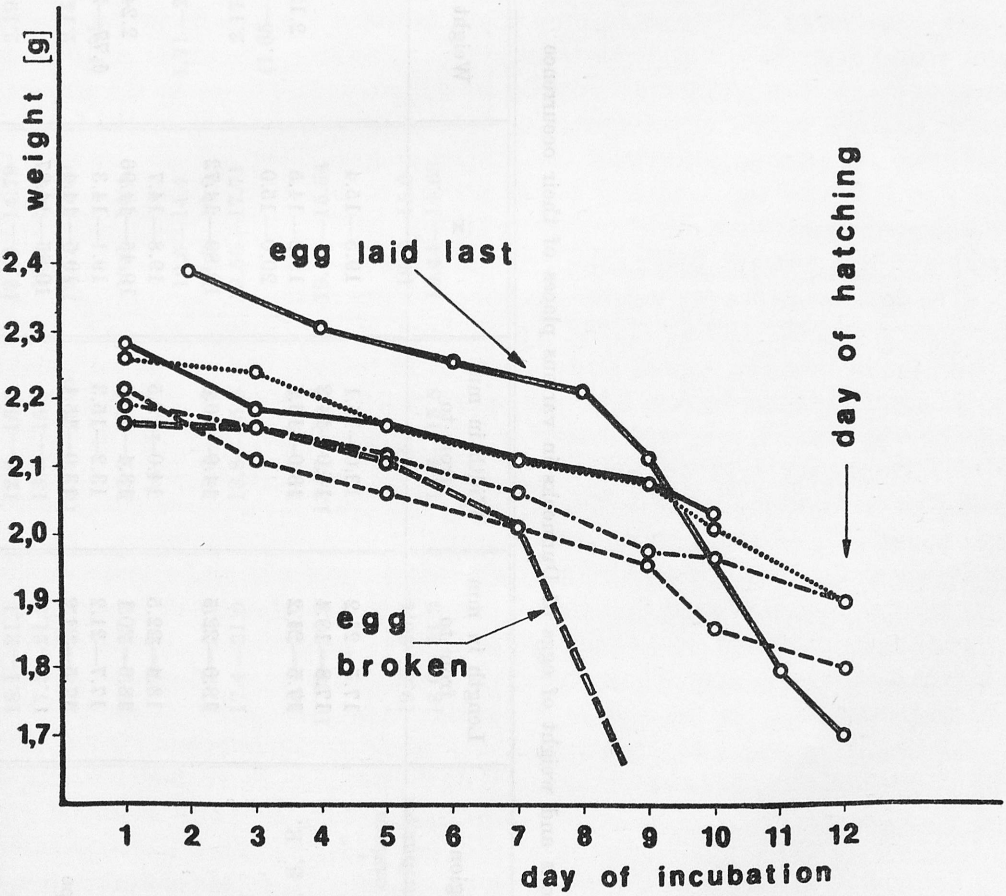

Fig. 2. Changes in egg weight during incubation

were losing on weight on the average about 0.03 g daily, i.e. throughout the incubation period they became lighter by about 16% of the initial weight (Fig. 2).

Table V

Dimensions and weight of eggs of Dunnocks in various places of their occurrence

Region	Length in mm from-to	Width in mm from-to	$\overline{x}$	Weight in g	Author
Europe	17.5—21.2	13.0—15.1	19.5—15.4		HARTERT, 1905
Europe	17.8—18.4	14.0—14.2			NAUMANN, 1905
Europe	17.5—21.2	13.0—15.5	19.2—14.5	2.13	SCHÖNWETTER, 1971
Germany			20.0—15.0		CAMPBELL, FERGUSON-LEES, 1972
Great Britain	18.0—22.5	14.0—16.0	19.89—14.72		VERHAYEN, 1967 after JOURDAIN
Great Britain	18.4—22.5	14.0—15.5	19.8—14.7		SCHÖNWETTER, 1971
Great Britain	18.6—20.1	13.4—15.9	19.45—14.96	2.24	MAKATSCH, 1976
Belgium	17.7—21.2	13.2—15.3	19.1—14.3	1.77—2.33	VERHAYEN, 1967
Western Europe	17.5—21.2	13.0—15.1	19.5—14.4		DEMENTEV et al. 1954
Switzerland			19.85—14.87		POCHELON, in: GLUTZ a and BAUER, 1985

Central Europe	18.1—21.1	12.8—16.0	19.53—14.79	2.19	Makatsch, 1976
	17.5—21.2	13.0—15.1	19.0—14.4		Makatsch, 1976, after Rey
Czechoslovakia	17.5—24.2	13.45—16.95	19.51—17.49	2.14 (1.81—2.66)	Hudec et al., 1983
Czechoslovakia	17.5—22.5	13.2—16.0	19.2—14.4		Hanzak, 1972
Poland	17—20	14—15.5			Taczanowski, 1882
Poland			19.5—14.4	1.71—2.25	Szczepski, Kozłowski, 1953
Poland	17.5—22.0	13.0—15.5	19.5—14.5		Gotzman, Jabłonski, 1972
Poland, ONP	17.4—21.0	13.8—15.5	19.56—17.71	2.17 (1.65—2.60)	present materials
Byelorussian S. S, R.	18.4—24.0	14.4—14.9			Fedyushin, Dolbik, 1967
U. S. S. R.	18.28—20.8	13.97—16.5	19.56—15.54		Dementev et al. 1954 after Menzbir
U. S. S. R. — eastern boundary of distribution	19.5—20.4	15.0	19.9—15.0		Molodovskiy, 1979
Sweden	18.0—21.3	13.7—15.5	19.44—14.68		Makatsch, 1976 after Rosenius

Both the dimensions of the eggs from ONP and their weight were similar to those found in the whole area of occurrence of Dunnocks. The dimensions of eggs given from the territory of the Soviet Union (MENZBIR, in DEMENTEV et al., 1954; MOLODOVSKIY, 1979) were somewhat larger and so were those given by CAMPBELL and FERGUSON-LEES (1972), these last writers did not give the range of variation, but probably only the mean values. According to the remaining authors (Table V), the mean values of the egg-size were similar to or somewhat smaller than those found in ONP, these differences being of the order of 0.05 mm. The weight of eggs given by a small number of authors (Table V) was slightly smaller (on the average by 0.1 g) than in our material.

The variation of the egg-size in the Dunnock, reaching 0.6×0.2 mm within a clutch was stated by NAUMANN (1905), who did not write which eggs, as regards their order of laying, were larger and which smaller. FEDYUSHIN and DOLBIK (1967) also found differences in dimensions between the eggs from one clutch and wrote that they may even reach 3 mm. However, the small number of measurements does not permit any far-reaching conclusions as to the changes in the size and weight of the eggs of one clutch as they are laid by the female, the more so, because sometimes the difference was slight 0.2 mm or 0.11 g. All this indicates the tendency for Dunnocks to lay larger and larger eggs (notably the last one), which agrees with the hypothesis of "brood-survival strategy" put forward by SLAGSVOLD et al. (1984).

The decrease in the egg weight with time was due to the evaporation of water through the shell. DRENT (1975), PRINZINGER et al. (1979), AR and RAHN (1980) found that the eggs of birds lost from 15 to 20% of their initial weight in the course of incubation. The eggs examined in the present study, losing about 16% of their weight, behaved in a typical manner. The loss in weight in the Dunnock's eggs during incubation is probably the same in different places of its occurrence; according to DRENT (1970), the eggs of this species lose about 17% of their weight. The possibility for measuring errors to creep in during the weighing of eggs under field conditions did not permit me to determine the decrease in the weight of eggs more accurately and to find, among other things, whether it was regular all through the period of incubation despite the fact that the graph in Fig. 2 suggests a change in its rate, namely, a greater fall in weight towards the end of incubation.

3.4. Incubation of eggs

3.4.1. Behaviour of female

The female laid eggs in the complete nest, as a rule, in the morning, soon after sunrise, at 24-hour intervals. Having laid the penultimate egg, she started incubation. The female left the nest to get food (only once I observed the feeding of the incubating female by the male). The breaks in incubation took from several to some dozen minutes and the more numerous the breaks were, the shorter they lasted. For instance, a female incubating 4 eggs, observed on the 7th and 8th days of incubation, left the nest for periods from 2 to 50 minutes. One day, during the 15-hour-long daily activity (i.e. from her first leaving of the nest after the night till she settled down in it for the next night) the female got off the nest 12 times, staying away for 243 min. The mean break was 22.8 min. and the bird stayed away from the nest altogether about 29% of the time of its daily activity. The next day the same female left the nest 18 times during 11 hours of observation (including 4 times when she was scared away), staying away for 152 min. i.e. about 22.7% of the time of observation and the mean break in incubation lasted 8.4 min. The length of her absence from the nest

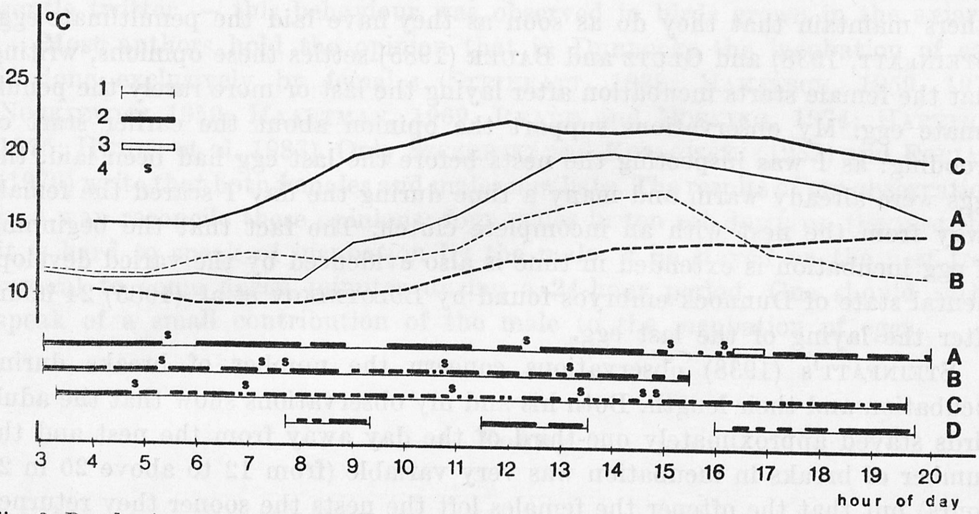

Fig. 3. Breaks in nest warming during the incubation of eggs and hatching of young on the background of temperature on given days, 1 — time of observation, 2 — presence of female on nest, 3 — incubation by male, s — female scared away. Incubation: A — 8 July 1976, B — 9 July 1976; hatching: C — 14 July 1976, D — 6 July 1978, A, B, C — the same female, D — another female

did not depend on the fact whether she had left it voluntarily or whether she had been scared away from it, for the females returned to their nests 37, 20, 12, 7 and even 1 min. after being scared away. In the period of the hatching of the young the number of breaks in incubation increased still more and simultaneously the female shortened the time of her absence from the nest. The female observed left the nest containing eggs and chicks 42 times during a day, her longest absence lasting 20 min. (the mean time of the absence from the nest was 7.26 min.). As a result of the frequent absence from the nest the total time of her staying away was somewhat longer than in the period of eggs incubation, i.e. 305 min. altogether, or 33.6% of the time of daily activity. The number and length of the breaks in the warming of the nest during the incubation of the eggs and the hatching of the young relative to the changing temperature are presented in Fig. 3. During several-hour-long observations other females behaved in a similar way and their cumulative absence from the nest on the days of hatching formed 37.1% of the time of observation.

The female left the nest containing eggs and chicks, among others, to acquire food for the young hatched by then. However, the feeding of the young was not the only reason for which she so often left the nest. This is evidenced by the fact that on her returning the female, which left the nest 42 times, only 22 times fed the young. In the remaining 20 cases she cleaned and tidied up the nest or settled down in it without doing any additional work.

Opinions differ as to the time of the start of the egg incubation period. Some authors think that the Dunnocks begin incubation after lying the last egg (Makatsch, 1976; Hudec et al., 1983; Szczepski and Kozłowski, 1953), others maintain that they do as soon as they have laid the penultimate egg. (Steinfatt, 1938) and Glutz and Bauer (1985) settles these opinions, writing that the female starts incubation after laying the last or more rarely the penultimate egg. My observations support the opinion about the earlier start of brooding: as I was inspecting the nests before the last egg had been laid, the eggs were already warm and many a time during the day I scared the female away from the nest with an incomplete clutch. The fact that the beginning of egg incubation is extended in time is also evidenced by the varied developmental state of Dunnock embryos found by Bolotnikov et al. (1985) 24 hours after the laying of the last egg.

Steinfatt's (1938) observations concern the number of breaks during incubation and their length. Both his and my observations show that the adult birds stayed approximately one-third of the day away from the nest and the number of breaks in incubation was very variable (from 12 to above 20 in 24 hours) but that the oftener the females left the nests the sooner they returned to them. In consequence, the adult birds stayed in the nests longer when they made more breaks. The time of absence of the female from the nest in the egg incubation period may have depended on ambient temperature: on a cooler day she stayed shorter away from the nest. However, the temperaure differences from 0.3 to 3.5°C (Fig. 3; A, B) do not account for so great differences in the number and duration of breaks in incubation in the same female. Neither are the breaks during a day differentiated in accordance with changes in the ambient temperature at the time of both incubation and hatching. A long stay off the nest therefore confirms Shilov's (1968) view that the birds that build nests with thick walls stay away from them much longer (about 4 hours) than the birds whose nests have thin, open-work walls (e.g. Warblers).

3.4.2. Behaviour of male

While the female was incubating the eggs, the male stayed in the proximity of the nest, giving signs of his presence by singing. He began singing soon after sunrise and sang at a distance of several to 20 and even 30 metres from the nest at a various frequency all through the day. He appeared close to the nest several to more than ten times daily but did not feed the incubating female. He replaced the female on the nest only exceptionally and for a short time at that. And so in one of the observed nests the male incubated the eggs for 34 minutes once a day; in another nest the male replaced the female for about 5 min. and in still another one for about 15 sec. After the hatching of the young he appeared at the nest much more frequently. As early as the day on which the young were hatching he brought food when visiting the nest and so he joined the feeding of the young actively from the first moment of their life. Then he sang at various distances from the nest but less frequently than before when the eggs were in the nest. After the hatching of the young, when the female left the nest, he behaved sexually towards her (somewhat raised tail, dropped, fluttering wings, gentle twitter — this behaviour was observed in birds grown in the aviary).

Most authors hold the opinion that in Dunnocks the incubation of eggs is done exclusively by females (Steinfatt, 1938; Makatsch, 1959, 1976; Noskiewicz 1959; Haartman, 1969, Reade and Hosking, 1974; Harrison, 1975; Hudec et al. 1983). Only Szczepski and Kozłowski (1952) and Ferianc (1979) write that both females and males incubate. The results of my observations in a way reconcile these opinions: four males in ten sat down on the nest, but it is hard to speak of incubation by the male, if he stayed on the nest from several to some dozen minutes during a 24-hour period. One should rather speak of a small contribution of the male to the incubation of eggs.

4. Young

4.1. Hatching

The young hatched 12 or 13 days (respectively, in 7 and 4 nests) after the start of incubation. The chicks did not hatch at the same time, but at intervals of several hours (the nests inspected on the day of hatching contained chicks already dry and others with down still wet and stuck together, and eggs — Phot. 3). The last chick usually hatched the following day and the one-day difference in development was distinct up to the end of the nestling period (cf. Development of young).

The phenomenon of asynchronous hatching of the young has already been observed by Steinfatt (1938), Noskiewicz (1959) and Krzywiński (1965). The asynchronism of hatching may be connected, among other things, with the earlier start of incubation, which aims at the shortening of the nestling period, during which the broods are heavily reduced by predators (Slagsvold, 1985). Then, in order to achieve the highest possible breeding success the Dunnocks adapted themselves by having relatively small clutches (better chance to feed the young) and shortening the nestling period (smaller pressure of predators on broods), at the same time with the survival of nearly all the chicks hathed owing, among others, to the increased size of the last egg of the clutch (Slagsvold et al., 1984).

4.2. Warming of young

After the hatching of the young the female still spent much time on the nest, brooding on it after her arrivals with food and also spending nights until the penultimate day of the stay of the young in it. The time given to the warming of the nestlings changed with their age (Table VI). The older the young were, the shorter was the time of warming and also the smaller was the daily number of warmings. The young did not cease to be warmed before the last day of their stay in the nest.

Table VI

Times of warming of young by female Dunnock in particular days of nestling period

Age of chicks in days	No of observation days	Total time of observation in min	Stay of female on nest in min	% of observation time	No of warmings	Mean time of 1 warming in min	Time of warming in min per 1 hr of life of chick	No of warmings per hour of life of chick
1 (Hatching)	1	875	551	62.9	41	13.4	37.7	2.8
2	1	120	56	46.6	3	18.6	23.0	1.5
3	1	460	213	46.3	23	9.3	27.6	3.0
5	3	1075	363	33.8	37	9.8	20.9	2.1
6	2	1185	347	29.3	34	10.2	17.6	1.7
7	1	840	125	14.9	18	6.9	8.5	1.3
8	3	1520	324	15.4	32	7.3	9.2	1.3
9	2	1357	206	15.2	26	7.5	9.1	1.2
10	1	875	34	3.9	6	5.7	2.3	0.4
11	1	465	—	—	—	—	—	—

Literature provides only a few data concerning the warming of the young by adult Dunnocks. NOSKIEWICZ (1959) and KRZYWIŃSKI (1965) wrote that the females stayed on the nests during the first days of life of the young, without giving a mention to the warming of the young in the night. On the other hand, STEINFATT (1938) maintained that they warmed the chicks until the 10th day of life (with the 13-day nestling period) and therefore similarly to the birds observed in ONP.

The authors who observed the warming of the young in open nests by, e.g., Hawfinches (KRÜGER, 1982) or Fieldfares (HAAS, 1982), found that the warming of the young was dependent on weather conditions. The shortening of the periods spent by the female on the nest with the development of the chicks indicates however that the warming of the young depends chiefly on thermoregulation acquired by them; it develops in nidicolous birds by degrees during their nestling period (SHILOV, 1968).

4.3. Feeding of young

The female Dunnock's began to feed their young soon after their hatching. The present observations show that the younger chicks were fed more rarely than the older ones (Fig. 7). Despite great individual variation in the frequency

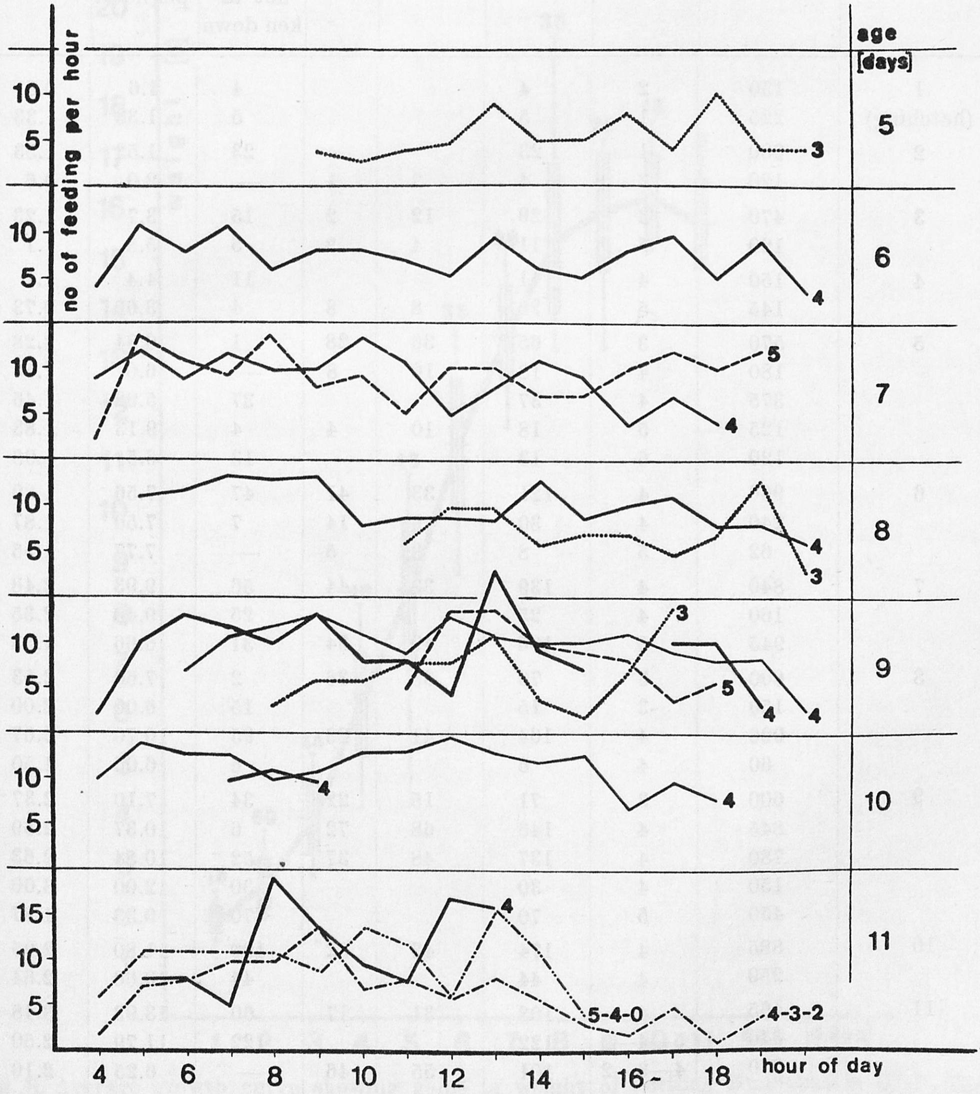

Fig. 7. The number of arrivals of adult birds with food at the nest in particularly hours of the day. The figures by the curves indicate the number of nestlings in the nest

Table VII

Number of feeding visits of adult birds and frequency of feeding of young during successive days of nestling period in Dunnocks

Age of young in days	Time of observ. of nest in min	No of young in nest	No of feedings	No of feeding visits: Female	Male	Sex undetermined or not taken down	Average number of feeding visits: per clutch per hour	per chick per hour
1	150	2	4			4	1.6	0.8
(hatching)	225	1	5			5	1.33	1.33
2	900	1	23			23	1.53	1.53
	120	3	4	3	1	—	2.0	0.6
3	470	3	29	12	2	15	3.7	1.23
	120	5	11	4	2	5	5.5	1.1
4	150	4	11			11	4.4	1.1
	145	5	20	8	8	4	3.69	0.73
5	570	3	65	36	28	1	6.84	2.28
	180	4	18	10	8	—	6.0	1.50
	375	4	37			37	5.92	1.46
	125	5	18	10	4	4	9.13	1.83
	120	6	13			13	6.5	1.08
6	960	4	121	33	41	47	7.56	1.89
	240	4	30	9	14	7	7.50	1.87
	62	5	8	3	5	—	7.77	1.55
7	840	4	139	39	44	56	9.93	2.48
	160	4	25			25	9.40	2.35
	945	5	105	40	34	31	6.66	1.33
8	600	3	76	38	36	2	7.60	2.53
	150	3	15			15	6.00	2.00
	920	4	164	41	28	95	10.70	2.67
	60	4	6			6	6.00	1.50
9	600	3	71	15	22	34	7.10	2.37
	845	4	146	68	72	6	10.37	2.59
	780	4	137	48	37	52	10.54	2.63
	150	4	30			30	12.00	3.00
	450	5	70			70	9.33	1.87
10	885	4	174	42	32	100	11.80	2.95
	250	4	44			44	10.60	2.64
11	465	4	108	31	17	60	13.93	3.48
	640	5—4—0	122			122	11.79	2.50
	970	4—3—2	101	55	46	—	6.25	2.10
Total			1545	545	481	519		

of feeding of the young of the same age, it can be stated that in larger broods the number of arrivals with food falling to one chick is somewhat lower than it is in smaller broods (Table VII).

The young Dunnocks were fed by both parents; the adult birds brought food in the bill and crop. Both the female and male fed the young directly, only twice the male was observed to deliver food to the female and next she fed it

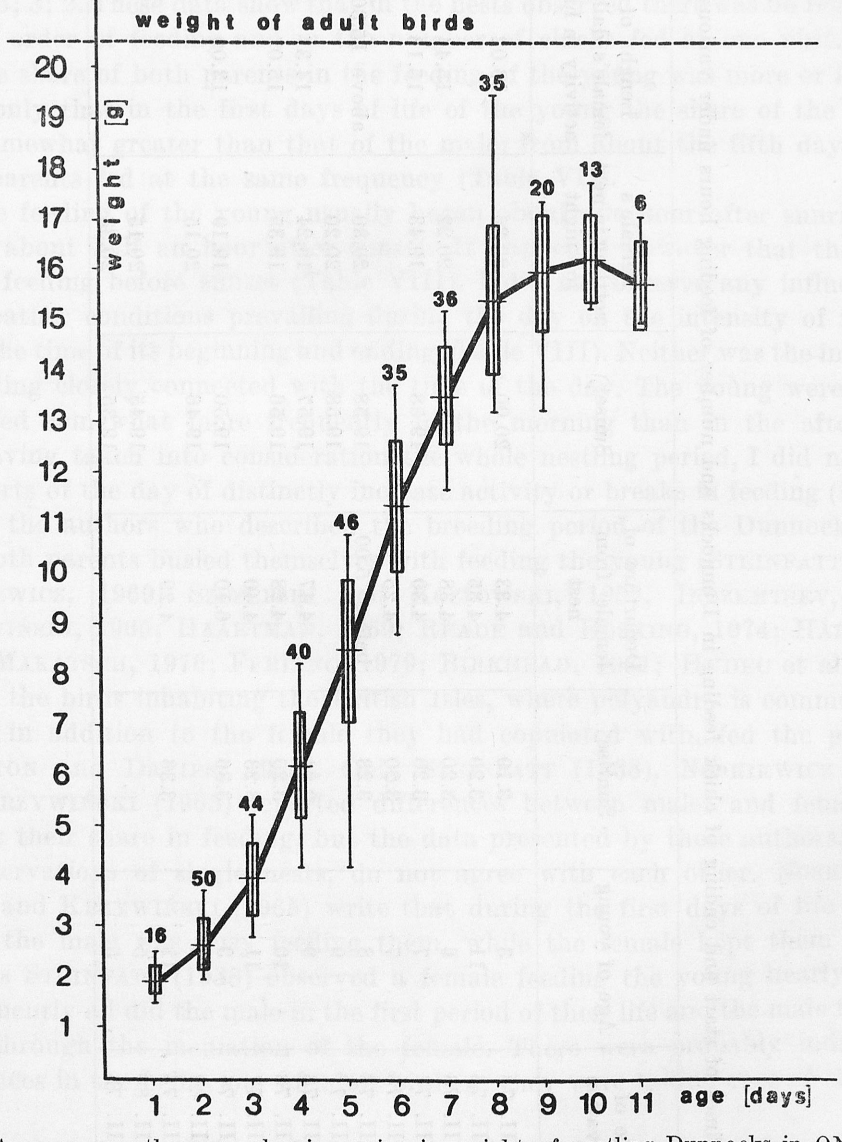

Fig. 8. Average growth curve showing gains in weight of nestling Dunnocks in ONP. The horizontal lines indicate the mean body-weigt, the vertical lines represent the weight ranges and the boxes enclose ± SD, the figures indicate the sample sizes

Table VIII

Times of start and ending of chick feeding in Dunnocks and number of feeding hours under various weather conditions

Date of observation	Age of young	Sunrise	Departure of female from nest	Sunset	Female's settling in nest for night	Lenght of female's daily activity in hrs	Weather
2. VII. 78	3	3.19	4.33	20.00	20.35	16.02	drizzle
3. VII. 78	11	3.20	4.35				sunny
4. VII. 78	6	3.20	4.38	19.58	20.22	15.44	fine
4. VII. 77	7	3.20	4.30	19.58	19.43	15.13	rain
5. VII. 78	7	3.20	4.25				downpour in evening
6. VII. 78	8	3.23	before 5.00	19.58	20.30	above 15.30	fine
6. VII. 77	9			19.58	20.20		light rain
7. VII. 78	9	3.24	4.47	19.57	19.24	14.37	rain at noon
8. VII. 78	10	3.25	4.28	19.56	19.35	15.07	rain at noon
8. VII. 77	11	3.23	4.40				fine
14. VII. 76	3	3.36	6.10	19.50	19.19	13.09	light rain
19. VII. 80	3			19.46	20.15		rain
19. VII. 75	11	3.36	4.29				rain
21. VII. 80	5			19.45	20.15		rain
27. VII. 78	5			19.35	20.33		sunny

to the young. One, two or three chicks were fed at one visit of an adult bird to the nest. Besides, if three chicks were fed, the ration of one of them was smaller than the rations of the other two chicks. The order in which the individually marked chicks received food was noted in three nests. And so during a period of about one hour in the nest with 5 chicks they received food successively, as follows: 1 and 3; 2 and 5; 4 and 1; 4; 5 and 1; ?; 5 and 1. In another nest with 4 chicks food was given successively to 1; 2; 2 and 3; ?, ?, ?; ??; 4; 2 and 4; ?; ?; and in a nest with 3 chicks the order of feeding was 1 and 2; 3; 1 and 3; 3; 2. These data show that in the nests observed there was no regularity in the order of feeding and in the number of chicks fed at one visit.

The share of both parents in the feeding of the young was more or less the same only that in the first days of life of the young the share of the female was somewhat greater than that of the male; from about the fifth day of life both parents fed at the same frequency (Table VII).

The feeding of the young usually began about one hour after sunrise and ended about half an hour after sunset. It happened however that the birds ended feeding before sunset (Table VIII). I did not observe any influence of the weather conditions prevailing during the day on the intensity of feeding or on the time of its beginning and ending (Table VIII). Neither was the intensity of feeding closely connected with the time of the day. The young were, to be sure, fed somewhat more frequently in the morning than in the afternoon, but having taken into consideration the whole nestling period, I did not find any parts of the day of distinctly increase activity or breaks in feeding (Fig. 5).

All the authors who described the breeding period of the Dunnock agree that both parents busied themselves with feeding the young (STEINFATT, 1938; NOSKIEWICZ, 1969; SZCZEPSKI and KOZŁOWSKI, 1953, INOZEMTSEV, 1963; KRZYWIŃSKI, 1965; HAARTMAN, 1969; READE and HOSKING, 1974; HARRISON, 1975; MAKATSCH, 1976; FERIANC, 1979; BIRKHEAD, 1981; HUDEC et al. 1983) and in the birds inhabiting the British Isles, where polyandry is common, the males, in addition to the female they had copulated with, fed the progeny (HOUSTON and DAVIES, 1985). Only STEINFATT (1938), NOSKIEWICZ (1959) and KRZYWIŃSKI (1965) reported differences between males and females as regards their share in feeding, but the data presented by these authors, based on observations of single nests, do not agree with each other. NOSKIEWICZ (1959) and KRZYWIŃSKI (1965) write that during the first days of life of the young the male was busy feeding them, while the female kept them warm, whereas STEINFATT (1938) observed a female feeding the young nearly twice as frequently ad did the male in the first period of their life and the male feeding them through the mediation of the female. There were probably individual differences in the behaviour of adult birds as they were taking care of the progeny.

The above-presented results of observations concerning the frequency of the feeding of the young agreed with the data published by INOZEMTSEV (1963) and STEINFATT (1938). STEINFATT (1938) found also that the frequency of arrivals with food increased with the age of the chicks (from 3.5 per hour in the nest with 3 chicks 1—2 days old to 6.5 with the same chicks aged 11—12 days). Both these authors state also somewhat more frequent arrivals with food in the morning hours. The change in the frequency of feeding with the time of the day was in general much smaller in the Dunnock than in other birds like *Passer montanus*, *Parus caeruleus* (GYURKO et al. 1949) or *Lullula arborea* (MACKOWICZ, 1970). The Dunnocks living in the lowlands (INOZEMTSEV, 1963; STEINFATT, 1938; the authoress' own material) show the rhythm of feeding similar to that of birds inhabiting the alpine zone, where the time of the day and weather conditions have no major influence on the change in the frequency of feeding (KOVSHAR, 1981). It may be assumed therefore that the Dunnocks, inhabiting, like the members of the whole genus *Prunella*, chiefly the alpine zone, keep their ways of life also in the lowlands.

4.4. Nest-helpers

I found the presence of nest-helpers at two nests in the twelve observed. At one nest the adult birds were caught and marked individually with coloured rings. The additional bird was a female or a young male (acc. to NAUMANN, 1905, the young male is coloured exactly like the female) and appeared at the nest very rarely. It fed the young only seven times right through the day and so its share in the feeding of the young was minute. Neither did this bird take part in incubation: having caught all the three birds appearing at the nest I found that the skin on the belly of the additional bird was not changed, while in the female it was changed in the typical manner of the incubating birds and in the case of the male the skin of the belly bore traces of incubation for only a short period of time.

The phenomenon of polygyny or polyandry and in this connection the feeding of the young by more than two parental birds encountered very commonly in the Dunnocks inhabiting the British Isles (SNOW and SNOW, 1982; BIRKHEAD, 1981; DAVIES and LUNDBERG, 1985; HOUSTON and DAVIES, 1985) found no confirmation in the birds living in the European continent. Here the existence of "families" consisting of more adult specimens than 1 female and 1 male has been observed, in addition to ONP, only on Lake Ladoga (YAKOVLEVA, 1983). The markedly rarer occurrence of such "families" as compared with the British population was probably the result of another manner of colonization of the area. In the British Isles the Dunnocks are stationary and have their fixed territories which are rather their "zones of influences" (SNOW and SNOW, 1982), whereas in the continent the Dunnocks fly away to winter quarters and on arriving occupy their territories in spring. The factor influencing the formation of numerous families may also be the density of population. With the considerably lower density of these birds in the east of Europe the possibility of the overlapping of the territories of particular birds is far smaller. This hypothesis is corroborated by the above-discussed existence of nest-helpers in ONP and so in the biotope where the density of Dunnocks was much higher than in the neighbouring areas (i.e., in the lowlands of Poland and in Slovakia). Unfortunately, theree are no observations at all of the behaviour of the birds inhabiting the continental part of Western Europe or the regions where the Dunnock is a sedentary inhabitant of parks and gardens and so living in similar conditions to those it has in the British Isles. For this reason it is hard to infer whether the differences in the behaviour of birds under discussion resulted only from the different character of their occurrence or also from their belonging to two different subspecies (the British Isles are inhabited by the subspecies *Prunella modularis occidentalis* (HARTERT 1910)). The occurrence of co-operative breeding may however be a characteristic features of the genus *Prunella*, for apart from both subspecies of *Prunella modularis*, DYRCZ (1977) found it also in the Alpine Accentor *Prunella collaris*.

4.5. Attention to nest sanitation

The maintenance of cleanness in the nest consisted of "dabbing in the nest", removal of egg shells and taking away excrements. The action of dabbing in the nest was done exclusively by the female. In addition to the changing of the position of the eggs, it probably aimed at the removal of objects that found themselves in the nest, the repairing of the structure of the nest and perhaps the clearing of parasites from it. The egg-shells left after the hatching of the chicks were eaten up by the female (the unhatched eggs — added and those with dead embryos — remained in the nest until the fledglings flew away). Except for the shells, the objects removed from the nest were mostly so small that they were invisible to the observer; they were probably also eaten up, for I did not see anything being taken away from the nest. The removal of a wire from the nest was the only exception; the wire had been used to make a comparison ring placed on the neck of a chick, which was later thrown out together with this chick (the chick was 6 days old, still unfledged and the wire on its neck was well seen). The wire with the chick fell directly under the nest and so could easily be found and the chick was placed back in the nest.

The female mended the nest and dabbed in it at varying frequency, decreasing with the age of the chicks (Table IX).

Table IX

Changes in frequency of female Dunnock's dabbing in nest with age of chicks (there were 3 chicks in the nest)

Age of chicks in days	Length of observation in min	No of action of dabbing in nest	No of action of dabbing in nest per hour
3	470	16	1.98
5	684	7	0.61
8	546	5	0.55
9	589	1	0.10

Table X

Frequency of defecation in young Dunnocks and of removal of faeces by adult birds on successive days of nestling period

Age of chicks in days	Lenght of observation of nest, in min (no of chicks)	No of capsules of faeces removed from nest (= 100%)	No of capsules of faeces removed per chick per hr	Percentage of capsules of faeces removed by			Percentage of capsules of faeces	
				Female	Male	Sex undetermined	Eaten	Carried away
2	120 (3)	4	0.06	50	50	—	100	—
3	470 (3)	12	0.53	75	25	—	100	—
4	145 (5)	3	0.25			100		
5	570 (3)	34	1.19	47.1	38.2	14.7	26.5	73.5
	125 (5)	7	0.67	42.9	28.6	28.6	28.6	71.4
	435 (4)	22	0.86			100.0	45.5	54.5
6	62 (5)	3	0.58	33.3	66.6	—		
	960 (4)	29	0.45			100.0	13.8	86.2
	240 (4)	12	0.75			100.0	16.7	83.3
7	945 (5)	27	0.34	44.4	25.9	29.6	100,0	—
	840 (4)	31	0.55			100.0	3.2	96.8
	160 (4)	12	1.13			100.0	25.0	75.0
8	600 (3)	24	0.80	41.7	50.0	8.3	8.3	91.7
	920 (4)	55	0.90	18.2	23.6	58.2		
9	600 (3)	18	0.60	44.4	27.7	27.7	—	100.0
	845 (4)	42	0.75	42.8	52.4	4.8	2.4	97.6
	780 (4)	41	0.79	24.4	39.0	36.6	—	100.0
10	885 (4)	44	0.75	25.0	13.6	61.4	—	100.0
	250 (4)	11	0.66			100.0	—	100.0
11	970 (4—3—2)	32		53.1	34.4	12.5	—	100.0
	465 (4)	38	1.23	28.9	21.1	50.0	—	100.0
	235 (4)	16	1.02			100.0	—	100.0

The chicks' excrements were removed from the nest by the adult birds. The parents usually removed the faecal capsules from the nest after feeding the young. The several first visits of the adult birds to the nest after the night break, when they only took the faeces out of the nest, without feeding the young, were an exception. The chicks evacuated their bowels more or less regularly throughout the day. The frequency of evacuation increased somewhat with their age (Table X). The mean frequency of evacuation all through the nestling period was about 0.74 portion/chick/hour. Both the parents removed faeces between them, their share in this being similar. Faecal capsules were either eaten up by the adults birds or taken away from the nest. In the first days of life of the chicks they were more often eaten up, later, the older the chicks were, the oftener their faeces were taken away from the nest (Table X).

The present observations agree with those published by Steinfatt (1938), who states the eating of faeces in the first days of life of the chicks, their being next taken away from the nest, similar shares of the female and male in their removal and the similar frequency of evacuation in the young (0.58 portion/chick/hour at the age of 8 and 9 days and 0.85 portion/chick/hour at the age of 11—12 days). Noskiewicz (1959) also mentions the removal of faeces from the nest by both parents, whereas Krzywiński (1965) maintains that for the first three days the female warmed the young continuously and the other bird took away faeces after each feeding, i.e. every 15—30 minutes. The data of the latter author would evidence that there may exist the above-mentioned individual variation in the behaviour of Dunnocks (perhaps depending on external conditions). However, it seems in sum that the division (more or less equal) of duties connected with raising the progeny between the two parental birds occurred more frequently, except for warming which belonged exclusively to the duties of the female.

4.6. Diet of young

Dunnocks as a rule forage on the ground. Small invertebrates living on the ground, in litter, on the plants of undergrowth,on tree trunks and branches lying on the ground fall victims to them. The food brought to the young was crushed; the portion a chick received at a visit of a parent consisted of several or even some dozen invretebrates and only exceptionally of one specimen. The largest portion in respect of the number of components comprised 122 specimens, including, among others, 93 aphides. The volume of an average portion of food was ca 0.5 cm³. The numbers of specimens going into the making of one portion of food received by a chick and one portion brought by an adult bird to the nest are presented in Tables XI and XII. The values in the tables may be somewhat underrated, for they do not include the part of food which the chicks managed to swallow before it had been removed (in several cases the compression rings were placed inaccurately).

The mean portion of food received by a chick calculated from the findings of 3 years consisted of 25.5 specimens and the mean portion brought by an adult bird of 34.4 specimens.

Table XI

No of specimens of invertebrates fed to one chick at a feeding visit

No of specimens	No of portions			
	1978	1980	1981	Total
1	2	—	—	2
2—10	21	9	7	37
11—20	25	7	7	39
21—50	42	5	1	48
51—100	11	—	—	11
above 100	1	—	—	1
Total	102	21	15	138

Table XII

Number of specimens of invertebrates brought by adult bird at one feeding visit to nest

No of specimens	No of portion			
	1978	1980	1981	Total
1	—	—	—	—
2—10	8	6	3	17
11—20	12	4	5	21
21—50	30	7	3	40
51—100	19	—	—	19
above 100	2	—	—	2
Total	71	17	11	99

The food of chicks was not only disintegrated but also diversified. The frequency of particular groups of food established for one portion brought by an adult bird at its visit to the nest is given in Table XIII. The food of animal origin predominates considerably over the vegetable food. In the samples analysed the vegetable components were found 32 times; these were for the most part seeds of the wood sorrel *Oxalis acetosella* and also 3 small twigs of moss

Table XIII

Specific composition and frequency of particular groups of invertebrates in food of young Dunnocks

Systematic group	No of specimens				Frequence			
	1978	1980	1981	Total	1978	1980	1981	Total
Malacostraca — *Isopoda*	7	5	14	26	7	2	8	17
Arachnida — *Pseudoscorpionidea*	3			3	2			2
Opilionidea	92	13	12	117	38	8	7	53
Araneae	118	13	24	155	45	7	7	59
Acarina (*Ixodes* sp.)	3		1	4	3		1	4
Myriapoda — *Chilopoda*	1			1	1			1
Insecta — *Collembola*	292	15	32	339	57	11	9	79
Coleoptera — larvae	11		2	13	7		1	8
pupae	1	2	2	5	1	2	1	4
imago	17	4	2	23	5	4	2	11
Neuroptera	4	1		5	3	1		4
Trichoptera		1		1		1		1
Lepidoptera — larvae	14	7	2	23	12	6	2	20
pupae	2			2	2			2
imago	13	6	1	20	13	5	1	19
Diptera — larvae	8	2		10	8	1		9
pupae	20	1	31	52	15	1	13	29
imago	507	77	9	593	56	16	6	78
Hymenoptera — larvae	15	1	3	19	13	1	3	17
imago	5	1		6	5	1		6
Psocoptera	8	7	40	55	7	4	11	22
Homoptera — larvae	6			6	4			4
imago	1530	30	64	1624	69	14	9	92
Heteroptera — larvae		1		1		1		1
imago	33	2	2	37	12	1	1	14
indet. larvae	89	6	4	99	33	4	4	41
insect eggs	6	1	44	51	1	1	5	7
Gastropoda	10	18	5	33	10	7	3	20
plants	39	30	32	101	15	9	8	32
pebbles	2			2	2			2

as well as a seed and a needle of the spruce *Picea excelsa*. Out of the invertebrates entering into the composition of the food of Dunnock chicks the occurrence of the *Arachnida* and *Insecta* was the highest.

Arachnids occurred in the food of the Dunnock frequently, but not in very large numbers; they were members of four orders: *Opilionidea*, *Araneae*, *Pseudoscorpionidea* and *Acarina*. A total of 279 specimens belonging to at least 42 species have been identified in the food analysed. The specific composition of the *Arachnida* from the orders *Opilionidea* and *Araneae* is presented in

Table XIV

Arachnids of orders *Opilionidea* and *Araneae* distinguished in food of chicks of Dunnock (determined by Dr W. Staręga)

Species	Juv.	Female	Male	Total
Opilionidea:				
Oligolophus tridens	79	—	—	79
Lacinius ephippiatus	7	4	3	14
Platybunus bucephalus	—	8	—	8
Leiobunum rupestre	7	—	—	7
Mitopius morio	3	2	3	8
Paranemastoma quadripunct.	1	—	—	1
Total	97	14	6	117
Araneae:				
Helophora insignis	19	—	—	19
Enoplognatha ovata	9	—	—	10
Linyphia triangularis	21	—	—	21
Lopophilio palpinalis	21	—	—	21
Batyphantes nigrinus	1	4	3	8
Leptyphantes cristatus	1	6	—	7
L. tenebricola	2	4	1	7
L. alecris	—	6	—	7
L. modifer	—	1	—	1
L. obscurus	—	1	—	1
L. sp.	10	—	—	10
Diplocephalus latifrons	—	3	—	3
Drapesticta socialis	4	—	—	4
Floronia bucculenta	4	—	—	4
Pachygnatha listeri	—	2	1	3
Polyphantes alticeps	3	—	—	3
Robertus lividus	—	—	2	2
Cryphaeca silvicola	1	1	—	2
Gonatinum isabellinum	2	—	—	2
Micrargus herbigradus	—	2	—	2
Bathyphantes gracilis	—	2	—	2
B. alticeps	1	—	—	1
Macrargus rufus	—	1	—	1
Dicymbium nigrum	—	1	—	1
D. tibiale	—	1	—	1
Cycloca conica	—	—	1	1
Nerina peltata	—	—	1	1
N. clathrata	—	1	—	1
Meta squamata	1	—	—	1
M. mengei	—	1	—	1
Theridion mystaceum	—	1	—	1
Diplostyla concolor	—	1	—	1
Pityohyphantes phryianus	—	1	—	1
Maso sundevalli	—	1	—	1
Micronota varia	—	1	—	1
Linyphiidae	1	—	—	1
Erigonidae	1	—	—	1
Total	102	42	11	155

Table XIV. It can be seen from Table XIV that the Dunnocks most often took juveniles (altogether 199 specimens or 73.1%), adult females being much fewer in the food (56 specimens, 20.6%) and adult males quite rare (17 specimens, 6.3%.)

Table XV

Springtails *Collembola* distinguished in food of chicks of Dunnocks (determined by Prof. A. SZEPTYCKI)

Species	No of specimens
Orchesella flavescens	191
Allacma fusca	36
Orchesella multifasciata	3
Entomobrya muscorum	5
Tetradontophora bielanensis	1
Isotomurus sp.	2
Tomoceridae	101
Total	339

Table XVI

Beetles *Coleoptera* (imagines) distinguished in food of chicks of Dunnocks (determined by Dr A. KUŚKA)

Species	No of specimens
Phyllobius calcaratus	4
Ph. arborator	2
Ph. argentatus	2
Polydrurus impar	2
Cidnorhinus quadrimaculatus	1
Brachysomus echinatus	1
Ceutorhynchus erysimi	1
Cantharis nigricans	1
Podabrus alpinus	1
Malthodes sp.	2
Agriotes sp.	1
indet.	5
Total	23

In respect of abundance and frequency in the food the group of springtails (*Collembola*) resembled that of arachnids; the specific differentiation of this group of insects was however far smaller, for its 339 specimens belonged to about 10 species (Table XV). Members of the group *Tomoceridae*, numbering 4 species, could not be identified exactly because of their being heavily damaged. The example of springtails shows that Dunnocks take food selectively: *Tetradontophora bielanensis*, which is a common species in ONP (Szeptycki, 1967) was consumed reluctantly.

Table XVII

Butterflies *Lepidoptera* distinguished in food of chicks of Dunnocks (determined by Mr E. Palik)

Family	Number of specimens		
	Larvae	Pupae	Imagines
Geometridae	7	1	2
Noctuidae	7		1
Lycaenidae	5	—	
Arctinae	1	—	—
indet.	3	1	17
Total	23	2	20

Table XVIII

Dipterans (imagines) distinguished in food of chicks of Dunnocks (determined by Dr W. Krzemiński)

Species *Nematocera*:	No of specimens	Species (cont.)	No of specimens
Austrolimnophila ochracea	9	*Nephrotoma* sp.	6
Ormosia albitibia	5	*Ormosia* sp.	6
Cheilotrichia cinerascens	3	*Limonia* sp.	3
Sylvicola cincta	3	*Gonomyia* sp.	2
Limonia sylvicola	3	*Dicranomyia* sp.	2
L. tripunctata	2	*Pilaria* sp.	2
L. taurica	2	*Dicronata* sp.	1
Gonomyia lucidula	2	*Ula* sp.	1
Ula molissima	2	*Cheilotrichia* sp.	1
Sylvicola punctata	1	*Sciaridae*	7
Limonia rubeculosa	1	*Mycetophilidae*	3
L. trivittata	1	*Limoniinae*	3
Meolimnomyia numeralis	1	*Anisopodidae*	2
Tipula sp.	14	*Cecidomyidae*	1
Molophilus sp.	7	*Chironomidae*	1
Molophilus cinereifrons	2		
		Total of *Nematocera*	99
		Total of *Brachycera* (indet.)	494

Members of the order *Coleoptera* occurred sporadically in the food brought to the nest. There were beetles of 11 different forms among them (Table XVI). Only imagines of these insects are included in Table XVI, whereas the larvae and pupae have not been identified; anyway, they were still less numerous than the imagines.

The butterflies *Lepidoptera* were also of minor importance as a food component. This order was represented chiefly by larvae: 45 lepidopteran remains identified belonged to 4 different families (Table XVII).

Table XIX

Homoptera distinguished in food of chicks of Dunnocks (determined by Prof. A. Szeptycki)

Systematic group	No of imagines
Aphiododea	1422
Psyllodea	5
Coccodea	10
Other homopterans indet.	187
Total	1624

Table XX

Snails *Gastropoda* distinguished in food of chicks of Dunnocks (determined by Dr E. Stworzewicz)

Species	No of specimens
Euconulus fulvus	14
Monachides vicina	8
Clausiliidae (juv.)	7
Trichia sp. (juv.)	2
Punctum pygmaeum	1
Zonitoides hammonis	1
Total	33

The dipterans were one of the main components of the diet of the young. They were brought to the nest fairly often: out of the 99 portions examined, 88 contained larvae, pupae and imagines of this order. About a quarter of the "flies" found in the food were classified in more than 15 genera of the *Nematocera*. The numbers of the different dipteran forms are given in Table XVIII.

The *Homoptera* formed the most numerous group of insects making up the food of the young. Their composition is given in Table XIX. The number of aphides in the food was strikingly large; they constitute the most abundant component (about 40% of the specimens in the food). As these insects are of rather small size, it seems that although they probably played an essential role in feeding, they were not the main component as regards biomass. On the other hand, this large proportion of aphides in the food may indicate the role of the Dunnock in the reduction of these insects.

The *Gastropoda* were the last closely analysed group of the invertebrates found in the food of the young. The adult birds brought their chicks both whole snails and empty shells. And so the shell fragments may have fulfilled the function of stones in the stomachs of chicks or provided mineral components. The specific composition of the snails occurring in the food analysed is presented in Table XX.

The specific composition of the invertebrates which entered into the food changed from year to year. For instance, aphides and dipterans were brought predominantly in 1978, whereas the *Isopoda* and *Psocoptera* were proportionally more numerous in 1981. The small number of food samples permits no inferences as to the causes of such a differentiation. It can only be concluded from the data presented in Table XIII that the main components of the food of the Dunnock's chicks were the *Arachnida*, *Collembola*, *Diptera* and *Homoptera*, and the constant components though taken in small numbers included the *Coleoptera*, *Lepidoptera* and *Gastropoda*.

The bringing of small-sized animals as food for the young is characteristic of the Dunnock and was found by all the authors who analysed the food (Inozemtsev, 1963; Emmrich, 1975; Davies and Lundberg, 1984; Petrusenko and Talposh, 1985). The mean portion of food brought to the nest in the material under study (calculated as the sum of all the components divided by the number of portions) consisted of 34.4 specimens. According to the data provided by Inozemtsev (1963), one portion was composed on the average of 11 specimens and Emmrich (1975) found up to 250 specimens, averaging 50—100, in the food obtained from 5 chicks during 2—3 hours. A food portion consisting of such a large number of invertebrates was not met with in other bird species of the Dunnock size (Gyurko et al., 1959; Bösenberg, 1964; Mentzel, 1971; Kaczmarek et al., 1981). The much larger Starlings, which forage on the ground like Dunnocks, brought on the average 16.6 specimens to their chicks during one hour (Bogucki, 1974), the Woodlarks about 5 specimens in one portion (Mackowicz, 1970) and the Blackbirds 2—9 specimens (Kaczmarek et al., 1981). The collecting of small-sized animals as food for the young is characteristic of the genus *Prunella*, for Kovshar (1981) found that a portion of food for the young of other members of this genus (i.e. *Prunella collaris*, *P. fulvescens*, *P. atrogularis*) consisted even of several times as many specimens ad did the portions of other bird species inhabiting the same alpine environment.

Not only did the Dunnock's food consist of a large number of specimens but it was also diversified. One portion of food contained several tens of taxonomic units, which agrees with the results obtained by Emmrich (1975). The fact that in various places of the Dunnock's occurrence the same groups of

Table XXI

Percentage frequency of main groups of organisms in samples of food of chick Dunnocks in various places of occurrence

Systematic group	Place of study and No of samaples (N)						
	ONP (present study)	Great Britain (BISHTON, 1985)	USSR (INOZEMTSEV, 1963)	Ukraine (PETRUSENKO, TALPOSH, 1985)	GDR (EMMRICH, 1975)	GDR (RIESS, 1976) *	East Prussia (Lithuanian SSR. STEINFATT 1938)
	N = 99	N=105	N=73	N=48	N=10	N=6	
Oligochaeta		11					
Arachnida	78	51	86	15.1 **	88	4 ***	+
Collembola	79		4.2	+	60		
Coleoptera	21	75	5 ***			11 ***	
Lepidoptera	30	27	30 ***		5	6 ***	+
Diptera	88	75	25 ***	46.3 ****	+	74 ***	+
Hymenoptera	21					2 ***	
Homoptera	89		100	18.4 ****		absent	
Heteroptera	15	22					
Gastropoda	20	20	20	1.6 **	+		
Plants	32	+	+		44		+

* — % of weight; ** — % of species; *** — approx. values, calculated on the basis of the author's data; **** — % of number.

animals, namely, the *Arachnida*, *Diptera*, *Lepidoptera* and *Gastropoda* were present in its food, showing similar frequencies, indicates that there is a kind of constant trend in the food composition (Table XXI). Seeds also constituted constant food components, but all the authors agree that they were of no nourishing significance. The role of seeds was rather their presence as hard parts, for they were not digested by chicks (Bishton, 1985). A comparison of the present results with those of an analysis of faeces made by Bishton (1985) shows that most of the invertebrate groups occurred at similar frequencies (Table XXI); there were however some differences: the coleopteran remains were relatively often found in the faces, whereas there were no traces of the *Collembola* and *Homoptera*. These differences were probably due to their various degrees of availability. The bodies of the *Collembola* and *Homoptera* have very few chitinous parts and could be digested nearly wholly (except for the hardly perceptible claws). Therefore I think that the percentage occurrence of the *Coleoptera* in the food was much smaller than might be judged from the analysis of the faeces; this opinion is also supported by the fact that all the results of analyses of the food obtained with the use of neck rings show a small proportion of these insects (cf. Table XXI). The absence of the collembolan remains from the faeces may be closely connected with the dependence of their occurrence upon the dampness of the habitat: in a dry habitat and in dry spells during the year there may have been no springtails on the litter (Szeptycki, pers. comm.). This is very probably why the springtails either occurred in the food very abundantly or were completely absent from it (Table XXI). Probably, wherever they occurred they were readily taken by Dunnocks and so were aphides (whose occurrence was dependent upon the presence of host plants). Other insects willingly eaten by Dunnocks were the Diptera, which has also been stated by Bishton (1985) and Petrusenko and Talposh (1985). The equally high proportion of dipterans was found only by Bösenberg (1964) in the food of *Ficedula hypoleuca*, whereas in other birds foraging in forest it was markedly lower (Pfeifer and Keil, 1959; Mackowicz, 1970; Kaczmarek et al., 1981). The Dunnocks brought dipterans at various times of the day (I collected food samples from 08.40 to 18.45) and not only in the morning and in the evening as suggested by Bishton (1985). The high proportion of dipterans in the food was the more striking, because the Dunnock foraged on the ground. This besides may evidence a great specialization of these birds in catching insects resting on plants. Collection of insects resting on plants was also suggested by Petrusenko and Talposh (1985), who analysed the food of the Dunnock in respect of the 24-hour activity cycle of the insects.

4.7. Development of young

Several dozen minutes after hatching the chicks began to receive food. As a result, their body-weight increased from the first day of life onwards and during their 11-day stay in the nest it grew by about 7 times, from about 2 to about 16 g (Fig. 5). The growth of the young in the nestling period can be divided into 3 stages: the period of postembryonic growth lasting for the first three days of life, in which the yolk derived from the egg was being absorbed, the chicks were fed more rarely than in the following periods and the body--weight increased to be twice as great; the period of rapid growth, from the 3rd to the 7th day of life, in which the young were fed more frequently and they reached the weight eight times as high as that they had had on the day of hatching; and the period of slow growth and in some cases a slight loss of body-weight of the young during the last two days of their stay in the nest, when they were fed also frequently. Departing from the nest on the 11th day after hatching, the young reached about 77% of the body-weight of adult birds, their weight averaging 16 g against the mean weight of adults of 20.7 g (in spring and autumn). The differences in body-size and weight between particular chicks of a brood at the end of the nestling period were distinct, for they differed in age by 1, exceptionally 2 days. These differences persisted up to the end of their stay in the nest (Fig. 6a, b). Food deprivation for about 2—3 hours during a day-and-night period did not affect the growth rate of the body-weight until the third day after the break in feeding (e.g. after the use of a neck ring). The young were however capable of making up this loss: the chicks which had compression rings put on on the 6th day of life, as early as the 10th day reached the body-weight similar to or even somewhat higher than the mean weight obtained for the chicks which had had no breaks in feeding (Fig. 6c). The appearance of the young also changes in the nestling period. These morphological changes and some forms of behaviour are as follows:

Day of hatching (1st day of life). Chicks blind, their backs, heads and wings covered with wet and stuck-together ashen-gray down. Skin over whole body yellow-orange-pink except places where the down feathers grew and the eyelids, which were also ashen-gray. Bill yellow-brown on outer side, with lighter egg--tooth on mandible and shields of external nostrils. White skin folds at the edges of the bill, well seen whether the bill was open or shut. The inside of the bill was orange, with three back spots on the tongue, one on its tip and two at its base (Plate VII).

2nd day of life. Skin somewhat lighter in colour. Down feathers dιy, about 12 mm long. The young formed a pyramid in the nest, their heads being turned towards the centre.

3rd day of life. Further growth of body, consiting in its lengthening of the trunk, wings, legs and head.

4th day of life. The remiges began to erupt, their pinfeathers being up to 2 mm long, averaging 0.5 mm, in some chicks. Some chicks, besides, changed their position and lay with their heads turned towards the edge of the nest.

5th day of life. The dark spot on the tip of the tongue disappeared in some chicks, about 50% of them began to see. The pinfeathers of the remiges were 1 to 7 mm long (mostly 2—3 mm). The dorsal pinfeathers appeared, reaching a length of 2.5 mm. The young moved their heads from under the sitting female and began to utter begging voices at feeding.

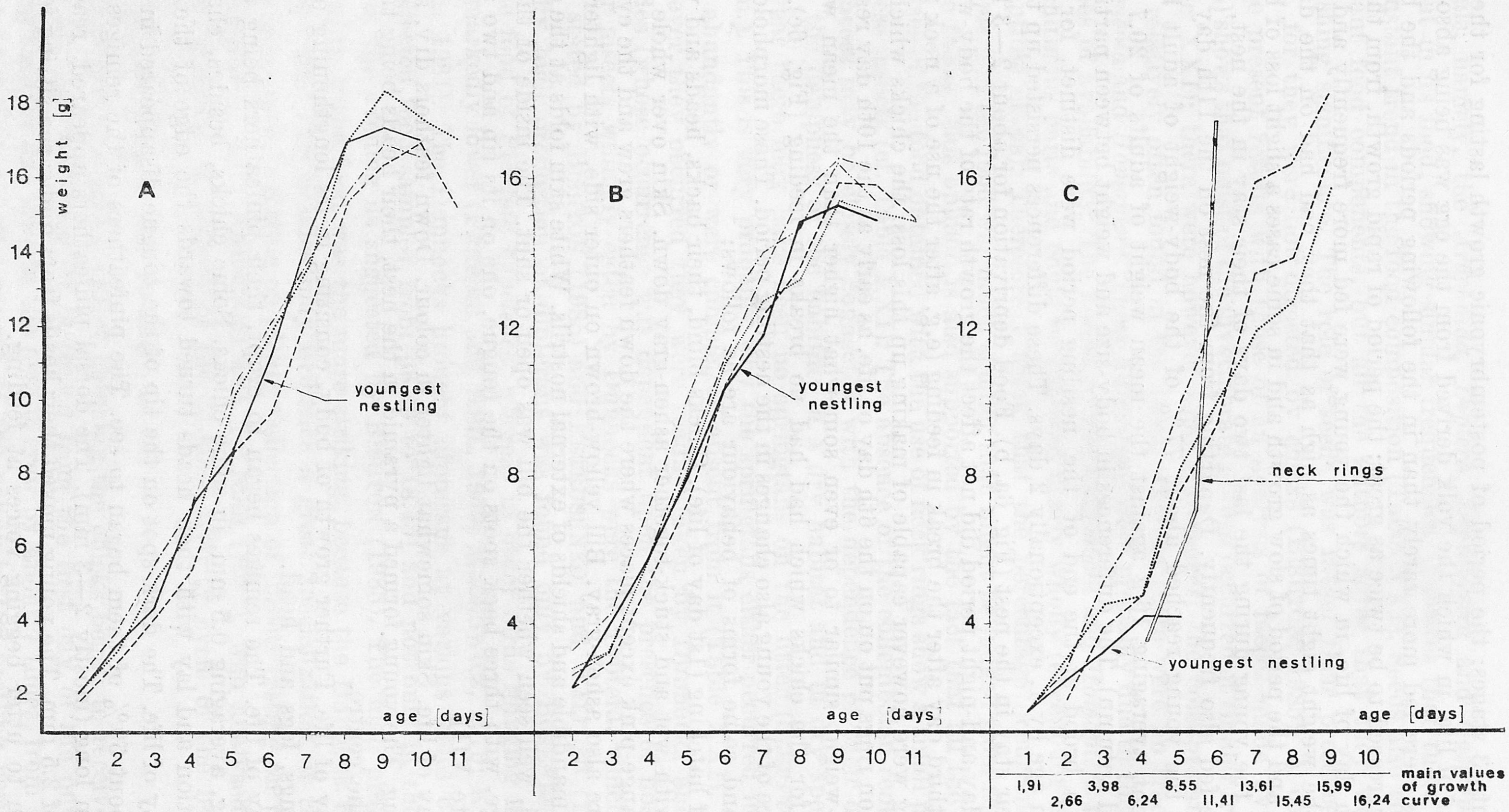

Fig. 6. Changes in the daily increments in weight of particular nestlings from one nest. A, B — nestlings fed normally, C — nestlings with rings placed on necks

6th day of life. All the young saw. Remex pinfeathers 2—12 mm long, most frequently 6—10 mm. Back, belly and flanks covered with pinfeathers, which began to burst. Two or 3 chicks in 10 had the pinfeathers burst open already, with the feathers growing out of them: brown on the back, rusty on the belly and yellow on the flanks of the body. On the same day the retrices began to grow and reached a length of 0.5—2 mm.

7th day of life. The remex pinfeathers were 8—15 mm long, in some chicks they began to burst. The pinfeathers on the back, flanks and belly were open and most of them ended with vanes, about 1 mm and sometimes up to 3 mm long. In most chicks the retrices were still at the stage of pinfeathers 1—2 mm long. The specimens whose retrices began to grow on the previous day, had already tails in the form of burst pinfeathers reaching 4 mm in length. The chicks with their feathers best developed, while sitting in the nest, gave the impression of being already fledged.

8th day of life. Some chicks still had pinfeathers (remiges) on the wings, in most of them however the pinfeathers were burs open. Some remiges were ended with vanes, 1 to 5 mm long. Only a small number of chicks had their feathers on the back, flanks and belly in the form of pins. In most chicks the body was covered with feathers the vanes of which were 2—3 mm long. The retrices were 2—10 mm in length, the longest ones with vanes.

9th day of life. Remiges, up to 25 mm long, with vanes (only about 4% of the chicks had them still in the form of pins). Body (back, flanks and belly) covered with well-developed feathers. Retrices, 5—10 mm long, either as opened pinfeather or with vanes up to 2 mm in length. It was not until that day that pinfeathers began to grow on the head. The nestlings began to prune the feathers by the themselves, stretched their wings and flapped them.

10th day of life. The remiges reached a length of 40 mm, the retrices 10—13 mm; pinfeathers were present only on the frons.

11th day of life. The young with tails more than 10 mm long began to fly out of the nest, often following the calls of the adult birds (especially when the nest was situated rather high), whereas the non-volant chicks went out (of the nests placed low above the ground). After leaving the nest, the young were fed by the adult birds on the ground and they never returned to them, though they stayed in its vicinity. For instance, on of the young observed returned to stay overnight close to the nest, settling down for sleep on twigs almost just under the nest, although it was placed hardly a dozen centimetres or so above the ground and it would not have been specially difficult for the chick to get into it.

12th day of life. The chicks that had not flown out of the nest on the previous day were leaving it.

The shape of the growth curve for the chicks in ONP resembles that for Dunnocks fed by two parental birds in Great Britain (BIRKHEAD, 1981). In both cases a period of rapid growth is followed by a setback in the growth of the body-weight in the last days of the nestling period. There was however a difference in the growth of the chicks: the birds weighed by BIRKHEAD (1981) reached the body-weight of the adult birds at the time of their departure from the nest, whereas the young from ONP, when leaving the nest, were lighter than adult birds by about 23%. This may have been due to the fact that young Dunnocks of ONP left the nests earlier, whereas, according to some authors, these birds stay in the nest for 12—14 and even 15 days (STEINFATT, 1938; SZCZEPSKI and KOZŁOWSKI, 1953; MAKATSCH, 1959; WITHERBY in HAARTMAN, 1975; SCHIFTER, 1970; READE and HOSKING, 1977; HARRISON, 1975; AICHHORN, in GLUTZ and BAUER 1985, HUDEC et al., 1983). On the other hand, however, the quick growth of the plumage, similar to that observed by AICHHORN (in GLUTZ and BAUER, 1985). and much quicker than the growth described by HEINROTH and HEINROTH (1966), according to whom, the 9-day-old chicks had only burst pinfaethers and their body was wholly unfledged, would indicate that the inspections of the nest did not exert a harmful influence on the development of the young. At the same time the decrease in the body-weight found in chicks in many species of the passerine birds before their leaving the nest (RICKLEFS, 1968a; O'CONNOR, 1975, and others) and also the phenomenon of chicks of some species departing from the nest before reaching the weight of adult birds (RICKLEFS, 1968b; KRÜGER, 1982, and others) suggest that the growth of the chicks under study proceeded normally. The differences in the growth and development of young Dunnocks from ONP in relation to those presented by BIRKHEAD (1981) and HEINROTH and HEINROTH (1966) show that the growth and development of chicks may take a varied course and the data presented in this paper may be characteristic of the population inhabiting the territory of Poland, which is confirmed by the observations made by KRZYWIŃSKI (1965).

5. Breeding success

The losses of eggs and those of chicks at particular stages of nestling period and the results of calculations of the breeding success carried out separately for the Dunnocks from ONP and on the basis of the data obtained from the Nest and Breeding Index Cards of Wrocław University are presented in Table XXII. It shows that the cumulative number of eggs and chicks destroyed by predators forms 53.8% (ONP) or 55.5% (Index Cards) of the eggs laid and that of the young flying from the nest only 33.3% (ONP) or 39.1% (Index Cards) of them. The numbers of unproductive eggs were also similar. The unfertilized eggs and those with dead embryos formed together about 10%. The young that did not live to leave the nest but had not been killed by predators constituted the smallest losses, which formed 4.8% (ONP) or 2.7% (Index Cards) of the young hatched or, respectively, 3% and 1.2% of the eggs laid. It is noteworthy that there is no convincing evidence the broods were lost owing to unfavourable weather conditions, for, as I have observed, even a heavy downpour did not affect the behaviour of the female brooding or feeding the young in a visible manner.

Table XXII

Losses of egg and chicks at particular stages of nestling period in Dunnocks and breeding succes in study area and acc. to data from Nest and Breeding Index Cards for Polish territory

	Broods of numbers of eggs and chicks known				Broods fate which is known but not always known number of eggs or chicks			
	ONP(1977—1978)		Index Cards		ONP(1974—1986)		Index Cards	
	specimens (broods)	%	specimens (broods)	%	broods	%	broods	%
Eggs laid	132 (28)	100	335 (70)	100	83	100	84	100
Eggs destroyed or abandoned	35 (9)	26.5	153 (34)	45.7	44	53.0	37	47.0
Eggs unfertilized, dead embryos	13 (9)	9.8	34 (23)	10.1				
Chicks hatched	84 (19)	63.6	148 (36)	44.2	39	47.0	47	56.0
Dead chicks	4 (4)	3.0	4 (4)	1.2				
Chicks destroyded by predators	36 (8)	27.3	33 (10)	9.9	13	15.7	13	15.5
Eggs + chicks unhatched, dead	17	12.9	38	11.3				
Flew from nest	44 (11)	33.3	111 (26)	33.1	26	31.3	34	40.5
No of departing chicks calculated for one nest built (on basis of mean clutch size for ONP and Index Cards)	1.68		1.60		1.42 *		1.74 *	

* — after the subtraction of the mean number of unfertilized eggs and dead chicks in the nest.

In the nests in which the number of eggs and young was recorded during the two years of investigation carried out in ONP (1977—1978). the losses of eggs were smaller than in materials collected at random from all over Poland for a much longer period (1968—1983). The losses of chicks were greater in ONP in the analogous periods. In consequence, the losses caused by predators were almost the same in ONP as in the whole territory of Poland; otherwise, if the predators did not manage to destroy enough eggs, they later made up arrears by killing chicks (The greater losses in the broods of Dunnocks in ONP during the nestling period found in the two years of study were possibly connected with the activity of other predators in that period, e.g. the squirrels, which were more numerous than in other years).

It can be seen from Table XXII that there is a great difference in the number of reduced eggs according to the fact whether the basis for calculation included the nests with the numbers of eggs known or all the destroyed nests that had contained eggs (the difference comes to about 23.5%). It arose from the fact that some eggs had been destroyed before the first inspection of the nest and so were not at first used in the calculations based on the number of eggs laid. When such nests, found with the fragmentary shells of broken eggs in them, were taken into consideration, it appeared that the losses caused by predators were greater than the figures obtained from the calculations based on the broods observed. In the material covered by the Index Cards all the nests found with the eggs already destroyed have been omitted and, as a result, the value obtained for the breeding success on the basis of the Index Cards seems to be too high. The breeding success may be also somewhat overestimated, if only the nests with the shells of broken eggs have been used in calculations. At frequent visits to the nests I observed that a certain number of broods had been eliminated after the laying of 1—2 eggs or just after the hatching of chicks. The contents of the nest disappeared completely during a day or a night, although the structure of the nest remained undamaged. Such predators as squirrels, jays penetrating the area closely and wood mice, were probably responsible for the disappearance of the brood (in one of the nests watched till dark the contents disappeared during the night — at dawn it was already empty). Such nests, looking as if newly built, had already fallen a prey to predation. Assuming that all the empty nests had been destroyed by predators, I calculated the breeding success for ONP, adjusted to one nest built (Table XXIII).

Assuming that the mean clutch in ONP was 5.14 eggs per nest, I subtracted the mean number of unproductive eggs and that of chicks lost in the nest and obtained the mean number of chicks flying from the nest, equal to 1.21 chicks per nest built or 29.5% of the full clutch. On the assumption that in the remaining territory of Poland the percentage of nests destroyed before the first inspection was similar to that in ONP, I calculated the presumable breeding success for the Polish population of Dunnocks; it is about 1.13 chicks per nest built.

The above-presented breeding success of Dunnocks, calculated for the study area and the whole territory of Poland, was the lowest of the values so far given from different places of its occurrence.

The number of chicks departing calculated for 1 nest built or for the number of eggs laid obtained for ONP is half the number for Czechoslovakia (HUDEC et al. 1983). Seeing that the configuration of these two regions, the stands of trees and the Dunnock's ethology in them are similar, it is hard to explain

Table XXIII

Breeding success of Dunnocks in ONP calculated for one nest built

	No of nests	%
Nests built	98	100
Nests empty, given up, with destroyed eggs	59	60.2
Nests with chicks hatched	39	39.8
Chicks destroyed by predators	13	13.3
Total of nests eliminated	72	73.5
Effective nests	26	26.5

this difference (in Czechoslovakia the Dunnock is also a wood bird which flies away for winter and is most numerous in the mountains). The breeding success of the Dunnock in Poland was also somewhat lower from that found for the birds living in Great Britain, where it was about 1.5 chicks per nest (calculated on the basis of the data from the papers by SNOW, MAYER-GROSS, 1967; BIRKHEAD, 1981; and SNOW and SNOW, 1982). A comparison of the reductions of Dunnocks at particular stages of the nestling period in Great Britain and Poland shows that in Poland, especially in ONP, much more nests were destroyed by predators, whereas in Great Britain more nests were effective, i.e. from which at least one chick flew off. The larger number of nests destroyed by predators in ONP than in Great Britain may be associated with the greater pressure of predators on the birds in more primitive environments than in those altered by man, which has been found by WESOŁOWSKI (1985).

The number of effective nests of the Dunnock in the territory of Poland, expressed as the percentage of the nests built was similar to that of other species of birds building open nests, like the Hawfinch *Coccothraustes coccothraustes* (KRÜGER, 1982), Willow Warbler *Phylloscopus sibilatrix* (WESOŁOWSKI, 1985) and other (MROCZKIEWICZ, 1974). At the same time, the percentage of effective nests was considerably higher in hole-nesting birds, e.g. sparrows *Passer domesticus* and *Passer montanus* (MACKOWICZ et al., 1970), House Martin *Delichon urbica* (HUND and PRINZINGER, 1979) and Tree Creeper *Certhia familiaris* (LÖHRL, 1979). Consequently, the losses of nests of the open-nesting birds were higher than those of the hole-nesting ones and did not depend on the height above the ground at which the nest was situated (Willow Warbler build their nests on the ground, Dunnocks about 1 m above it and 75% of the nests of Hawfinches were placed at a height of 1—6 m).

The small difference in breeding success between the British and the Polish population, although the reduction of nests was smaller in Great Britain, was caused, among other things, by a relatively high percentage of unfertilized eggs, 16—20% (Snow and Snow, 1982) or 11—16%, acc. to the data of BTO (Snow and Snow, 1982), or there was at least one unfertilized egg in very other nest, i.e. 1 or more in 13 eggs laid (acc. to Birkhead's data, 1981). The larger number of unfertilized eggs in Great Britain would indicate that the formation of "families" consisting of more parental birds than a femal and a male has an unfavourable influence on the fertility of the eggs. I should therefore accord with Birkhead's (1981) opinion that the broods of monogamous families are more effective.

V. ACKNOWLEDGMENTS

I wish to express my thanks to Dr W. Staręga of the Institute of Zoology, P.A.Scs, in Warsaw, Prof. A. Szeptycki, Dr W. Krzemiński, Dr E. Stworzewicz, and Mr E. Palik of the Institute of Systematic and Experimental Zoology, P.A.Scs, in Kraków and Dr A. Kuśka, for their help in the determination of the specimens making up the food of chicks. I also thank Dr T. Wesołowski of Wrocław University for giving me access to the Nest and Breeding Index Cards and Mr J. Partyka of the Administration of the Ojców National Park for providing me with meteorological data from the ONP area.

I am also indebted to the students of biology, particularly B. Błaszak, S. Grzankowski, Z. Kopczyński, B. Kuchna, M. Łuczak, E. Michalska, K. Okońska, K. Ostrowska, E. Świerczyńska and Ł. Wenta, treinees at the Institute of Systematic and Experimental Zoology, and Mr T. Oleś (former worker of the Institute) for their help in field work. Special thanks are due to Prof. Z. Bocheński and Dr A. Tomek for their valuable remarks.

Translated into English
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STRESZCZENIE

Obserwacje zbierano w latach 1974—1986 w okresie od końca marca do początku sierpnia. Łącznie dotyczą one 148 gniazd. Przy 12 gniazdach prowadzono obserwacje łącznie podczas 270 godzin w bezpośrednim sąsiedztwie gniazda w okresie wysiadywania jaj i karmienia piskląt. Szczegółowe pomiary i opisy 52 piskląt z 13 gniazd dostarczyły materiału do określenia tempa ich wzrostu i rozwoju, a od piskląt z 5 innych gniazd pobrano 138 porcji pokarmu, które pozwoliły na analizę pożywienia pokrzywnic w okresie gniazdowym. Prócz materiału z Ojcowskiego Parku Narodowego wykorzystano materiały pochodzące z całej Polski, z Kartoteki Gniazd i Lęgów Uniwersytetu Wrocławskiego (141 kart), oraz z Kartoteki Gniazd Zakładu Zoologii Systematycznej i Doświadczalnej PAN w Krakowie (17 kart spoza OPN), a także obserwacje własne pochodzące z terenu Polskich Karpat.

Ptaki przylatywały na teren późniejszego gnieżdżenia się z końcem marca lub na początku kwietnia. W latach dużej liczebności (1974—1978) terytorium jednej pary obejmowało około 1 ha; po spadku liczebności w latach następnych (1979—1986) na parę lęgową ptaków przypadało 2,5—3 ha lasu. Do budowy gniazda część pokrzywnic przystępowała w drugiej połowie kwietnia, a pozostałe ptaki w pierwszej połowie maja. Budowa gniazda trwała kilka (3—7) dni, po czym do gotowych gniazd składane były jaja. Terminy przystępowania do lęgów w OPN i na terenie całej Polski przedstawiono w tab. I. Trzecia dekada kwietnia, pierwsza i druga dekada maja oraz pierwsza i druga dekada czerwca były terminami I i II lęgu; jaja znoszone w pozostałych okresach należały do lęgów powtarzanych. Istnieje zależność między terminem przystępowania do lęgów przez pokrzywnice a przebiegiem izotermy +5°C na kontynencie europejskim (ryc. 1).

Liczba jaj w pełnym zniesieniu wahała się od 2 do 6 (tab. II); największe zniesienia miały pokrzywnice w czerwcu, a najmniejsze w lipcu (tab. III). Wielkość znoszonych jaj wahała się w granicach: długość 17,4—21,0 mm, a szerokość 13,8—15,5 mm (średnie wymiary: 19,56 ×14,71 mm). Ciężar świeżo zniesionych jaj wahał się od 1,78 do 2,60 g (średni ciężar — 2,17 g). Jaja należące do jednego zniesienia często różniły się między sobą zarówno pod względem wielkości, jak i ciężaru. Ciężar jaj spadał w miarę upływu czasu wysiadywania, łącznie o około 16% początkowego ciężaru (ryc. 2). W kilku gniazdach stwierdzono zwiększanie rozmiarów oraz ciężaru u kolejno znoszonych jaj (tab. IV). Ciężar i rozmiary jaj znoszonych przez pokrzywnice w OPN nie odbiegają od wartości podawanych z całego areału występowania (tab. V). Jaja znoszone były w odstępach około 24 godzin i po zniesieniu przedostatniego samica rozpoczynała wysiadywanie. Przerwy w wysiadywaniu trwały od 1 do 50 minut; podczas klucia ilość przerw w wysiadywaniu była większa, ale równocześnie krótszy czas nieobecności samicy na gnieździe (ryc. 3). Nie zaobserwowano zmiany czasu przebywania samicy na gnieździe w zależności od pory dnia, również brak dużego wpływu warunków atmosferycznych na aktywność wysiadywania (ryc. 3). Podczas wysiadywania jaj samiec przebywał w odległości kilku do kilkunastu metrów od gniazda, wyjątkowo tylko ogrzewał gniazdo przez krótki czas (kilka do kilkudziesięciu minut w ciągu doby). Inkubacja trwała 12—13 dni; pisklęta kluły się nierównocześnie, przeważnie jedno pisklę kluło się dopiero następnego dnia. Pisklęta w gnieździe były ogrzewane przez samicę (tab. VI).

Karmienie piskląt rozpoczynało się niedługo po ich wykluciu. Pisklęta młodsze otrzymywały pokarm rzadziej niż pisklęta starsze (tab. VII, ryc. 4), a w lęgach liczniejszych przeważnie na jedno pisklę przypadała mniejsza ilość przylotów ptaków rodzicielskich z pokarmem niż w lęgach mniej licznych (tab. VII). Pokarm przynosiły obydwa ptaki rodzicielskie (tab. VII) karmiąc zwykle bezpośrednio pisklęta. Pokarm otrzymywało 1, 2 lub 3 pisklęta podczas przylotu ptaka dorosłego z pokarmem. Nie stwierdzono większej zależności częstotliwości karmienia od warunków atmosferycznych panujących w ciągu dnia (tab. VIII), ani też od pory dnia (ryc. 5).

Obydwa ptaki rodzicielskie utrzymywały gniazdo w należytym stanie, z tym że poprawianie konstrukcji gniazda, dziobanie w nim, usuwanie przedmiotów, które znalazły się w gnieździe, a także prawdopodobnie usuwanie pasożytów wykonywała wyłącznie samica. Częstotliwość dziobania samicy w gnieździe zmniejszała się wraz z wiekiem piskląt (tab. IX). Równy podział obowiązków między samicą a samcem panował przy usuwaniu kału. Woreczki z kałem ptaki dorosłe początkowo zjadały, w miarę wzrostu piskląt kał był coraz częściej wynoszony poza gniazdo (tab. X). Pisklęta wydalały kał z średnią częstotliwością 0,74 porcji przez pisklę w ciągu godziny; częstotliwość oddawania kału przez pisklęta zwiększała się nieznacznie z wiekiem piskląt (tab. X).

Dorosłe pokrzywnice pokarm dla piskląt zbierały na ziemi, ściółce, roślinach runa lub też na leżących gałęziach. Zarówno porcja pokarmu przyniesiona jak i otrzymana przez pisklę składały się od kilku do kilkudziesięciu komponentów (tab. XI i XII). Pokarm piskląt był urozmaicony. Głównymi składnikami pokarmu były pajęczaki *Arachnida*, skoczogonki *Collembola*, muchówki *Diptera* i pluskwiaki równoskrzydłe *Homoptera*. Stałymi składnikami pokarmu, lecz występującymi w małych ilościach były chrząszcze *Coleoptera*, motyle *Lepidoptera* i ślimaki *Gastropoda* (tab. XIII). Dokładniejszą analizę składu gatunkowego niektórych grup organizmów wchodzących w skład pokarmu przedstawiono w tabelach XIV—XX. Porównując skład pokarmu pokrzywnic z różnych miejsc ich występowania (tab. XXI) stwierdzono, że cechą charakterystyczną dla gatunku może być podobna frekwencja występowania w pokarmie wymienionych wyżej grup bezkręgowców oraz nie spotykana u innych gatunków ptaków wróblowatych zawartość jednej porcji, w skład której wchodzi do kilkudziesięciu jednostek taksonomicznych bezkręgowców.

W rozwoju piskląt wyróżnić można 3 okresy: wzrostu postembrionalnego (3 pierwsze dni życia), szybkiego (do 7 dnia życia) i wolnego wzrostu, a nawet nieznacznego spadku ciężaru ciała podczas ostatnich dwóch dni przebywania w gnieździe. Pisklęta opuszczające gniazdo osiągały około 77% ciężaru osobników dorosłych (ryc. 5, 6a, 6b). Przerwy w karmieniu odbijały się niekorzystnie na tempie przyrostu ciężaru ciała dopiero na trzeci dzień; pisklęta jednak były zdolne niedobór ten uzupełnić w krótkim czasie (ryc. 6c). Świeżo wyklute pisklęta miały ciało pokryte ciemnopopielatym puchem. Lotki u piskląt zaczynały wyrzynać się w 4 dniu ich życia, pałki piór grzbietowych, brzucha i boków ciała 5 dnia, ogona — 6 dnia życia. Najpóźniej, bo dopiero 9 dnia, zaczynały wyrzynać się pałki na czole. Pałki zaczynały pękać i pióra były zakończone chorągiewkami w dwa dni później. Pisklętom pękały powieki i zaczynały one widzieć 5 lub 6 dnia życia. Pisklęta opuszczały gniazdo 11 lub 12 dnia po wykluciu. Około połowa lęgów była niszczona przez drapieżniki (sójki, wiewiórki, myszy) w okresie znoszenia lub inkubacji jaj, a dalsze 15% gniazd padało łupem drapieżników już po wykluciu się piskląt. Na 100 zniesionych jaj około 10 było niezapłodnionych lub zarodki obumierały przed wykluciem. Najmniej, bo tylko 2—3, pisklęta (na 100 zniesionych jaj) ginęły w gnieździe nie przeżywając do wylotu z innych powodów niż drapieżnictwo (tab. XXII). W Ojcowskim Paku Narodowym tylko 26,5% gniazd było efektywnych, tj. wyleciało z nich co najmniej jedno pisklę (tab. XXIII), a z jednego założonego gniazda przeciętnie wylatywało 1,21 piskląt, tj. 23,5% pełnego zniesienia. W Polsce na jedno założone gniazdo pokrzywnice wychowują prawdopodobnie 1,13 piskląt.

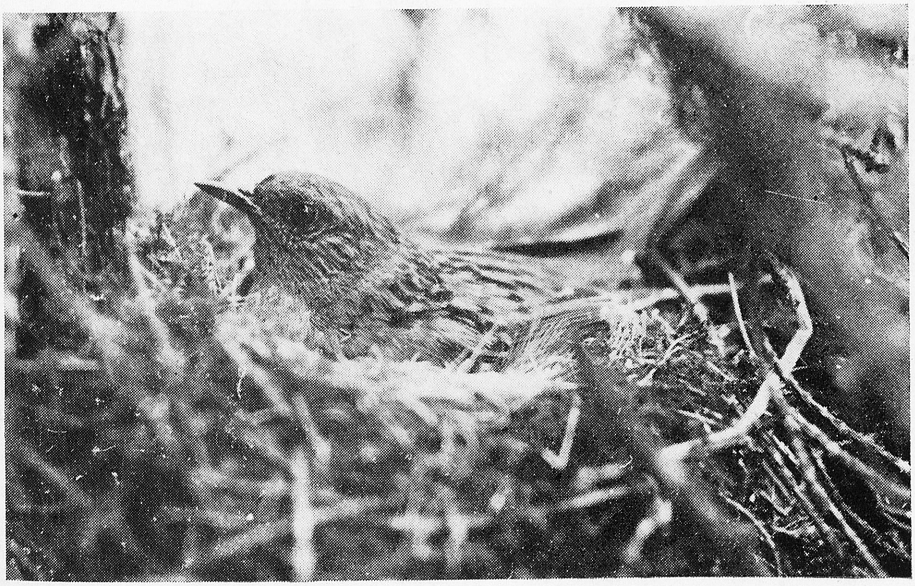
Redaktor pracy: prof. dr Z. Bocheński

Plate V

Phot. 1. The nest built in the place of the last-year nest

Phot. 2. An incubating female

Phot. 1



Phot. 2

T. Tomek

Plate VI

Phot. 3. 2-day-old nestlings and egg in the nest

Phot. 4. A female Dunnock feeding a nestlings

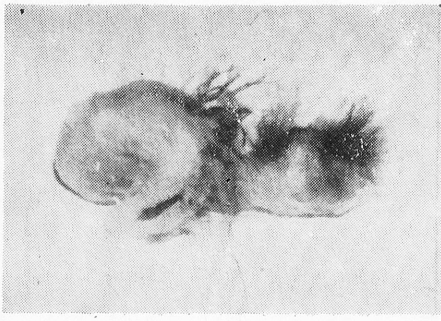
Phot. 3

Phot. 4

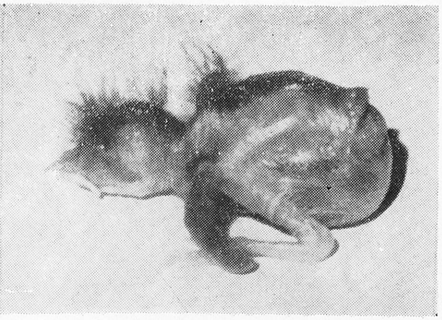
T. Tomek

Plate VII

The development of the nestlings. The figures indicate the age of nestlings



1



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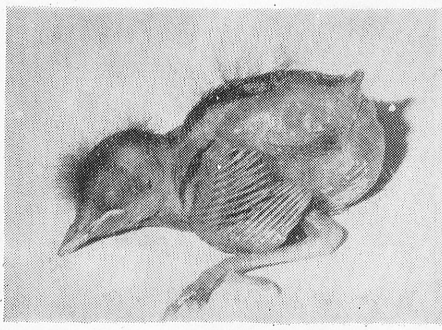

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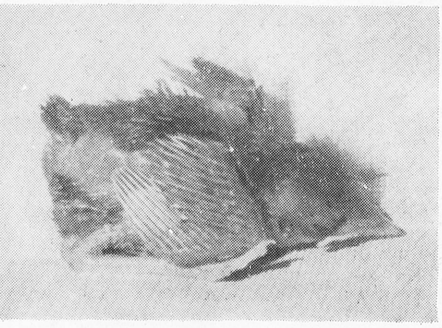

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9

T. Tomek