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FECUNDITY, MORTALITY, NUMBERS AND BIOMASS DYNAMICS OF A POPULATION OF THE TREE SPARROW (*PASSER M. MONTANUS* L.)

An analysis has been carried out on the fecundity, mortality, and numbers and biomass dynamics of a population of the Tree Sparrow. The number of young birds raised by a pair in the breeding season is quite considerable (8.70). The reproductive output depends on the number of pairs raising third broods, while the number of young raised from all broods depends on the extent of egg loss which amounts on average to 1/4 of the total number of eggs laid. The total biomass of the population changes during the year by 3–5 fold. In view of the considerable biomass of the population (500 birds per 1 km²) and its seasonal changes Tree Sparrows play a significant part in the energy flow through field ecosystems.

Contents

1. INTRODUCTION

The purpose of the present investigation is to analyse the fecundity and mortality of a population of the Tree Sparrow (*Passer m. montanus* L.) and their relation to the numbers and biomass dynamics of this species. Making use of the results presented in papers previously published on the annual cycle of the breeding colony, autumn sexual display, dispersal of young birds from their place of birth and breeding habitat preference, all of the same population, it will be possible to analyse, as comprehensively as possible, the above mentioned problems (Pielowski and Pinowski 1962, Pinowski 1965a, 1965b, 1966, 1967a, 1967b, 1967c).

Although thirty years have already passed since the first of the classical investigations of this type (Nice 1937) on a population of Song Sparrows(*Melospiza melodia* Wilson), Kendeigh and Baldwin (1937), on the House Wren (*Troglodytes aedon* Viellot), there have been few papers published which describe fully the annual cycle, fecundity and mortality of sedentary populations of small birds (Kluyver 1951, Lack 1954, 1966, Perrins 1965, 1966).

Knowledge of numbers, biomass and energy flow through the given population is of fundamental importance in ecology.

2. OUTLINE OF THE ECOLOGY OF THE INVESTIGATED POPULATION OF THE TREE SPARROW

An optimum breeding ecosystem for the Tree Sparrows habitating the area analysed in connection with the present investigations are villages and shelterbelts surrounding them. Breeding colonies, each comprising a number of nest-boxes, were put up for the Tree Sparrows at the villages and shelterbelts. A large proportion of nest-boxes in village colonies was occupied both in the breeding season and during the period of autumn sexual display. Forest colonies were established 100–1000 metres from the forest edge. The degree of occupation by the Tree Sparrows in this case was lower than that of village colonies and it also decreased when the distance from the forest edge increased. In those years when the population of the Tree Sparrow was high the degree of occupation by them of the majority of forest colonies was relatively high, on the other hand it decreased for years when the population of Tree Sparrows was low. After the severe winter of 1962/63 when the numbers of the population of the Tree Sparrow decreased, Tree Sparrows ceased nesting in the majority of forest colonies, while the degree of occupation of nest-boxes in village colonies fell less and quickly returned to the previous state (Pinowski 1967a).

In the period of autumn sexual display when the numbers of the population of the Tree Sparrow exceeded by many times the numbers in the breeding season, young Tree Sparrows in particular also accupied nest-boxes in forest colonies situated deeper in the forest, however after the winter reduction of the population, when many nest-boxes lost their occupants, they moved back to village colonies in the period of autumn sexual display. These observations indicate that the optimum breeding ecosystem for the Tree Sparrow are village areas surrounded by fields, and that forest areas are marginal ecosystems, occupied to a variable degree depending on the extent to which, in turn, the village boxes are occupied, and this is, dependent on the size of the population (Pinowski 1967a).

After leaving the nest young Tree Sparrows stay for a period of two to six weeks in the vicinity of the breeding colony, the place of their birth, in small flocks numbering, as a rule, less than a hundred birds. Later they join the large flock that gathers in the surrounding fields. This flock roams about a definite area amounting in our case to about 3 km². The area of the flock usually includes a village and surrounding fields. The flock consists of young birds born in village and forest colonies situated in its area or in the nearest vicinity. Only about 20% of young birds emigrate in the juvenile period, i.e. before beginning to moult, to neighbouring flocks and roughly the same number joins from the neighbouring flocks (Pinowski 1965b). Old birds, that have bred in the flock make up, as a rule, not more than 5% of its total. The size of the flocks depend on the size of the population of the Tree Sparrow, and each flock usually includes about 2,000 individuals, just after the breeding season about the middle of August. Birds belonging to a particular flock roost together in a chosen section of cover at the edge of a forest or in a clump of trees in the field, every year in the same place (Pinowski 1967a).

From the beginning of September moulted birds, mainly old birds and young from first broods, spend the morning in the breeding colonies where the autumn sexual display takes place. The birds occupy nest-boxes, form pairs and make nests. Later in September more and more fully-moulted birds stay each morning in the breeding colonies; at noon they move to the flock on the fields. To about mid-September still about a half of birds spend the night at the communal roosting place but as the season advances increasingly more birds separate from the flock before evening and fly to the breeding colonies; here they roost in the canopies of trees or in bushes. They start roosting in nest-boxes at the end of October. At the beginning of November, as it becomes colder with less sunshine, the period of autumn sexual display terminates and the birds fly straight from the breeding colony to the fields and form one flock. But in the evening the flock again breaks up as birds return again to their breeding colonies to roost. In the period of snow cover the flock often divides into small groups which feed around farmyards. When the average temperature in the daytime increases to about 0°C spring sexual display commences. As in autumn, birds stay in breeding colonies in the morning and only at noon do they fly to the flock in the fields. When the average temperature reaches about 10°C, egg-laying begins and breeding continues until the second half of August (Pielowski and Pinowski 1962, Pinowski 1965a, 1965b, 1966, 1967a, 1967b).

3. DESCRIPTION OF THE STUDY AREA

Investigations were carried out in an area of about 25 km^2 and situated between the bed of the Vistula river and the Kampinos Forest about 15 km NW from Warsaw (52 20'N, 20 50'E). The area is under crop – rye, wheat, oats, potatoes, beetroot, and vegetables. In the more sandy area, nearer the forest, only rye, oats and potatoes were grown. The agrotechnical level, particularly of the poorer sandy soils, is very low, as a result of which the fields are, as a rule, covered with weeds. In the southern part of the study area, nearer Warsaw, there is quite a number of newly established gardens and orchards. The more fertile area next to the Vistula has a number of shelterbelts consisting mainly of pollarded willows. Sandy fields adjacent to the Kampinos Forest are completely bereft of trees outside human settlements. The villages were isolated from each other by 2–3 km strips of fields, and only the southern part of the study area was occupied by more compact, suburban dwellings. Detailed descriptions of the area, together with maps have already been published (Pinowski 1959, 1966, 1967a).

From 36 to 120 (most frequently 72) nest boxes were hung in each of the separate villages and in chosen parts of the forest in the years 1960–1963, they formed six forest colonies and four village ones. A detailed description of the environment of each of the colonies and their history have already been given (Pinowski 1966, 1967a).

Forest breeding colonies (Nos. 1–W, 2–W, 3–W, and 5–W) were not farther than 1,000 metres from the forest edge. Of these colonies 1–*W*, and 2–*W* were situated near buildings in the forest (a sanatorium and scientific station); colony 3–*W* was 1,000 m from the edge in the depth of the forest and far from the buildings; colony 4–*W* was 3 km from the above mentioned colonies and only 100–400 metres from the forest edge. All the above mentioned forest colonies were situated in a pine forest containing also a number of broad-leaved trees. Colony 6–*W* was stretched between antiflood ditches of the Vistula and its bed, and was situated in a broad-leaved wood growing in a meadow near the river.

Colonies Nos. 1–*D*, 2–*D*, 3–*D*, 4–*D* were located in villages, and consisted of nest-boxes hung in trees growing along country roads or in farmyards, as a rule, not more than 100 metres from the buildings.

Breeding colonies Nos. 1–*W*, 2–*W*, 3–*W*, and 5–*W* were located in the area of flock *A* or in the vicinity. Colonies 1–*D*, 2–*D*, 4–*D*, and 4–*W* were situated in the area of flock *B*, and colony 3–*D* in the vicinity of flock *F*. The position of colony 6–*W* in relation to the areas of Tree Sparrow flocks was not determined. The distribution of breeding colonies and the areas covered by various Tree Sparrow flocks was shown in Figure 1 of the paper by Pinowski (1967a).

4. METHODS AND MATERIAL

The investigations were carried out from the spring of 1960 to the autumn of 1966, using 616 nest-boxes of type *A* (Sokołowski 1954), that is the ones with entrance holes of the right size for the Tree Sparrow and too small for the House Sparrow (*Passer domesticus* L.). Only in colony, 2–*D* containing 36 nest-boxes, the holes were sufficiently big for the House Sparrow to get into.

All the nest-boxes were checked at least once a week in the breeding season, from April to September in all the years when the investigations were carried out. The aim was to determine which nest-boxes were occupied by Tree Sparrows; the number of eggs in the nest, whether the eggs were warm, and whether they were broken. Those eggs from which no nestlings hatched were later broken open to check whether they contained a dead embryo. If no embryo was found there then the egg was described us infertile. If nestlings were found in the nest their number was recorded and they were aged.

When a dead nestling was found in the nest its age was recorded. Nestlings, at least eleven days old, were individually marked with an aluminum ring of the Ornithological Station of the Institute of Zoology, Polish Academy of Sciences. The nestlings were weighed every other day in 1965, but in 1966 the nestlings were weighed only once, when they were 10–12 days old.

In all, 31,140 inspections of the nest-boxes were carried out in the years 1960–1965 and the course of 1,417 broods of Tree Sparrows was followed (only part of the data collected in 1966 was used for the purposes of the present paper). A total of 4,881 nestlings were ringed.

Throughout the year Tree Sparrows were caught in mist nets, particularly intensively during the breeding season in the vicinity of colony 1–W. In all 8,461 Tree Sparrows were ringed, 1,382 recaptured at least once, and because some individuals were captured a number of times the total number of recaptures amounted to 3,783 (of which certain proportion was weighed and sexed).

In the autumn and winter a nocturnal inspection of nest-boxes was carried out once a month in order to record the number of Tree Sparrows roosting in the nest-boxes and their ring numbers. In all, 4,500 nest-boxes were inspected in this way.

Meteorological data – air temperature, precipitation, depth of snow – were taken from the meteorological station operating at Dziekanów Leśny attached to the Field Station of the Institute of Ecology, Polish Academy of Sciences, and data concerning the amount of sunshine for Legionowo (10 km E from Dziekanów Leśny) and Bielany (10 km S from Dziekanów Leśny) for the period were taken from the State Institute of Hydrology and Meteorology. For the sake of comparison we carried out our own observations on the amount of sunshine for Dziekanów Leśny in the summer of 1961 and 1962.

5. PHENOLOGY OF THE BREEDING SEASON

5.1. The onset of egg-laying and the role of climatic factors

The onset of spring sexual display varies in timing from year to year. The earliest date when sexual display commenced was on 4th March (1961) while in the next year it started on 28th March (the latest date recorded) (Fig. 1). When weather conditions deteriorate and the temperature falls below 0°C sexual display stops (Pinowski 1966). Intensive nest building starts when the average temperature in the day-time is 8–10°C. In 1963 after a very cold winter Tree Sparrows started building their nests only five days before the onset of egg laying (Fig. 1).

In 1961 both spring sexual display, and the onset of egg laying was the earliest recorded, but in the time between the two events the average temperature in the daytime did not fall below 0°C. In other years there was no connection between the date of the onset of spring sexual display and the date of the onset of egg-laying (Fig. 1).

The number of clutches started early is most dependent on the average temperature of the very week preceding the laying of the first egg in a given nest. This correlation works only in the case of temperatures below the average temperature arrived at after taking into account the whole material because the

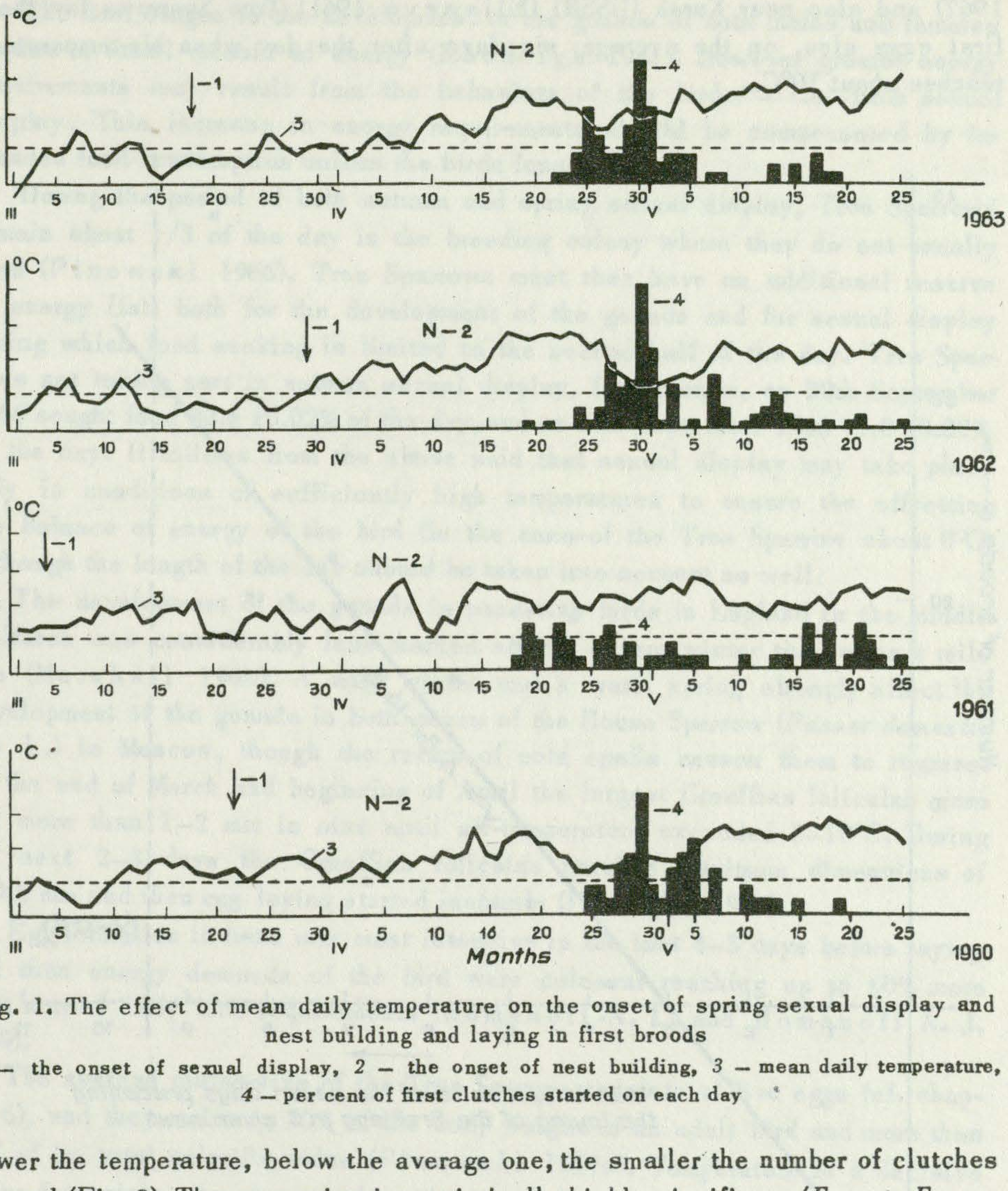

Fig. 1. The effect of mean daily temperature on the onset of spring sexual display and nest building and laying in first broods

1 – the onset of sexual display, *2* – the onset of nest building, *3* – mean daily temperature, *4* – per cent of first clutches started on each day

lower the temperature, below the average one, the smaller the number of clutches started (Fig. 2). The regression is statistically highly significant ($F_{cal.} > F_{0.01}$; 35.54 > 9.16). Temperatures above the average do not result in an increase in the number of clutches started. The average temperature of the week preceding the laying of the first egg of first broods amounted to 9.5 ±0.1°C in the years 1960–1965. The lowest average temperature of the week preceding the laying of the first egg was 3.3°C. Since the average temperatures in the day-time during second and third broods do not fall below 9.5°C, and as a rule they are much higher, temperature cannot be a significant factor affecting the time of the onset of the second and third broods. In the vicinity of Oxford (England) (Seel

1967) and also near Kursk (USSR) (Eliseeva 1961) Tree Sparrows lay their first eggs also, on the average, six days after the day when air-temperature reaches about 10°C.

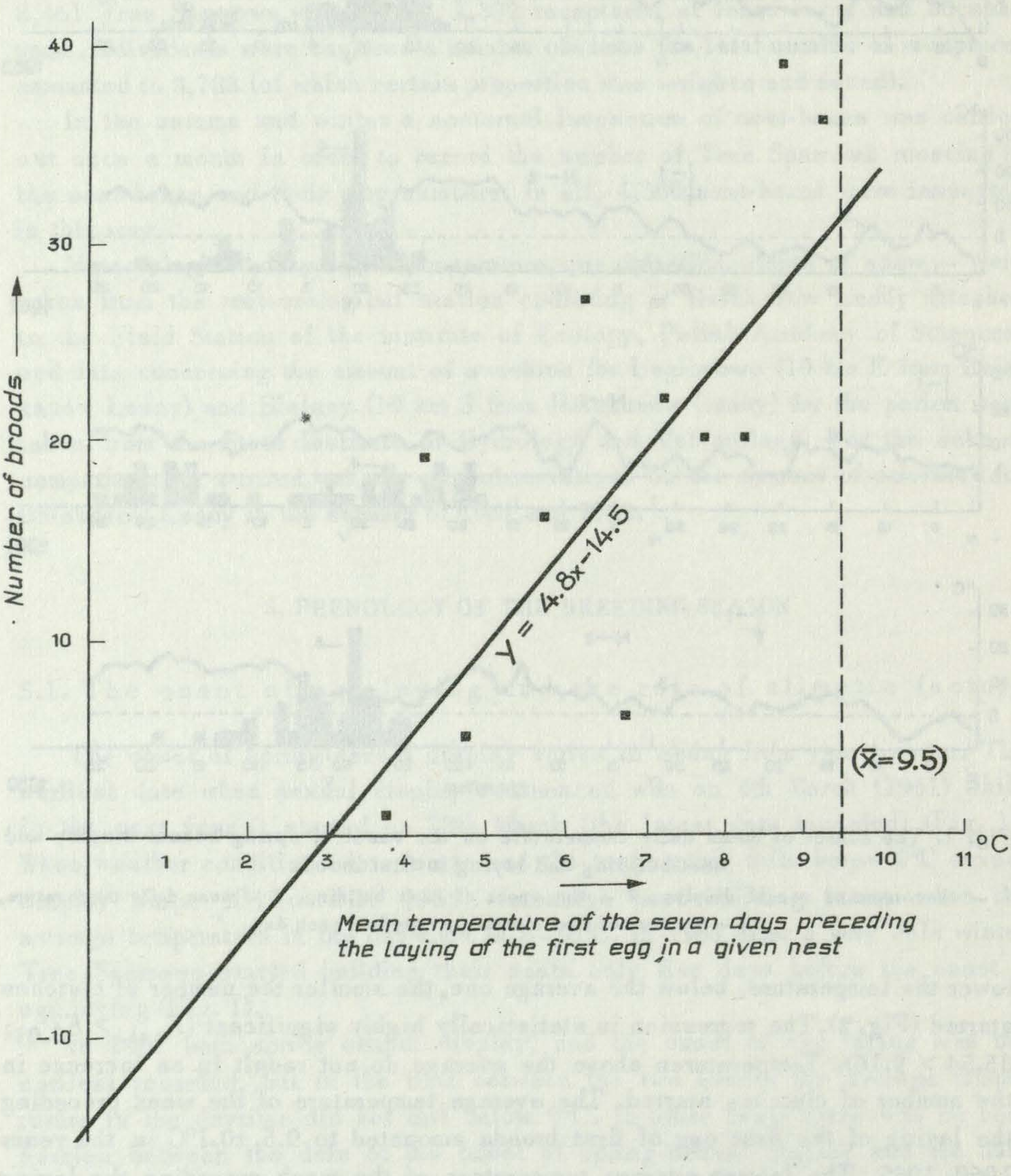

Fig. 2. The relationship between the mean temperature of the week preceding the laying of the first egg and the number of first broods started

Broken line – mean temperature of the week preceding the laying calculated for all the first broods ($\bar{x}$ = 9.5)

The first stages in the development of the gonads of both males and females require a small amount of energy (Kendeigh 1941). However greater energy requirements may result from the behaviour of the birds – i.e. from sexual display. This increase in energy requirements should be compensated by increased food-consumption unless the birds lose weight.

During the period of both autumn and spring sexual display, Tree Sparrows remain about 1/3 of the day in the breeding colony where they do not usually feed (Pinowski 1966). Tree Sparrows must then have an additional reserve of energy (fat) both for the development of the gonads and for sexual display during which food seeking is limited to the second half of the day. Tree Sparrows not taking part in autumn sexual display, for example, on 20th September 1966 sought food 83.6 ±0.02% of the day, and on 26th September 1966 71.0 ±0.02% of the day. It follows from the above said that sexual display may take place only in conditions of sufficiently high temperatures to ensure the offsetting the balance of energy of the bird (in the case of the Tree Sparrow about 0°C) – though the length of the day should be taken into account as well.

The development of the gonads in passerine birds in England in the middle of March was considerably less marked after a severe winter than after a mild one (Marshall 1949). A mild winter and a warm spring strongly affect the development of the gonads in both sexes of the House Sparrow (*Passer domesticus* L.) in Moscow, though the return of cold spells causes them to regress. At the end of March and beginning of April the largest Graaffian foliculas were not more than 1–2 mm in size until air-temperature exceeded 6–10°C. During the next 2–3 days the Graaffian foliculas reached maximum dimensions of 9–9.5 mm and then egg laying started instantly (Ill'enko 1958).

Egg-formation in hens was most intensive in the last 4–5 days before laying and then energy demands of the bird were colossal reaching up to 60% more than normal daily food requirements (Romanoff A. L. and Romanoff A. J. 1959).

The average clutch-size of the Tree Sparrow consists of five eggs (cf. chapter 6), and they make up 50% of the body weight of an adult bird and more than 30% of its total calorific value (Pinowski 1967a). Temperature is a decisive factor determining the moment of egg laying in the conditions when it approaches the level necessary to offset the balance of energy of the bird, i.e. in the place during first broods (Nice 1937, Kendeigh 1941, 1963a, Myres 1955, Ill'enko 1958, Curio 1959, Marshall 1961, El-Wailly. 1966, Lack 1966 and others).

Tanner (1966) analysing abundant data for five species of birds (*Parus major* L., *Sturnus vulgaris* L., *Sialia sialis* (L.), *Junco heymalis* L.) on the effect of temperature, sunshine, precipitation, the amount of food and development of the vegetation on the onset of laying recorded that only beginning from the middle or end of winter until the moment of ovulation temperatures affect the time of egg laying. However Ill'enko (1958) recorded an evident effect of the number of days with a complete sunshine on the development of the gonads and spermatogenesis of the House Sparrow in Moscow. According to our data the seasonal rise in air-temperature is one factor deciding the onset of laying in the Tree Sparrow.

5.2. The number of broods and the duration of the breeding season

Tree Sparrows from the study area have three broods in a year (Fig. 3). First and second broods are usually equally numerous, but the number of third broods is smaller by about 1/3 (Tab. I). Only in 1961 there were less first broods than second ones but this was due to the fact that nest-boxes were

Percentage of pairs having *I*, *II*, *III* broods

Tab. I

Brood			Total number of broods	Year
I	*II*	*III*		
15.IV–16.V	17.V–24.VI	25.VI–3.VIII		
45.2% (1)	28.8% (0.6)	26.0% (0.6)	122	1960
27.6% (1)	49.8% (1.8)	22.6% (0.8)	291	1961
38.5% (1)	36.0% (0.9)	25.5% (0.7)	429	1962
38.5% (1)	35.8% (0.9)	25.7% (0.7)	174	1963
37.0% (1)	37.0% (1.0)	26.0% (0.7)	189	1964
40.7% (1)	38.8% (0.9)	20.5% (0.5)	44	1965

The figures in parentheses show the ratio of the percentage of second and third broods to first broods.

hung too late. In those nest-boxes in which there were third broods, first broods started earlier than in the boxes in which only two broods were raised. In the nest-boxes in which three broods occurred 91.7 ±2.8% of first broods were started by 6th May, whereas in the nest-boxes in which only first and second broods occurred only 77.9 ±2.0% ($P < 0.01$). Eliseeva (1961) near Kursk stressed that only those Tree Sparrows which laid the eggs of the first brood in the first ten days of May later had third broods. Berger (1959) in Germany in 1958, when the spring was very late, did not record third broods in the Tree Sparrow at all. In the southern part of Sakhalin (USSR) Tree Sparrows have three broods only in those years with an early spring (Gizenko 1955). Also in the Spanish Sparrow (*Passer hispaniolensis* Temm.) near Alma-Ata (Kazakhstan) only those

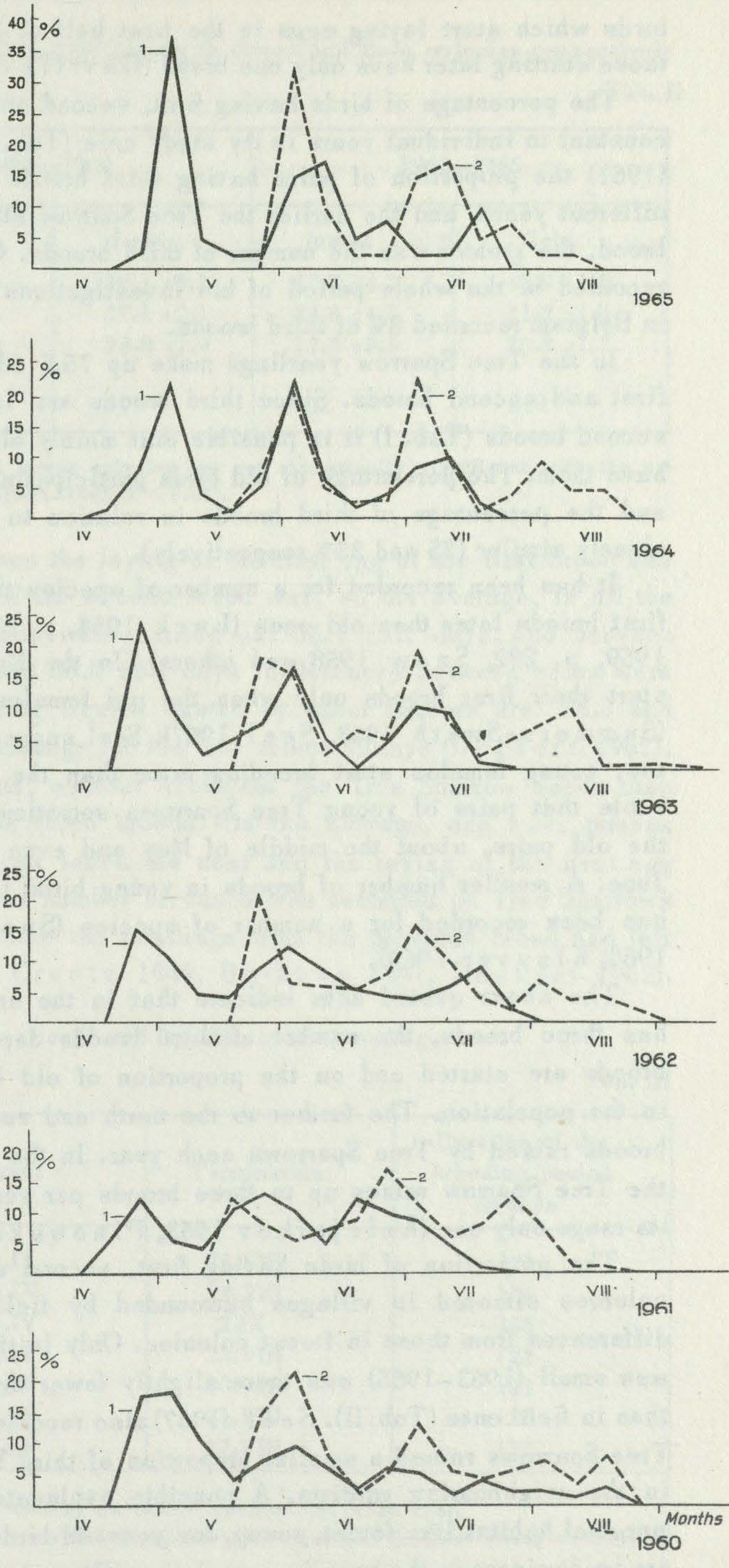

Fig. 3. Per cent of clutches started and nests left by nestlings each week through the season. The figures are expressed as a percentage of the total number of clutches started or of nest left by nestlings produced over the season as a whole
1 — the onset of laying,
2 — fledglings

birds which start laying eggs in the first half of May have second broods and those starting later have only one brood (G a v r i l o v 1962).

The percentage of birds having first, second and third broods was relatively constant in individual years in my study area (Tab. I). According to E l i s e e v a (1961) the proportion of pairs having third broods varied between 8 to 24% in different years, and the earlier the Tree Sparrow started laying eggs of the first brood, the greater was the number of third broods. C r e u t z (1949) near Dresden recorded in the whole period of his investigations 17%, and B e t h u n e (1961) in Belgium recorded 8% of third broods.

In the Tree Sparrow yearlings make up 75.5 ±3.8% of birds participating in first and second broods. Since third broods are less numerous than first and second broods (Tab. I) it is possible that mainly old birds (at least 2 years old) have them. The percentage of old birds participating in first and second broods, and the percentage of third broods in relation to first and second broods are closely similar (25 and 33% respectively).

It has been recorded for a number of species that young females start their first broods later than old ones (L a c k 1954, p. 62, V a n T y n e and B e r g e r 1959, p. 292, S n o w 1958 and others). In the House Sparrow, young females start their first broods only when the old females are starting second broods (S u m m e r s - S m i t h 1963, S e e l 1967). Seel suggests that, in the Tree Sparrow too, young females start breeding later than the old ones. B e t h u n e (1961) wrote that pairs of young Tree Sparrows sometimes lay eggs much later than the old pairs, about the middle of May and even as late as the beginning of June. A smaller number of broods in young birds in their first breeding season has been recorded for a number of species (S n o w 1958, S u m m e r s - S m i t h 1963, K l u y v e r 1963).

The above quoted data indicate that in the areas where the Tree Sparrow has three broods, the number of third broods depends on the date when first broods are started and on the proportion of old birds (at least 2 years old), in the population. The further to the north and east the smaller the number of broods raised by Tree Sparrows each year. In the south and temperate regions the Tree Sparrow raises up to three broods per year while in the very north of its range only one (K e l e j n i k o v 1953, P i n o w s k i 1966).

The proportion of birds having first, second and third broods in breeding colonies situated in villages surrounded by fields did not show significant differences from those in forest colonies. Only in the years when the population was small (1963–1965) was there slightly fewer third broods in forest colonies than in field ones (Tab. II). S e e l (1967) also recorded that near Oxford (England) Tree Sparrows raised a smaller proportion of third broods in a small forest than in the neighbouring gardens. A possible explanation seems to be that in the marginal habitat like forest, young, one year old birds, raising fewer third broods, are predominant in the breeding population (P i n o w s k i 1967a).

Percentage of pairs having *I*, *II* and *III* broods in forest and field colonies respectively

Tab. II

Period of investigations	1960–1962		1963–1965	
Colonies	forest	field	forest	field
Broods *I*	38.6 ±2.5	36.1 ±2.1	47.7 ±4.3	43.0 ±1.9
Broods *II*	36.5 ±2.5	37.1 ±2.1	34.8 ±4.1	31.2 ±1.8
Broods *III*	24.9 ±2.2	26.8 ±1.9	17.5 ±3.3	25.8 ±1.7
Total number of broods	357	501	132	618

Differences between field and forest colonies are not statistically significant with the exception of third broods in the years 1963–1965 ($P < 0.05$).

The length of time between the laying of the first egg of the first brood and the laying of the first egg of the second brood was, on the average, in all the years when the investigations were carried out 36.4 ±5.1 days, and between the second and the third brood 38.0 ±5.1 days (differences between years were not significant). Corresponding figures quoted by other authors are: 38.3 and 37.1 (Bethune 1961), the average for the two values 32 days (Deckert 1962), 38.5 ±4.3 (Seel 1967). Thus, without accidents the Tree Sparrow needs then about 110–115 days to raise three broods. On the average, one week passes between the date the nestlings leave the nest and the laying of the first egg of the next brood, but a great number of cases was recorded of Tree Sparrows laying eggs into the nest before the nestlings from the previous brood had left (Berndt, Frieling 1939, Creutz 1949, Bethune 1961, Deckert 1962).

The onset*, termination** and duration of the breeding period

Tab. III

Year	Onset	Termination	Duration of the breeding period in days
1960	26.IV	25.VIII	121
1961	18.IV	22.VIII	126
1962	19.IV	2.IX	136
1963	22.IV	23.VIII	123
1964	19.IV	20.VIII	123
1965	25.IV	24.VIII	121
1966	22.IV	17.VIII	117

* The onset of breeding is indicated by the date of the first egg of the year.

** The termination of breeding is indicated by the date on which the last young of the year left the nest.

For the population as a whole, the breeding season lasted 117–136 days (Tab. III), and so it was not considerably longer than for individual pairs[1]. It indicates that the Tree Sparrow goes through its broods as quickly as possible, and this fact was also stressed by Seel (1967). Among a few thousand nests of the Tree Sparrow investigated by many authors during many breeding seasons only Bethune (1961) in Belgium found two fourth broods, and in one of these all the eggs were infertile, while there were no fledglings from the other one. In the previous broods of these pairs there was also a considerable number of infertile eggs. The pairs involved consisted of exceptionally old birds. In the House Sparrow fourth broods are not infrequent, and sometimes even fifth broods may occur (Weaver 1943, Summers-Smith 1963).

What then are the factors conditioning the number of broods and the length of the breeding season in the Tree Sparrow? A female Tree Sparrow lays in a breeding season a limited number of eggs which can not be increased by their removing them from the nest (Puhlmann 1914, Eisenhut and Lutz 1936). Also females of the Spanish Sparrow lay a limited number of eggs (Gavrilov 1962). In contrast to both the above mentioned species, female House Sparrows may be made to lay a few times greater number of eggs than they normally do in the breeding season (Rey 1912, Puhlmann 1914, Witschi 1935, Eisenhut and Lutz 1936). The comparison of the history of first, second and third broods clearly indicates that considerably fewer nestlings hatch from the eggs of third broods than from earlier broods (cf. chapter 7, Tab. VII). They are either infertile eggs or eggs which disappeared probably thrown away by the parents. Also Creutz (1949) and Eliseeva (1961) stressed that in third broods there was a greater per cent of eggs from which no nestlings hatched than in the earlier broods. Eliseeva tried to connect it with a higher number of addled eggs resulting from exposure to excess cold but she not distinguish infertile eggs from addled ones. Our data do not indicate any direct connection between the percentage of hatched nestlings and air-temperature during the incubation of third broods (cf. Fig. 12).

In order to assess mortality in eggs and nestlings in final broods, 109 broods, chosen in the following way, were analysed: from each of the breeding colonies during all the years the last 3–5 broods of the season were taken into account. Among these broods the number of infertile eggs was higher than even in the earlier third broods. On the other hand the mortality of nestlings of the last 3–5 third broods was even smaller (Tab. IV).

The termination of the breeding season in the Tree Sparrow may be conditioned, through natural selection, by different selection pressures acting on birds from later broods than from earlier ones. Moulted and sexually active Tree

[1]The breeding season of the population as a whole lasts from the date of the first egg of the year to the date on which the last young of the year left the nest.

Sparrows appear in breeding colonies at the beginning of September. They are either old birds or young ones from early broods. They occupy the best nest-boxes (holes) in the optimum habitats (Pinowski 1965a). Young birds from later broods finish moulting later (Fig. 4) and appear in breeding colonies at the end of September when all the most suitable sites for building nests are already occupied, particularly in the summers when the population is large.

Comparison of losses of eggs and nestlings in the last 3–5 broods of the season from each of the colonies with all third broods in all years

Tab. IV

	The last broods	Third broods
Number of broods	109	386
Number of eggs laid	499	1841
Average clutch-size	4.57 ±0.73	4.77 ±1.04
Per cent of eggs destroyed with the rest of the clutch	6.41 ±1.09	5.26 ±0.60
Per cent of eggs lost or destroyed in nests from which at least one nestling fledged	8.22 ±1.22	17.33 ±0.80
Per cent of infertile eggs	8.42 ±1.24	6.43 ±0.57
Per cent of eggs from which nestlings hatched	76.95 ±1.88	70.98 ±1.06
Per cent of nestlings which perished in the first five days of life and of undetermined age (percentage in relation to the number of eggs laid)	3.41 ±0.81	6.98 ±0.60
Per cent of nestlings which perished between 6th and 10th day of life	3.61 ±0.83	2.33 ±0.36
Per cent of nestlings which perished between 11th day of life and leaving the nest	0.60 ±0.34	0.91 ±0.22
Total per cent of mortality in nestlings	7.62 ±1.18	10.22 ±0.70
Per cent of nestlings which left the nests, in relation to the number of eggs laid	69.34 ±2.06	60.80 ±1.18

In the period of autumn sexual display Tree Sparrows not only occupy nest-boxes, form pairs, build nests, and copulate, but are also connected with that nest-box and roost in it through the autumn and winter period (Pielowski and Pinowski 1962, Pinowski 1965a, 1967a). Young birds from later broods maturing at the end of September and in October, even if they take part in autumn sexual display and form pairs, only start building their nest or do not build at all. They also roost rarer in nest-boxes, and more frequently in the canopies of trees even in the period with severe frosts (Pinowski 1967a). Disregarding here the effect of overcrowding as a populational factor, the fact that they do not take full part in autumn sexual display and, connected with it, maintaining only loose contact with the hole or none at all in winter must reduce their chances of surviving till the breeding season. Roosting in the shelter of a nest-box enables birds to save a considerable amount of energy

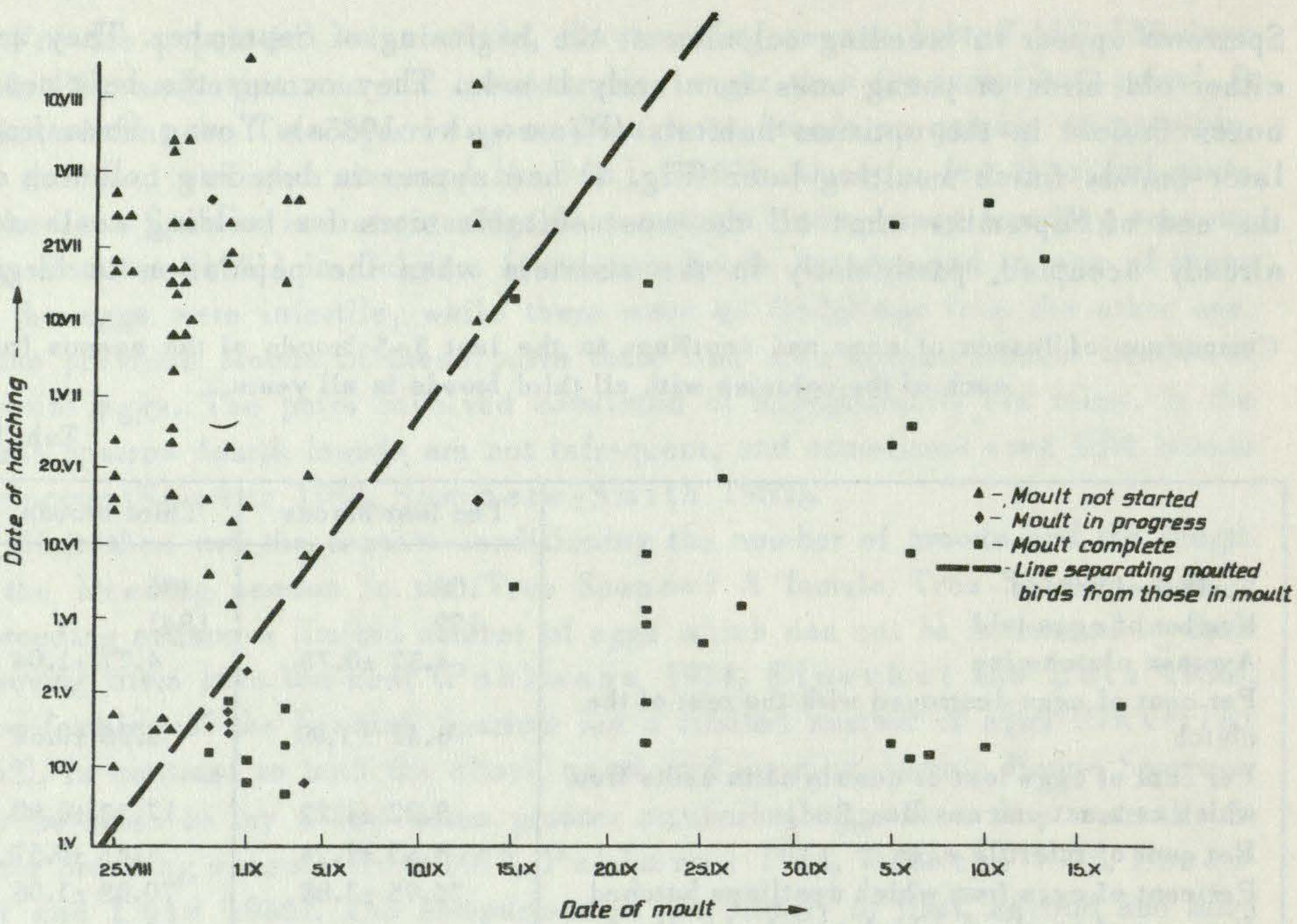

Fig. 4. The relationship between the date of hatching and the date of post-juvenile moult

in the winter period (Kendeigh 1961) and the more so roosting in a nest-box with a complete nest. Newton (1966) noted that those young Bullfinches (*Pyrrhula pyrrhula* L.), which moulted latest, had a smaller chance of surviving the winter than those which moult earlier.

Tree Sparrow populations moult from August till the middle of October. After 10th October unmoulted birds occur rather rarely (Fig. 5). Deckert (1962) (near Berlin) also stressed that from the end of October she did not find any moulting Tree Sparrows. Juvenile plumage differs from that of the adults in being weaker, looser in texture (Van Tyn and Berger 1959, p. 96, Newton 1966) and because of this it does not insulate so well so that young birds in juvenile plumage lose more heat than old birds (Kendeigh 1939). The process of moulting also requires a considerable amount of energy (Koch and de Bont 1944, Wallgren 1954, King and Farner 1961, Dolnik 1965, Newton 1966) and is much easier for birds to complete early in autumn, i.e. when temperatures are higher and feeding conditions better. Similarly, old birds terminating their breeding late, have a somewhat delayed moult with all its disadvantages.

I think that the disadvantages of a late moult in young birds from final broods and the resulting delay, or absence of autumn sexual display should be taken as the main selection pressure conditioning the end of the breeding season in the Tree Sparrow at a time when climatic and food conditions would still permit breeding.

The end of the breeding season (the date of leaving the nest by birds from final broods), determined on the basis of material from a few hundred nests every year distributed in a few breeding colonies in the radius of 5 km, varied only slightly from year to year (Tab. III). Only in 1962, which was an exceptionally cold and rainy year, was the end of the breeding season as late as 2nd September. In a cold and rainy period it takes longer for the young to develop and because of that the whole course of breeding takes longer. At the same time owing to the losses of the whole broods the synchronization of broods is reduced (Fig. 3). The later first broods commence, the shorter is the breeding season (Tab. III).

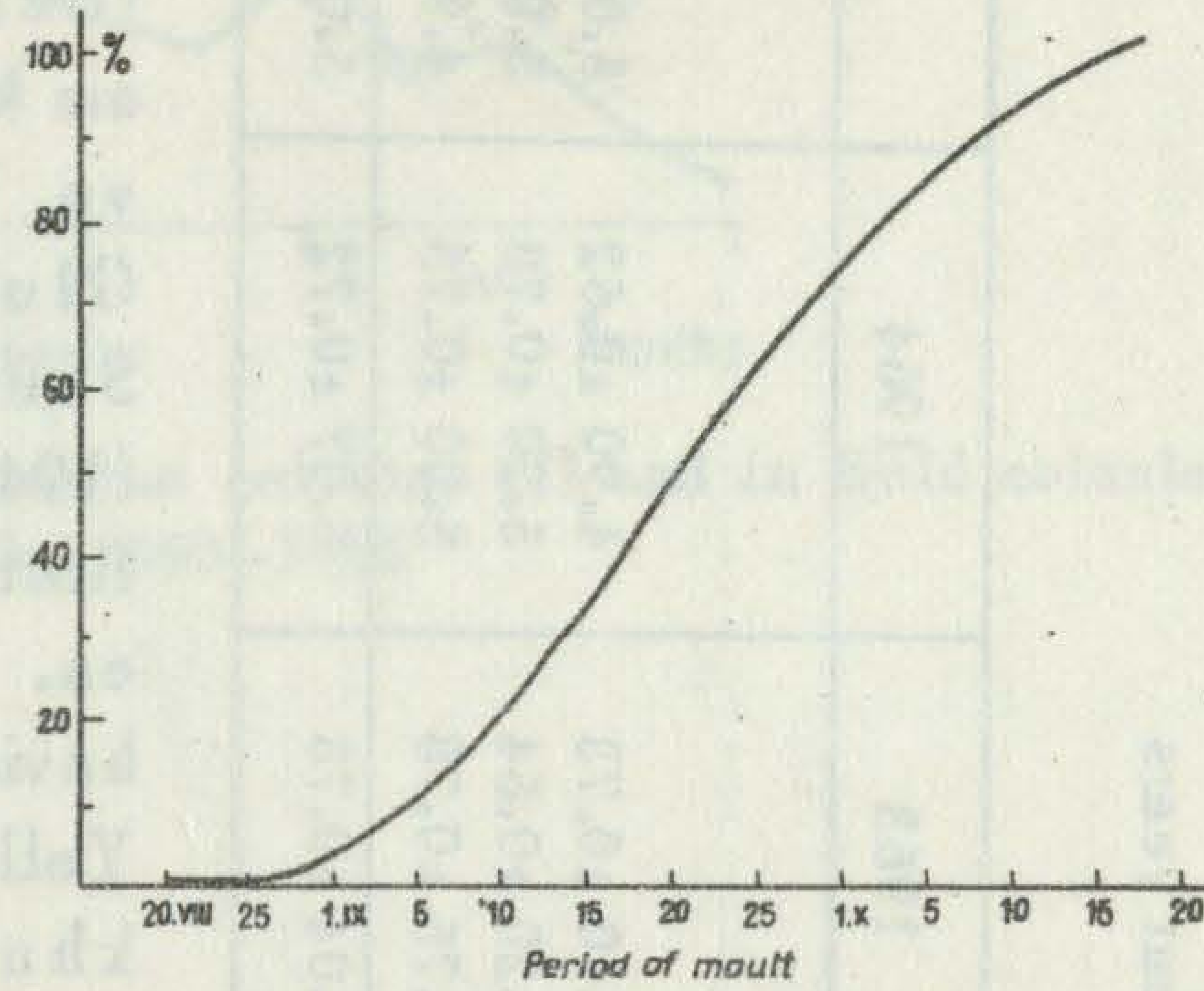

Fig. 5. The percentage of completely moulted young birds in the catches. Based on data for 1960–1965

6. CLUTCH-SIZE

6.1. Clutch-size in first, second and third broods, and seasonal variations in clutch-size

Clutch-size in the Tree Sparrow varies from 3 to 8 eggs. The average clutch-size in the sturdy area calculated on the basis of 1,417 clutches from the years 1960–1965 was 4.97 ±1.00 (Tab. V).

Usually the second clutch is the largest one, and third, is the smallest (Tab. V). First clutches are particularly small at the beginning of the breeding season in April, but in May clutch-size increases and remains high until the end of the breeding season in July when there is a drop (Fig. 6). Second clutches more often consist of 6 eggs make up a greater per cent than in first broods and it is mainly due to them that the average size of second clutches is higher (Fig. 7). Clutches of 7 eggs are also relatively rare even in second broods. A clutch of 8 eggs was recorded only once. First and third broods have more clutches of 3 and 4 eggs than second broods (Fig. 7). Average clutch-sizes of third broods were always smaller than in second broods, and only in 1962 were average clutch-sizes of first broods somewhat higher than of second broods (Tab. V). Final clutches, that is the latest of third broods, are of the smallest size (Tabs. IV, VI).

The majority of authors record that in the Tree Sparrow clutches of first and third broods are smaller than those of second broods (Berndt and Frieling 1939 – Frankfurt am Main, Bethune 1961 – Belgium, Eliseeva 1961 – Kursk (USSR), Steffan according to Glutz von Blotzheim 1962 – Switzerland, Seel 1964 – Great Britain). Only Creutz (1949) near Dresden recorded that the size of first clutches was larger than of second clutches. Similarly, in a number of other species having several broods each year, such as the Yellowhammer (*Emberiza citrinella* L.) (Parkhurst and Lack 1946), the Blackbird (*Turdus merula* L.), the Song Thrush [*Turdus philomelos* (Brehm)], the Robin (*Erithacus rubecula* L.) (Lack 1949), the Spotted Flycatcher (*Muscicapa striata* Pall.) (Summers-Smith 1952), early clutches are smaller than those laid in the middle of the breeding season; and generally clutches at the end of the breeding season are smaller (Davis 1952, Lack 1954, Welty 1962, and others).

Seel (1967) recorded in the Tree Sparrow a correlation between the size of broods and the length of the day and explained it (after Lack 1947, 1954) as an effect of the day-length on the amount of food brought to the young: the longer the day the more food can be obtained by the parents which are thereby able to raise a larger number of nestlings. In our investigations clutches reach the same average size in May as they do in June (Fig. 6). About 15 days are required for laying eggs and incubation, and so already at the beginning of June nestlings hatch from clutches of the same size as in the second half of this month when days are longest, however Lack (1947)

Tab. V

Clutch-size *I*, *II*, *III*, in different years

clutch	Number of clutches	1960	1961	1962	1963	1964	1965	Average
I	515	4.76 ±0.59	4.70 ±1.09	5.18 ±1.25	5.10 ±0.73	4.90 ±0.62	5.08 ±0.61	4.81 ±0.97
II	516	5.30 ±0.87	5.17 ±1.19	5.06 ±1.25	5.20 ±0.64	5.20 ±0.78	5.06 ±0.79	5.14 ±1.00
III	386	4.65 ±0.68	4.57 ±1.42	4.78 ±0.82	4.75 ±0.78	5.00 ±0.75	4.98 ±1.02	4.77 ±1.04
Average		4.91 ±0.77	4.88 ±1.08	4.81 ±1.16	5.04 ±0.78	5.07 ±0.72	5.04 ±1.06	4.97 ±1.00

has already stressed that the day-length was only one of the factors affecting, clutch-size and often not the most important one.

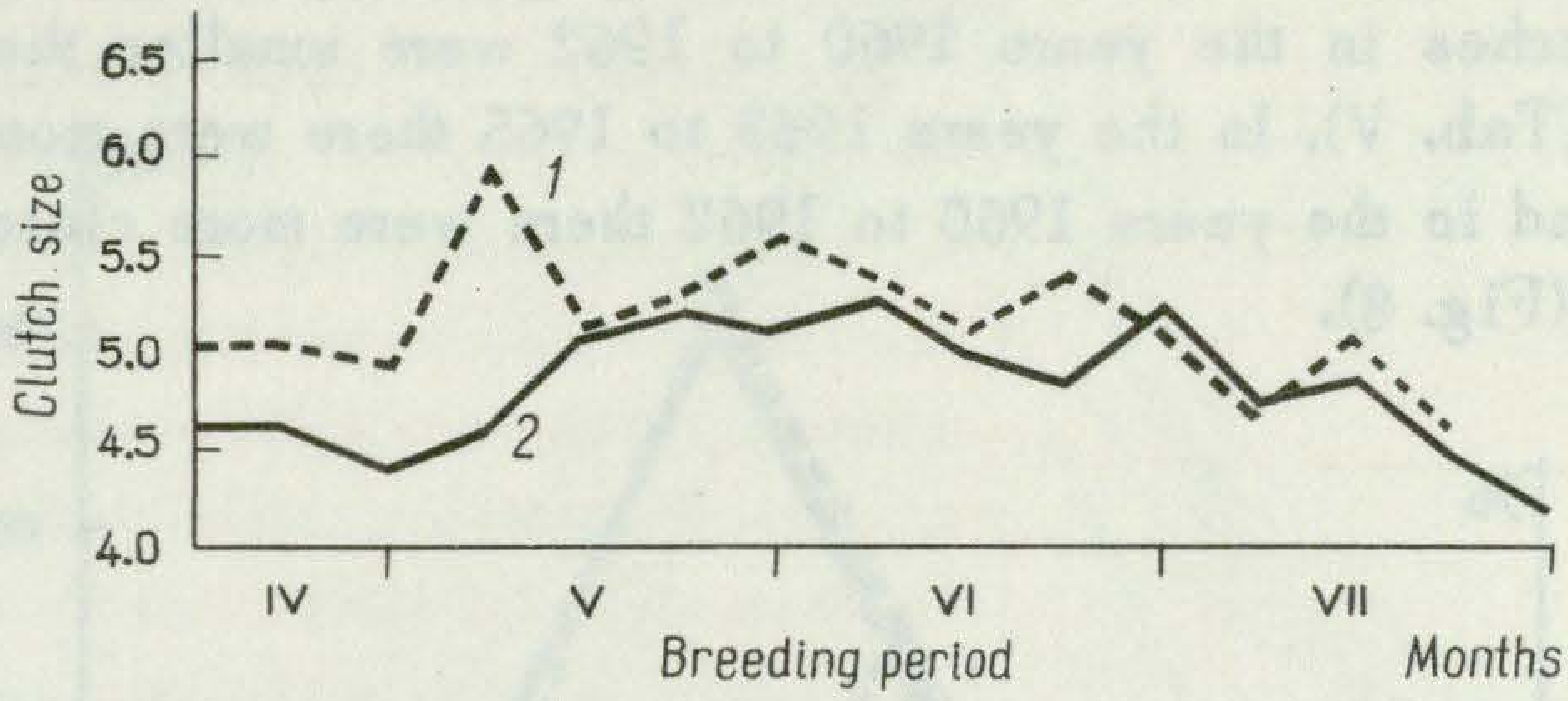

Fig. 6. Mean clutch-size through the season in forest colonies (*1*) and in field colonies (*2*). Based on data for 1960–1965

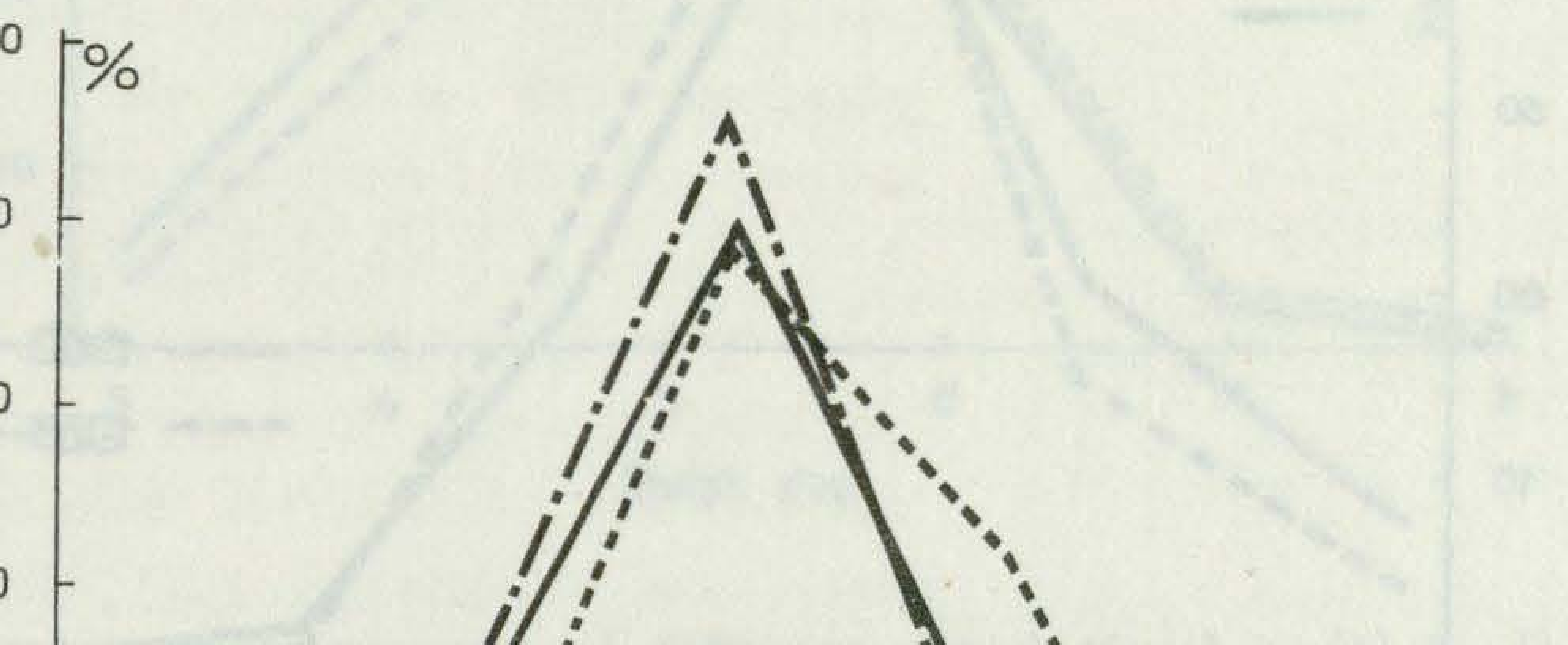

Fig. 7. The percentage occurrence of different sized clutches in first, second and third broods (*I* against *II* – $\chi^2 = 54.27$; $df = 4$; $P < 0.001$; *II* against *III* – $\chi^2 = 46.00$; $df = 4$; $P < 0.001$)

The percentage frequency of different clutch-sizes in third broods compared with the last 3–5 clutches of the season. Data for all years and all colonies have been combined

Tab. VI

Clutch-size	3	4	5	6	7	Total	Number of broods
Third broods	6.5	22.9	54.1	15.1	1.4	100.0%	384
Last Broods	9.2	29.4	50.9	5.5	0	100.0%	109

$\chi^2 = 11.8829$ df = 4 $P < 0.02$

6.2. Clutch-size in different years

Average sizes of clutches in different years vary from 4.88 to 5.07 eggs per nest. Clutches in the years 1960 to 1962 were smaller than in the years 1963 to 1965 (Tab. V). In the years 1963 to 1965 there were more clutches of 5 and 6 eggs, and in the years 1960 to 1962 there were more clutches consisting of 3 to 4 eggs (Fig. 8).

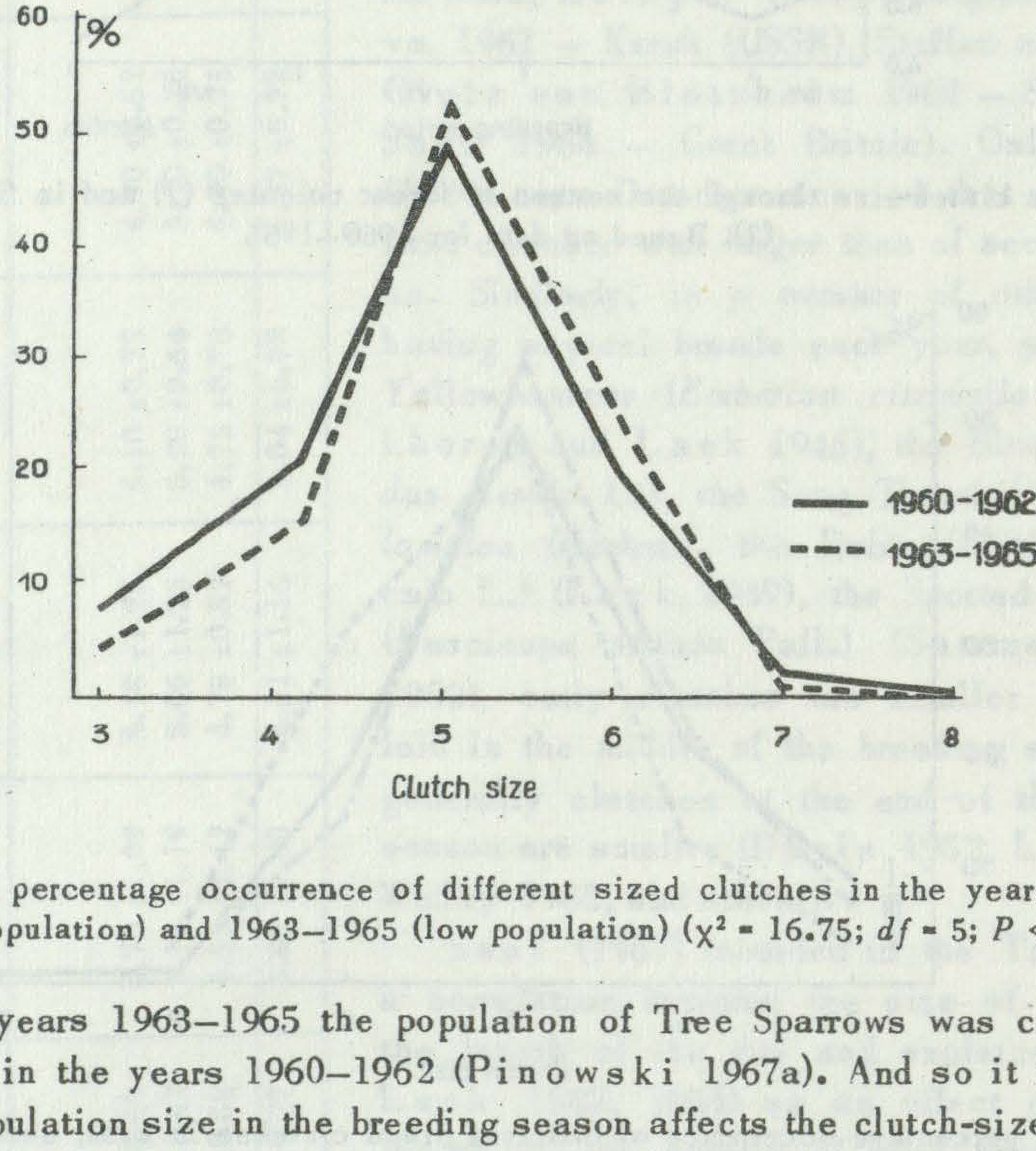

Fig. 8. The percentage occurrence of different sized clutches in the years 1960–1962 (high population) and 1963–1965 (low population) (χ^2 = 16.75; df = 5; $P < 0.001$)

In the years 1963–1965 the population of Tree Sparrows was considerably lower than in the years 1960–1962 (Pinowski 1967a). And so it is possible that the population size in the breeding season affects the clutch-size. Similarly, a lowering of clutch-size at high density has been recorded in the Great Tit (*Parus major* L.), the Blue Tit (*Parus coeruleus* L.), the Coal Tit (*Parus ater* L.), by Kluyver (1951), Lack (1955, 1958) and Perrins (1965), and in the Song Sparrow by Johnston (1956).

6.3. Clutch-size in forest and field colonies

In forest colonies clutches were somewhat larger than in field colonies; in the latter there were proportionally more clutches, of 3 or 4 eggs than in forest colonies (Fig. 9). Out of 23 weeks of the breeding season in different years of the investigations it turned out in 18 cases that clutches in forest colonies were larger than in field colonies ($\chi^2 = 7.34$, $df = 1$, $P < 0.001$). And so it seems that differences between the analysed habitats in fact really exist.

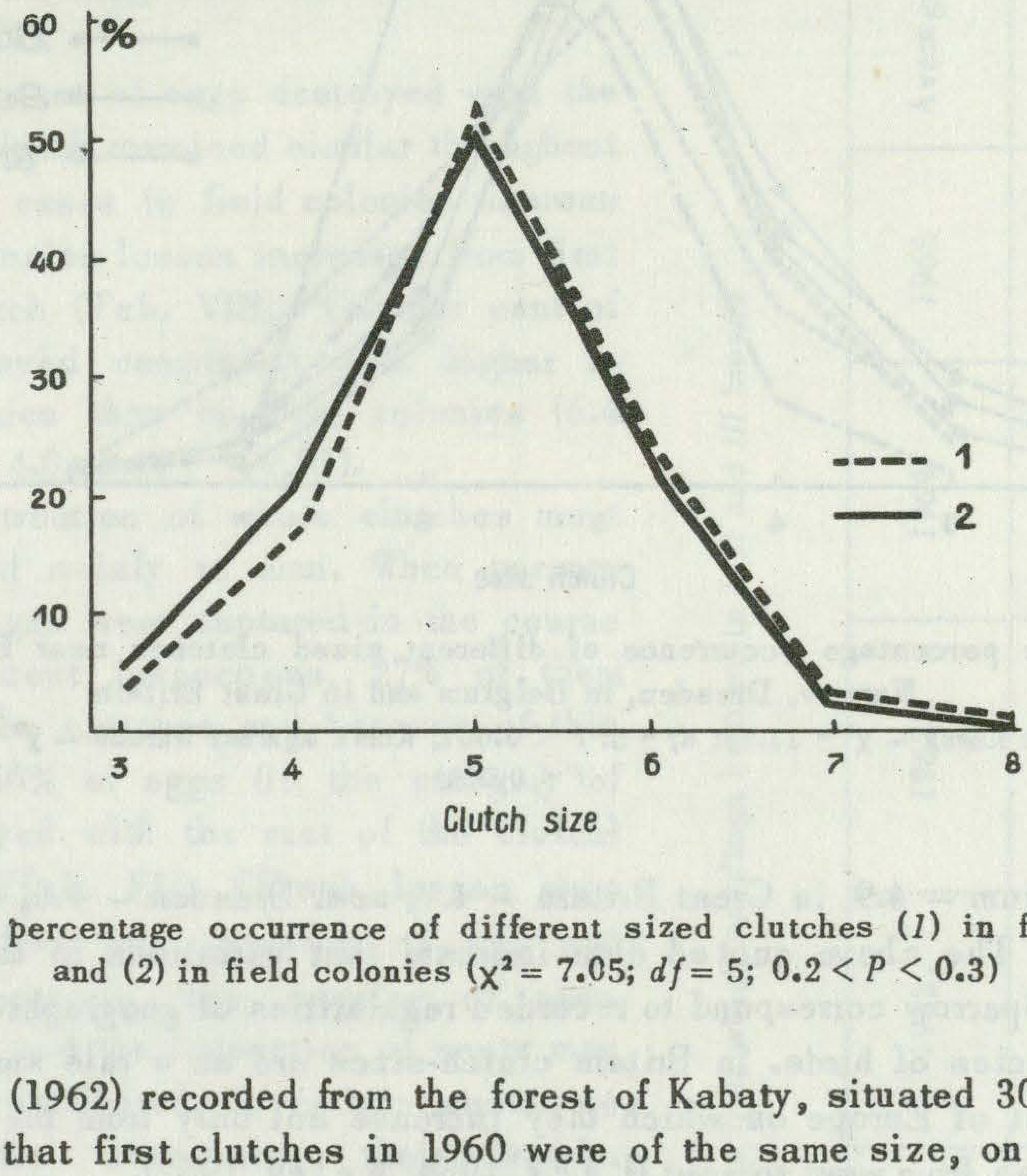

Fig. 9. The percentage occurrence of different sized clutches (*1*) in forest colonies and (*2*) in field colonies ($\chi^2 = 7.05$; $df = 5$; $0.2 < P < 0.3$)

Busse (1962) recorded from the forest of Kabaty, situated 30 km from my study area, that first clutches in 1960 were of the same size, on the average, of 4.88 ±0.31 eggs, i.e. the same number that was recorded in our area, but in 1961 they were much larger and amounted to 5.52 ±0.25 (Tab. V). Considerable variations in the clutch-size of the Tree Sparrow in different habitats were stressed also by Seel (1967).

The percentage occurrence of various clutch-sizes based on at least 50 nests are known to me from 7 regions: Peking (40°N, 116°E) (Chia et al. 1963); Kursk (52°N, 36°E) (Eliseeva 1961), Warsaw (52°20'N, 20°50'E) (data obtained by the author), Dresden (51°N, 14°E) (Creutz 1949), Belgium (51°N, 3°E) (Bethune 1961), Great Britain (Seel 1964). Clutches of 8 eggs were found only near Peking, Kursk, and Dresden. Clutches consisting of 7 eggs occurred frequently only near Peking, while in other areas they were rare. Clutches of 6 eggs were most frequent near Kursk, and clutches of 5 eggs in other areas (Fig. 10). At Singapore, among 21 nests analysed, the most frequent clutches consisted of 3–4 eggs (Ward – in a letter). The largest average clutches were recorded near Kursk – 5.5, near Peking they amounted to 5.0, near Warsaw to

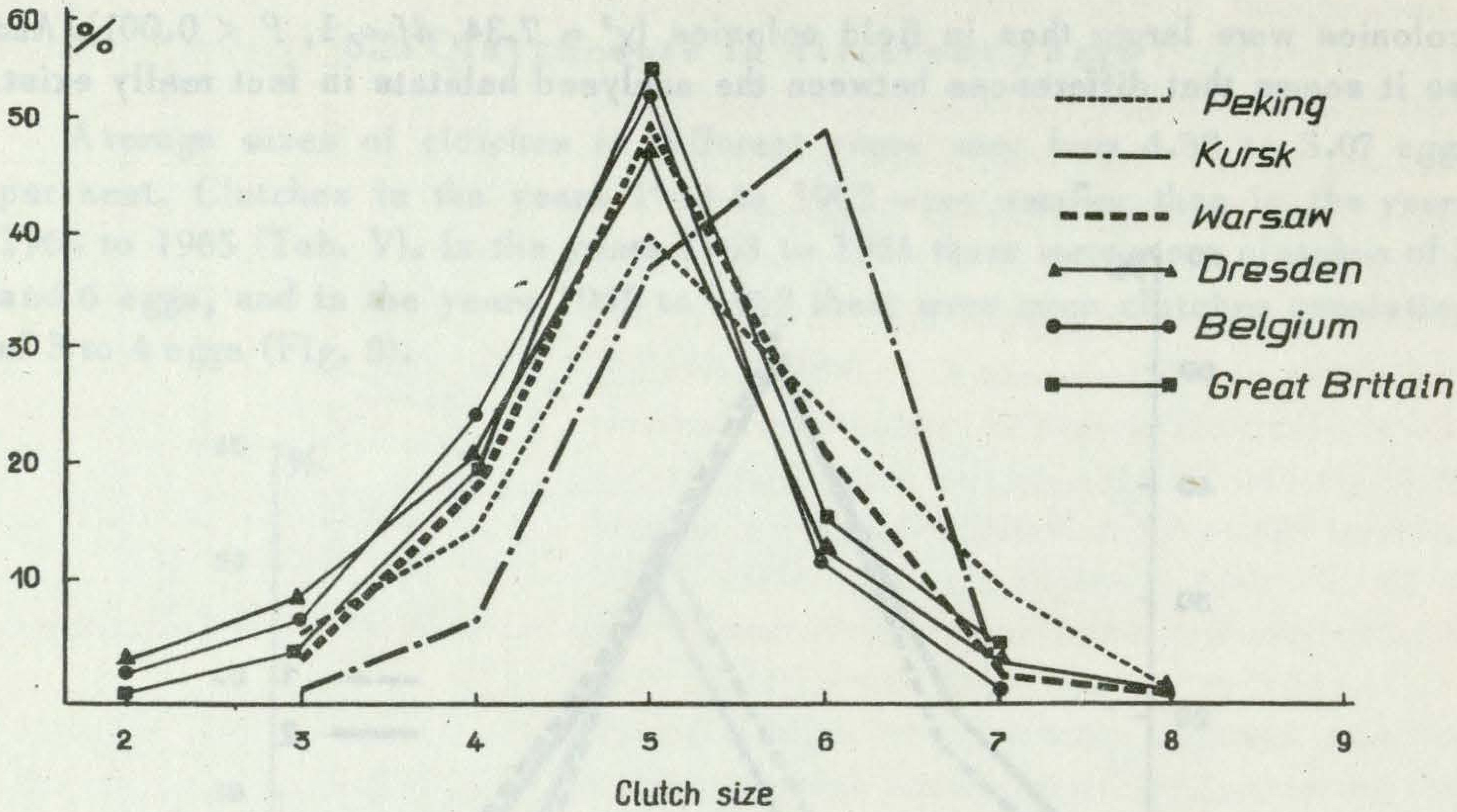

Fig. 10. The percentage occurrence of different sized clutches near Peking, Kursk, Warsaw, Dresden, in Belgium and in Great Britain

(Peking against Kursk – $\chi^2 = 31.73$; $df = 5$; $P < 0.001$, Kursk against Warsaw – $\chi^2 = 243.95$; $df = 5$; $P < 0.001$)

4.9, in Belgium – 4.9, in Great Britain – 4.7, near Dresden – 4.6, and at Singapore – 3.7. The above quoted data indicate that variations in the clutch-size of the Tree Sparrow correspond to recorded regularities of geographical variations in other species of birds. In Britain clutch-sizes are as a rule smaller than on the continent of Europe on which they increase not only from the south to the north, but also from west to east (Lack 1954, Welty 1962).

7. THE EXTENT AND CAUSES OF EGG-LOSS

7.1. The extent of egg-loss

On the average, 78.7 ±0.5% of all eggs laid hatched. Eggs laid in first broods were most successful and those in third broods least successful. Only in particularly cold springs, as in 1963 and 1965, the per cent of eggs hatched was higher in second than in first broods (Tab. VII). Otherwise, there were no significant differences in hatching success from year to year.

Over the study period as a whole, a smaller proportion of eggs in forest than in field colonies hatched successfuly (73.7 ±0.9 against 78.0 ±0.6; $P < 0.01$).

Eggs that failed to hatch were either destroyed together with the rest of the clutch or they were from nests in which one or more young hatched successfuly.

The per cent of eggs which were destroyed with the rest of the clutch was (with the exception of 1965) always smaller than the per cent of eggs lost from nests in which at least one hatching success was recorded (Tabs. VIII, IX).

The per cent of eggs destroyed with the rest of the clutch remained similar throughout the season, cases in field colonies whereas in forest colonies losses increased from first to third clutch (Tab. VIII). The per cent of nests destroyed completely was higher in forest colonies than in field colonies (6.4 ±0.5 against 4.0 ±0.3; $P < 0.01$).

The destruction of whole clutches must be attributed mainly to man. When parents incubating eggs were captured in the course of routine nest inspections, 27% of them abandoned the clutches and because of this more than 50% of eggs (in the category of eggs destroyed with the rest of the clutch) were lost (Tab. IX). (These losses were eliminated from the analysis of egg and nestling success). The opening of nest-boxes itself and the inspection of nests may have also contributed, in certain cases, to certain pairs abandoning their broods. Probably some birds were also scared off or their nests destroyed by children. Only four clutches were destroyed by Wrynecks (*Jynx torquilla* L.), and also a small number by Hornets (*Vespa crabro* L.), Wasps [*Dolichovespula saxonica* (F.)], *Paravespula germanica* (F.), and Bumblebees (*Bombus* sp.) (Pinowski 1967a).

The per cent of eggs from which no nestlings hatched but were laid in nests with at least one egg hatching successfully varied in different years from 15.0 to 21.1%. The majority of such losses were made up of eggs that were missing (Tab. IX). Tree Sparrows, like other species of birds, throw

Tab. VII

Per cent of eggs from which nestlings hatched in *I*, *II* and *III* broods

	1960	1961	1962	1963	1964	1965	Average	Total number of eggs
Brood *I*	80.9 ±2.5	86.1 ±1.7	90.6 ±1.1	77.8 ±1.9	84.0 ±1.8	65.9 ±3.6	83.3 ±0.7	2343
Brood *II*	66.6 ±3.3	78.3 ±1.8	78.5 ±1.4	83.7 ±2.0	81.0 ±1.9	84.4 ±2.4	79.2 ±0.8	2423
Brood *III*	54.4 ±4.4	74.2 ±2.3	73.3 ±2.0	76.3 ±2.5	77.2 ±2.9	65.5 ±2.8	71.8 ±1.0	1744
Average for the year	69.9 ±1.9	79.6 ±1.1	81.4 ±0.8	79.3 ±1.2	81.4 ±1.2	71.7 ±1.7	78.7 ±0.5	

Per cent of eggs destroyed with the rest of the clutch and per cent of eggs from which no nestlings hatched in nests in which at least one egg hatched

Tab. VIII

	Number of eggs laid	Per cent of eggs destroyed with the rest of the clutch	Per cent of eggs from nests which had at least one hatching success
Forest colonies			
Brood *I*	821	4.8 ±0.8	16.6 ±1.3
Brood *II*	778	6.5 ±0.9	18.9 ±1.4
Brood *III*	459	9.1 ±1.2	27.2 ±2.1
Field colonies			
Brood *I*	1,758	4.5 ±0.6	13.8 ±0.8
Brood *II*	1,868	3.4 ±0.6	17.9 ±0.8
Brood *III*	1,375	4.3 ±0.6	22.7 ±1.1
Total	7,059	4.7 ±0.3	18.4 ±0.5

Per cent of eggs destroyed with the rest of the clutch and per cent of eggs destroyed from clutches which had at least one hatching success, with a division of eggs into infertile, lost, slightly broken and addled

Tab. IX

Year	Eggs from broods completely destroyed	Eggs from broods partly destroyed	Infertile	Addled	Slighty broken	Lost	Total number of eggs laid
1960	13.8	19.0	5.8	0.0	2.6	10.6	536
1961	9.6 (5.3)	17.0	5.3	0.0	3.1	8.6	1402
1962	6.3 (3.8)	16.5	6.0	0.6	0.0	9.7	2280
1963	6.2 (5.7)	21.1	7.2	0.2	1.7	11.9	1177
1964	5.0 (3.8)	17.6	5.0	0.0	0.0	12.2	999
1965	24.2 (8.9)	15.0	3.5	0.3	0.8	10.3	735

In parenthesis per cent of eggs abandoned by parents after they were captured on the nest.

out of their nests slightly broken eggs (Armstrong 1955) and this most probably contributed to the great number of eggs which just disappeared. The greatest number of eggs disappeared from third broods (Tab. X). Infertile eggs made up 3.5 – 7.2% of the number eggs laid (Tab. IX). The greatest number of infertile eggs was in third broods (Tab. X). The number of eggs evidently addled or with a slightly broken shell was very small (Tabs. IX, X). In forest and field colonies the per cent of eggs that were lost through these various causes did not differ significantly from each other (Tab. X).

Per cent of eggs lost, infertile, addled and slightly broken from nests which had at least one hatching success

Tab. X

	Lost eggs	Infertile eggs	Addled eggs	Slightly broken eggs	Number of eggs laid
Forest colonies					
Brood *I*	11.8 ±1.1	4.7 ±0.7	0.1 ±0.1	0.0	821
Brood *II*	10.9 ±1.1	6.8 ±0.9	1.1 ±0.3	0.0	778
Brood *III*	18.7 ±1.8	8.5 ±1.8	0.0	0.0	459
Field colonies					
Brood *I*	8.5 ±0.6	4.2 ±0.5	0.0	0.9 ±0.2	1758
Brood *II*	10.7 ±0.7	5.3 ±0.5	0.0	2.0 ±0.3	1868
Brood *III*	15.1 ±0.9	5.7 ±0.6	0.0	1.8 ±0.3	1375
Average	11.6 ±0.3	5.4 ±0.2	0.2 ±0.0	1.1 ±0.1	7059

In different regions of the Tree Sparrow the per cent of eggs that hatch successfully varies considerably, but nowhere was it lower than 50%, Near Peking it amounted, on the average, to 85% (Chia et al. 1963), near Kursk it varied in different years from 81.3 to 84.5% (Eliseeva 1961), near Dresden it amounted to 60.2% (Creutz 1949), in Belgium 57.7% (Bethune 1961), in various parts of Great Britain – 88% (Seel 1964).

As in our investigations Creutz (1949) and Eliseeva (1961) also recorded that the smallest egg-loss was in first broods and the highest in third broods. Also the highest number of infertile eggs was recorded in third broods (Creutz 1949, Blagosklonov 1950, Eliseeva 1961). In England, the Tree Sparrow hatches its eggs more successfully than the House Sparrow (Summers-Smith 1963, Seel 1967), on the other hand in Germany the position is reversed (Creutz 1949, Encke 1965). In the Spanish Sparrow which nests in large colonies in trees, the per cent of eggs hatched successfully was very high at 95.1% (Gavrilov 1962). In the Black-faced Dioch (*Quelea quelea* L.), which nests in a similar site to the Spanish Sparrow, i.e. in large colonies, and which builds open nests, the per cent of hatched eggs was also very high (Ward 1965).

Nice (1957), analysing the hatching success of 12 species of hole-nesting birds on the basis of papers written by several authors and containing data on 34,000 laid eggs concluded that the percentage of eggs which hatched in hole-nesting birds amounted, on the average, to 77%, this is not significantly different from the data obtained for the Tree Sparrow in our study area (78%). The range of variation in the per cent of Tree Sparrow eggs hatching also corresponds with similar data for other species of hole-nesting birds (Gibb 1950, Creutz 1955, Lack 1955, 1958, Perrins 1965 and others).

7.2. The causes of egg-loss

Of all climatic factors only temperature seems to have a significant effect on the per cent of eggs hatched. The effect of the average day-time temperature during incubation on hatching success was marked only on first clutches, and only then when the day-time temperature of the period often dropped below 12°C (Fig. 11); the regression was statistically significant, ($F_{cal} > F$ 0.01; 23.11 > 9.07). In second and third broods, when the average daily temperatures were always higher than 12°C, there was no correlation between temperature and hatching success (Fig. 11).

The eggs were maintained at constant temperature during incubation through changes in the frequency and length of time they were warmed by the birds (Baldwin and Kendeigh 1932, Kendeigh 1952, 1963b, Armstrong 1955, Haartman 1956, Curio 1959, and others). The amount of time that a bird spends warming its eggs depends very much on the temperature of the environment (Kendeigh 1949, 1963b).

It seems that at average day temperatures below 10°C a discrepancy becomes evident between the amount of energy required for Tree Sparrows to incubate the eggs, and the length of time needed for this operation on one hand, and the extra feeding time needed to compensate this increased use of energy on the other. As a result of this, the bird takes longer to obtain its food and this may lead to the exposure of the eggs to excess cold and to the death of the embryos. Besides, in the Tree Sparrow, males incubate the eggs only in the afternoon. Quite a number of authors have stressed that a considerable drop of temperature during incubation sometimes causes the birds to abandon their nests (Musselman 1935, Armstrong 1955, 172 p., Myres 1955, and others). Low temperatures may prolong incubation (Kendeigh 1940, Haartman 1956, Curio 1959, and others) and result in an increase in the per cent of eggs which fail to hatch. If we take that incubation in the Tree Sparrow lasts 12 days and that 22% of eggs suffer reduction then the mean daily reduction amounts to 2.0% of eggs laid (cf. Tab. VII). Kendeigh (1940, 1952) states that low temperatures may prolong the 12–14 days period of incubation by 3–4 days, and an equivalent increase in the Tree Sparrow would result in a rise in egg-loss by 6–9%. However in the case of the Tree Sparrow low temperatures, caused a considerably higher loss of eggs (Fig. 11), and so consequently low temperatures must have contributed to a large extent to these losses. Eliseeva (1961) stressed that when unfavourable climatic conditions prevail (rain and low temperatures) there is an increase in the Tree Sparrow in the number of addled eggs, and this supports our thesis about a direct effect of the temperature on hatching success of this species.

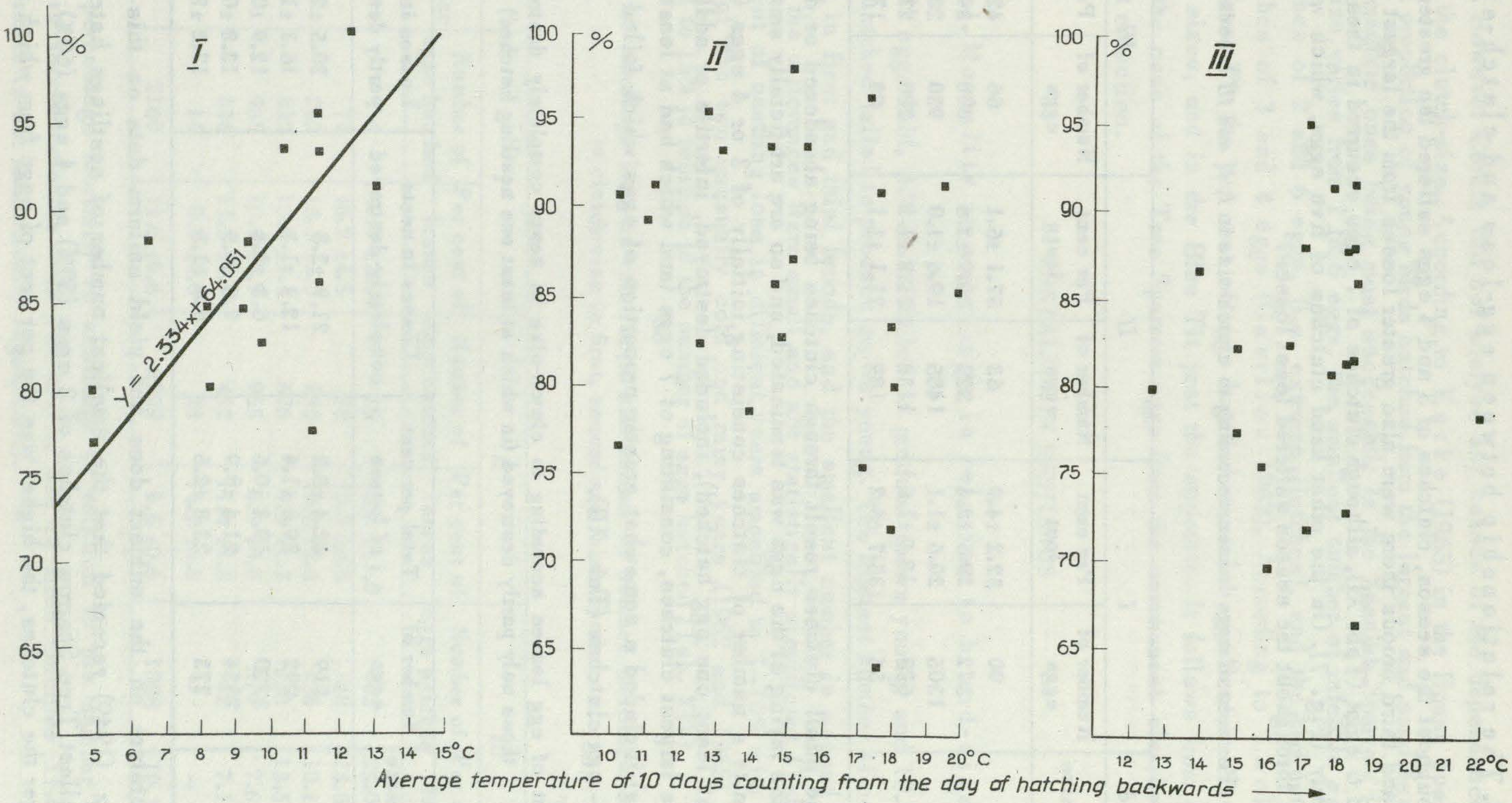

Fig. 11. The relationship between the mean temperature during incubation and the per cent of eggs hatched
I – first brood, *II* – second brood, *III* – third brood

7.3. The relationship between egg-loss and clutch-size

Throughout the season, clutches of 3 and 4 eggs suffered the greater losses. In first and third broods there were also greater losses from the largest clutches of 7 and 6 eggs (Tab. XI), although clutches of 7 eggs occurred in these broods only rarely (Fig. 7). On the other hand clutches of five eggs, which were most frequent throughout the season suffered least losses.

Per cent of eggs losses according to clutch-size in *I*, *II* and *III* broods

Tab. XI

Brood	*I*		*II*		*III*	
Clutch-size	Number of eggs	Per cent lost	Number of eggs	Per cent lost	Number of eggs	Per cent lost
3	90	32.2 ±4.9	63	57.1 ±6.1	66	42.4 ±6.1
4	372	19.6 ±2.4	320	30.9 ±2.6	300	39.6 ±2.8
5	1305	20.6 ±1.1	1485	19.6 ±1.0	930	20.5 ±1.3
6	628	18.9 ±1.6	1138	21.3 ±1.2	288	27.7 ±2.6
7	56	35.7 ±6.2	189	21.1 ±3.1	28	17.8 ±8.8

Some small clutches result through clutches being abandoned or destroyed before the laying of the eggs was terminated, and so are artificially small. However, quite a number of clutches consisting initially of 3 or 4 eggs (and from which at least one egg hatched), included destroyed, infertile or addled eggs. Also the largest clutches, consisting of 7 eggs (and which had at least one egg hatching) included a somewhat greater proportion of eggs which failed to hatch than 5 – egg clutches (Tab. XII).

Per cent of egg losses according to clutch-size in nests completely destroyed and those only partly destroyed (in which at least one nestling hatched)

Tab. XII

Clutch-size	Number of eggs	Total per cent of losses	Losses in nests completely destroyed	Losses in nests partly destroyed
3	219	42.4 ±3.3	21.9 ±2.8	20.5 ±2.7
4	992	29.0 ±1.4	12.9 ±1.3	16.1 ±1.1
5	3720	19.2 ±0.6	6.3 ±0.4	12.9 ±0.5
6	2054	21.4 ±0.9	7.6 ±0.5	13.8 ±0.7
7	273	23.8 ±2.5	6.6 ±1.5	17.2 ±2.2

Literature on the subject does not yield uniform data on this problem. Creutz (1949) recorded that the smallest number of nestlings hatched from the smallest Tree Sparrow clutches of 3 eggs (50%) and 4 eggs (60%), and that the larger the clutches, the higher was the per cent of eggs from which nestlings hatched. However Creutz did not analyse any causes of the dependence of egg loss on the clutch-size. According to Encke (1965) in the House Sparrow the smallest proportion of young birds hatched from the largest and smallest clutches intermediate ones being most successful; In the Spanish Sparrow in which clutch-size varies from 2 to 6 eggs, the smallest number of infertile eggs was in clutches of 2 and 6 eggs, (i.e. extreme clutches), and the highest number in clutches of 3 and 4 eggs (Gavrilov 1962). According to Lack (1955) in the Great Tit the per cent of eggs hatched was also smallest in clutches of extreme sizes, and in the Blue Tit just the opposite. It follows from our data that in the case of the Tree Sparrow eggs from the commonest clutches suffer the least reduction.

8. MORTALITY IN NESTLINGS

8.1. Mortality in nestlings in relation to brood-size

Of all eggs laid, 8.9 ±0.3% failed to produce grown young, and 10.5 ±0.4% of eggs hatched failed to produce grown young. The highest number of nestlings perished in first and third broods, and the smallest number in second broods, however the differences were small and not statistically significant (Tab. XIII). The extent of nestling loss in different years amounted to 7–10% with the exception of the two unusually cold and rainy years (1962 and 1965) when it amounted to 15% in relation to the number of eggs hatched (Tab. XIV).

Per cent of nestlings lost (in relation to the number of hatched nestlings) according to clutch-size in first, second and third broods

Tab. XIII

Brood	*I*		*II*		*III*	
Brood-size	Number of eggs hatched	Per cent of losses	Number of eggs hatched	Per cent of losses	Number of eggs hatched	Per cent of losses
1	6	50.0 ±20.4	19	36.8 ±11.0	12	25.0 ±12.5
2	74	16.2 ±4.5	58	13.7 ±4.5	48	14.0 ±4.9
3	243	13.5 ±2.8	135	10.3 ±2.6	138	10.1 ±2.5
4	532	12.0 ±1.4	576	9.6 ±1.2	338	13.5 ±1.7
5	955	10.5 ±0.9	955	6.5 ±0.8	510	7.6 ±1.1
6	336	11.3 ±1.9	432	11.4 ±1.5	42	7.1 ±3.9
7	14	0.0 ±0.0	28	14.2 ±6.6	–	–
Average	2160	11.6 ±0.6	2209	9.5 ±0.6	1088	10.7 ±0.9

The percentage mortality in nestlings in relation to the number of eggs hatched in forest colonies was 9.8 ±0.7%, and in field colonies 11.6 ±0.5% (the difference is not statistically significant).

Per cent of losses of nestlings (in relation to young hatched) in different years

Tab. XIV

Year	1960	1961	1962	1963	1964	1965
Young hatched	430	1203	1730	557	836	415
Per cent of nestlings lost	9.9 ±1.4	8.1 ±0.8	14.8 ±0.8	6.6 ±1.1	7.3 ±1.0	15.6 ±1.7
Total rainfall in mm (10.V–31.VII)	262.6*	188.7	281.5	146.5	158.4	237.2
Average temperature (10.V–31.VII)	14.4	15.8	14.5	19.6	17.5	14.7

*In 1960, in the last days of July rainfall amounted to 133.4 mm.

The highest mortality of nestlings was in the first five days of their life, and amounted to 63.7 ±2.9% of the total number of nestlings lost. From 6th to 10th day of life, 23.9 ±2.7% of nestlings perished, and in the last few days before leaving the nest, 12.4 ±1.8% of nestlings perished.

In the first five days of life 55.4 ±3.9% of nestlings perished with the rest of the brood, and from 6th to 10th day of life 7.6 ±2.9%, while from the eleventh day of life till the young bird leaves the nest-box 41.3 ±5.7% of the total number of nestlings which perished in the given age class. And so nestlings perish most frequently with the rest of the brood except in the middle age class.

The heaviest losses occurred in the broods of one nestling. Among larger broods of 2–6 nestlings the percentage loss was nearly the same (Tab. XV). This regularity occurred throughout the season (Tab. XIII). Nestling loss in broods of one nestling occurred mainly in the first 10 days of life. The percentage loss of complete broods did not increase with increasing brood-size (Tab. XV).

In 1964 and 1965, nestlings were weighed when they were 8–12 days old in order to obtain the degree of variation of nestlings in broods of various size. In broods consisting of 2–3 nestlings the maximum mean difference in the weight of nestlings amounted to 1.35 grams, in broods consisting of 4 nestlings – 2.55 grams, and in broods including 5–6 nestlings 2.97 grams. An increase in variations in the weight of nestlings was related to the increase in brood size, but only the difference between broods of 2–3 nestlings on the one hand and larger broods on the other was statistically significant ($P < 0.01$).

In 1962, the mortality in nestlings increased as a result of prolonged rain and cold which rendered it difficult for the parents to obtain sufficient food and warm their nestlings. In this year nestlings loss was the same in all brood, sizes of 3 or more. (Only in the two largest broods, consisting of 7 nestlings, there occurred higher mortality but these two broods can not be taken as a sta-

Per cent of nestlings lost (in relation to young hatched) according to brood-size. Data on losses in nests completely destroyed and nests which had at least one fledging success are separated

Tab. XV

Brood-size	Young hatched	Per cent of lost nestlings in all the broods	Per cent of nestlings lost in nests which were completely destroyed	Per cent of nestlings lost in nests which had at least one fledging success
1	37	37.8 ±7.9	37.8 ±7.9	–
2	182	16.0 ±2.7	10.0 ±2.3	6.0 ±1.7
3	516	12.0 ±1.4	4.1 ±0.8	7.9 ±1.1
4	1478	11.4 ±0.8	5.1 ±0.5	6.3 ±0.6
5	2430	8.5 ±0.5	2.5 ±0.3	6.0 ±0.4
6	816	11.4 ±1.4	5.1 ±0.8	6.3 ±0.8
7	42	9.5 ±4.5	0.0 ±0.0	9.5 ±4.5
	5501	11.4 ±0.9	5.0 ±0.1	6.4 ±0.3

tistical sample). In 1965, also a wet year there was no increase in mortality with increase in brood size (Tab. XVI).

Per cent of nestling losses (in relation to young hatched) according to brood-size in wet, cold years (1962 and 1965)

Tab. XVI

Year	1962			1965		
		Per cent losses			Per cent losses	
Brood-size	Young hatched	Broods completely destroyed	Broods partly destroyed	Young hatched	Broods completely destroyed	Broods partly destroyed
1	18	55.5 ±11.7	–	5	20.0 ±17.8	–
2	80	7.5 ±3.3	2.5 ±1.7	30	13.3 ±6.2	3.3 ±3.2
3	201	6.0 ±1.8	10.9 ±2.2	36	0.0 ±0.0	11.1 ±5.2
4	480	6.6 ±1.2	8.5 ±1.2	156	12.8 ±2.6	7.6 ±2.1
5	685	2.9 ±0.6	9.6 ±1.1	140	3.6 ±1.5	9.3 ±2.4
6	252	7.1 ±1.6	8.7 ±1.7	48	0.0 ±0.0	10.4 ±4.4
7	14	0.0 ±0.0	28.5 ±12.0	–	–	–

Nestling mortality in Tree Sparrows in relation to the number of eggs hatched amounted in Belgium to 8.1 ±1.0% (Bethune 1961), and near Kursk (USSR) in successive years was respectively 13.5%, 12.4%, 11.1% (Eliseeva 1961). These data are similar to my own on the average 11.4 ±0.9%. In Great Britain, however as many as 31% of nestlings hatched perished before they became old enough to leave the nest (Seel 1964). Eliseeva (1961) recorded that the smallest loss of nestlings occurred at the beginning and end of the breeding season and the heaviest loss in second broods just the opposite to what happened in my study area where the smallest loss was in second broods.

8.2. Causes of mortality in nestlings

8.2.1. Loss of whole broods

The highest number of nestlings perished in small broods of one nestling, they died in the first 10 days of life. It is possible that they hatched already weakened as they came from broods in which the majority of eggs did not hatch (practically no normal clutches consisting of one egg were found).

In 27 of 34 broods in which all nestlings perished, we failed to establish the cause. Of the remaining broods, one brood was destroyed by a Wryneck (*Jynx torquilla* L.), and one through the death of the female. In three nests we found dead nestlings covered with ants, in two cases they were *Lasius niger* L., and in one case some species of red ants [Bruns (1957) did not record any harmful effect of ants on broods of birds]. One nest was destroyed by a falling branch and two by an unknown predator. No harmful effect of other animals was recorded (Pinowski 1967a).

Long spells of rainy weather with a drop in temperature and a strong draught through the hole of the nest-box also caused the death of whole broods. For instance, on 5th June 1962, the minimum temperature was 6.4°C, and the maximum 10.2°C, the sky was completely overcast, it rained frequently and NNW wind was blowing through the entrance to nest-boxes, and the day before was slightly warmer but also overcast with heavy rain (28.6 mm). In 7 out of 12 broods, dead nestlings were recorded or complete lack of nestlings, while in other nests the nestlings were alive but cooler than the human hand. It seems likely therefore that those young that died suffered from excessive cold. There was in fact quite a high correlation between the per cent of nestlings leaving the nest and the mean minimum temperature ($r = 0.59 \pm 0.15$; $P < 0.01$) in different years.

Eliseeva (1961) wrote that some Tree Sparrows broods perished because of predators and the Wood Mouse [*Apodemus sylvaticus* (L.)], but the majority of them from bad weather, i.e. rain and low temperature, when it is extremely difficult for old birds to get the sufficient amount of suitable food for the nestlings and they have to feed them on unsuitable food from which they die. In Belgium where Bethune (1961) carried out his investigations considerable destruction of nests of Tree Sparrows was caused by dormice.

8.2.2. Losses of parts of broods

Nestlings which did not live to leave the nest were either found dead among their siblings or simply disappeared from the nest. Like other species of birds Tree Sparrows throw out of the nest dead or weakened nestlings which do not react with "begging" to their arrival at the nest (Berger 1959, Summers-Smith 1963, Luton 1965, Payn 1966, and others).

During laying Tree Sparrows devote progressively more time to warming, and incubation proper starts from the 3rd or 4th egg and as a result most of the eggs in a nest hatch on the same day (Seel 1967). Several authors, like myself, stated that the growth rate of different Tree Sparrow nestlings varies significantly, so that in each nest there are usually one or two nestlings smaller than the rest. This is usually caused by delayed hatching or by some nestlings receiving less food than the rest (Creutz 1949, Bethune 1961, Eliseeva 1961). However none of the above mentioned authors analysed the relationship between nestlings and brood-size. Only Seel (1964) wrote that he had not recorded any correlation between mortality of nestlings and brood-size.

In birds which feed their young on invertebrates the feeding frequency is higher in large broods than in small ones, but this increase is not directly proportional to the increase in the number of nestlings; as a result in large broods every nestling gets on the average a smaller amount of food (Kluyver 1933, Moreau 1947, Gibb 1950, Kendeigh 1952, and many others). Tree Sparrows feed their young almost exclusively on invertebrates, and in the first place with insects (Blagosklonov 1950, Pfeifer and Keil 1958, Berger 1959, and others).

In rainy and cold spells when it is difficult for parents to supply sufficient food, there should be a clear relationship between nestling-loss in the Tree Sparrow and brood-size, but I could detect no such relationship in my data even in the worst breeding season of 1962 (Tab. XVI).

There was an increase in mortality in nestling Spanish Sparrows as broods became larger. For instance, from clutches of 2 eggs 75% of nestlings left the nest, and from clutches of 6 eggs only 54% (Gavrilov 1962). In a different species of weaverbirds namely the Black-face Dioch (*Quelea quelea* L.) there was also recorded an increase in mortality in nestlings when brood size increased (Morel and Bourlière 1955, 1956, Ward 1965). Nestlings perished in the first few days of their life, most frequently from those eggs which were the latest to hatch while the hatching of nestlings in one brood was often spread over more than 24 hours (Ward 1965). A progressive increase in nestling mortality with increase in brood size has been recorded in many species of birds e.g., the Swift (*Apus apus*) (Lack D. and Lack E. 1951), the Blackbird (Snow 1958), and others. These data are in line with the thesis of Lack's (1947, 1954) that natural selection conditions the size of broods – the commonest brood sizes are those which give rise to most fledglings. In many species of birds, however as in the Tree Sparrow, there is either no correlation between brood-size and the mortality of nestlings or the correlation holds only in conditions particularly unfavourable for survival (Gibb 1950, Kluyver 1951, Lack 1950, 1954, 1955, Perrins 1965, and others). In such situations Lack (1954) came to the conclusion that young from large broods, although they leave the nest successfully have a smaller chance of surviving till the next breeding season and breeding themselves, and so the mechanism of natural selection would be the same. Starlings from larger broods perish more intensively in the first three months after leaving the nest than Starlings from smaller broods (Lack 1948). Mortality in young Blue Tits and Great Tits in the first three months after leaving the nest is higher among those which were raised in large than among those in small broods, and only in years with a small amount of food (caterpillars) in the period of feeding nestlings (Lack, Gibb and Owen 1957).

If however brood-size were conditioned, according to Lack's thesis, by natural selection, then an important thing would be not only the number of young birds surviving to the first breeding period but also the number of young raised per parents lifetime (Kluyver 1963). According to results obtained by Kluyver the highest number of young raised per female Great Tit are not produced by females raising the most frequently occurring broods, i.e. those producing 7–8 nestlings leaving the nest, but by females raising the largest broods, for from these broods the highest number of females survives to breed themselves.

In the Tree Sparrow there is no relationship between the size of the brood from which a bird comes and the chance of its surviving to the first breeding period. Both in large and in small broods the survival of young birds was nearly the same (Tab. XVII).

The effect of brood-size on the survival of fledglings

Tab. XVII

Brood-size	1–3	4	5	6–7
Number of nestlings hatched	318	648	1125	390
Per cent of young which survived at least 4 months after ringing	6.60 ±1.39	6.48 ±0.96	8.18 ±0.81	8.72 ±1.38
Per cent of young which survived till 1st May of the following year	1.25 ±0.62	1.39 ±0.46	2.75 ±0.48	3.85 ±0.97

If we accepted that there are no differences as to the number of nestlings in one breeding season raised by birds coming from large or small broods, then we could not accept Lack's conclusion on the role of natural selection in conditioning the size of broods in the Tree Sparrow. According to Kluyver (1963) differences in brood-size of Tits are evolved not by genetic but by phenotypic factors, and every Tit possesses an inborn ability to modify the brood-size and this ability may be evolved through natural selection.

In his latest work Lack (1966) analysed this problem in detail and also did not supply any data on the effect of clutch-size on the number of young surviving to the next breeding period, but only for three months after leaving the nest. Even as far as this period is concerned he stated that for some species there was no relationship between survival and brood-size, while for other species this relationship was evident only in some years. At the same time he stressed that there were considerable variations in clutch-size caused by phenotypic factors.

9. THE NUMBER OF EGGS LAID AND YOUNG BIRDS RAISED PER PAIR IN ONE YEAR

In all, in the years 1960–1965, 68.8 ±0.5% of eggs laid gave rise to fledged young. In most years, second broods were most successful and third broods least. Only in 1964 did a higher per cent of fledglings come from first than from second broods. The smallest number of fledglings (in relation to the number of eggs laid) was produced in 1965, and the highest number in 1963, the difference between the two years was only 10.7% (Tab. XVIII).

On the average, over the years 1960–1965, 3.24 nestlings left the nest from each clutch. The highest number of fledglings produced per nest occurred in 1964, and the smallest in 1965 (Tab. XIX). The highest number of fledglings per nest occurred in first and second broods and the smallest number in third broods. This pattern was maintained in all study years except 1963 when there were more fledglings in third broods than in 2-nd ones; in this year the cold spring caused considerable losses in the eggs and nestlings of 2-nd broods (Tab. XIX).

Taking into account all these data together with the per cent of pairs participating in first, second and third broods each year (Tab. I) it is possible to calculate the average number of eggs laid and young raised to fledging by one pair in a given year. On the average, for 1960–1965 one pair of Tree Sparrows laid in the breeding period 13.1 eggs and raised 8.7 young to leave the nest (Tab. XX). The highest number of eggs per pair occurred in 1962 and the smallest in 1960; the highest number of young raised per pair occurred in 1964 and the smallest in 1965 (Tab. XX).

Per cent of eggs laid in different broods and different years that give rise to fledged young

Tab. XVIII

Year	1960	1961	1962	1963	1964	1965	Average	Number of eggs laid
Brood *I*	76.5 ±2.8	70.3 ±2.2	74.2 ±1.7	73.1 ±2.0	74.7 ±2.1	55.0 ±3.7	72.2 ±0.9	2343
Brood *II*	59.0 ±3.5	71.5 ±2.0	72.8 ±1.6	75.5 ±2.3	70.6 ±2.3	72.5 ±3.0	71.7 ±0.9	2423
Brood *III*	41.6 ±4.4	63.5 ±2.5	66.9 ±2.1	69.3 ±2.7	45.3 ±3.4	58.5 ±2.9	60.8 ±1.1	1744
Average	62.4 ±2.0	68.9 ±1.3	71.8 ±1.0	72.8 ±1.3	68.1 ±1.4	62.1 ±1.8	68.8 ±0.5	6510
Number of eggs laid	550	1263	1920	1099	1003	675		

The number of fledglings raised from different broods in different years

Tab. XIX

Year	1960	1961	1962	1963	1964	1965	Average	Number of broods
Brood *I*	3.64 ±1.46	3.20 ±2.22	3.26 ±1.72	3.59 ±1.52	4.75 ±1.00	3.55 ±1.93	3.60 ±1.69	514
Brood *II*	3.63 ±2.06	3.62 ±3.01	3.52 ±1.81	2.08 ±2.27	4.52 ±0.76	3.14 ±1.78	3.42 ±1.91	512
Brood *III*	2.00 ±1.78	3.28 ±1.82	2.94 ±1.83	3.31 ±1.43	4.93 ±1.69	1.67 ±1.69	2.55 ±2.00	395
Average	3.22 ±1.88	3.38 ±2.43	3.28 ±1.77	3.04 ±2.00	4.70 ±0.87	2.63 ±1.94	3.24 ±1.92	
Number of broods	116	298	446	225	208	128		1421

The average number of eggs laid and young raised
by a pair of Tree Sparrows each year

Tab. XX

Year	Number of eggs laid	Number of young leaving the nest
1960	12.25	8.59
1961	12.89	8.98
1962	13.73	8.72
1963	13.62	7.85
1964	13.60	12.52
1965	12.63	7.59
Average	13.10	8.70

Since mean clutch-size varies in the Tree Sparrow only very slightly the number of eggs produced by a population depends primarily on the proportion of pairs laying third clutches. For example, in 1962 and 1965 the size of clutches was similar, but in 1962 70% of females took part in third broods against 50% in 1965 consequently the average number of eggs laid per pair was much higher in the 1962 breeding season than in 1965 (Tab. XX).

The number of young raised per pair in a breeding season depends on the number of eggs laid and on the extent of the losses of eggs or nestlings. Since 75% of these total losses occur in the egg stage the average number of young raised per pair depends mainly on factors conditioning egg loss (cf. chapter 6). The highest number of eggs and nestlings were lost from third broods and this lessened the effect of the per cent of pairs taking part in third broods on the mean number of young raised per pair each year.

The percentage occurrence of clutches of different sizes differs considerably from analogous percentage occurrence of different brood-sizes at the time the young leave the nest. Although most of the broods consisted of five fledglings, just like previously with five-egg clutches, then at the same time there increased per cent of broods consisting of 1–4 fledglings, and per cent of such broods but of the largest size decreased (Fig. 12).

The highest annual egg production in the Tree Sparrow was recorded by Bethune in Belgium (1961) where most pairs had three broods and some of them even four. The lowest annual egg production was recorded by Creutz (1949) near Dresden where not all of the pairs had second broods and only a small fraction of them had third broods. Blagosklonov (1950) did not record any third broods near Kamyshyn (USSR) and that is why in spite of a relatively high clutch-size the annual egg production of the Tree Sparrow in this region was low. Eliseeva (1961) stressed that in years when spring came late a very small number of Tree Sparrow pairs had third broods and that this considerably lowered the annual egg production of the population.

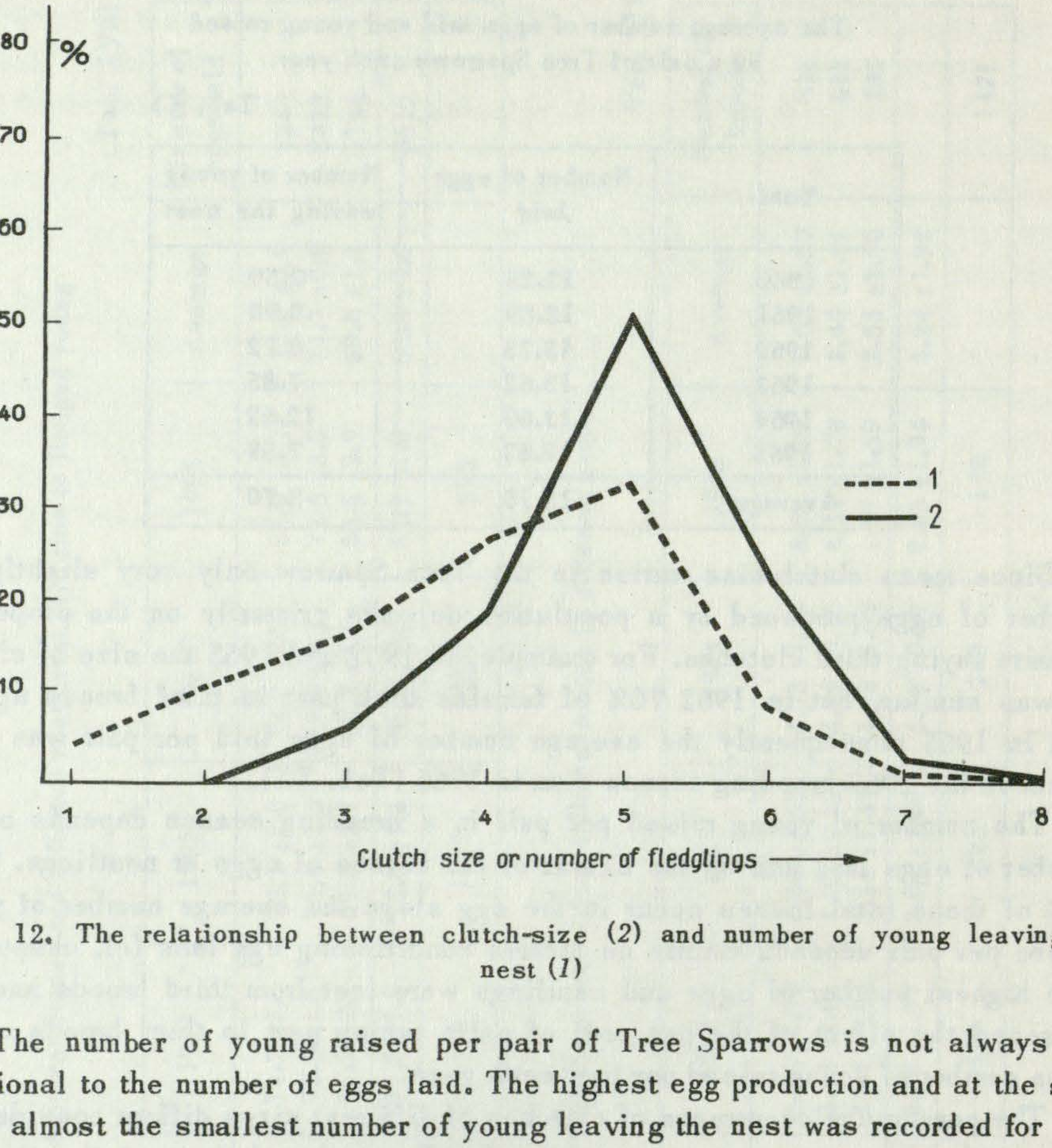

Fig. 12. The relationship between clutch-size (*2*) and number of young leaving the nest (*1*)

The number of young raised per pair of Tree Sparrows is not always proportional to the number of eggs laid. The highest egg production and at the same time almost the smallest number of young leaving the nest was recorded for Tree Sparrow population investigated in Belgium by Bethune (1961). Such a small number of fledglings raised per pair was the result of an enormous number of infertile eggs, particularly in the older birds which also laid most clutches. A considerable number of nests was destroyed by the Dormouse. Near Kamashyn, in spite of low annual egg production each (11.1) pair raised successfully (10.4) young owing to a small number of infertile eggs and small loss of eggs and nestlings (Blagosklonov 1950).

As a rule, House Sparrow has more broods than the Tree Sparrow living in the same area; this although the number of eggs in its clutch is smaller, average annual egg production per pair is usually higher. In the Spanish Sparrow average clutch-size is only slightly larger than in the Tree Sparrow, and annual egg production in a given year mainly depends on the per cent of pairs producing second broods which may vary from 45 to 4%. The number of pairs participating in second broods (similarly as in the case of third broods in the Tree

Sparrow) depends mainly on the date on which first clutches are started (G a v r i l o v 1962). In the African weaverbird, Black-faced Dioch, which like the Spanish Sparrow, nests in enormous colonies, annual egg production is even lower when it broods in nests made in tree branches and it has only one brood per year (M o r e l, B o u r l i è r e 1955, 1956, W a r d 1965).

10. SURVIVAL, AGE-COMPOSITION AND POPULATION DYNAMICS OF THE TREE SPARROW

Data on the survival of Tree Sparrows were obtained by recovering birds which had been ringed as nestlings.

In the forest breeding colony 1–W at Dziekanów Leśny, a very intensive capturing of Tree Sparrows in mist nests was carried out in the breeding seasons of 1961 and 1962. In 1961 only 9.8 ±3.82 were not captured in the first month after leaving the nest but caught in subsequent months, in 1962 6.3 ±2.3%.

In 1961 55.9 ±4.7% of all birds ringed as nestlings were captured at colony 1–W in the first month after they had left the nests, and in 1962 58.2 ±3.5%. The above quoted percentage, together with necessary corrections 9.8% and 6.3%, were accepted as survival indices of young birds in the first month after leaving the nest.

In the second and third months of life young birds gather in large flocks in fields and in spite of intensive netting those young which had been ringed as nestlings made up only a small part of birds captured. As a result it was impossible to take these recaptures as a basis for analysing the degree of survival of young birds. From November however when most birds already occupy nest-boxes and lead a sedentary life (P i n o w s k i 1965a, 1965b), the degree of survival of young Tree Sparrows and the average life expectancy were calculated according to the methods of F a r n e r (1952) and H a l d a n e (1955). Most recent information on the survival of birds ringed as nestlings came from re-captures in mist nets or in nest-boxes they do not give the full life-span of the birds for they went on living after the latest capture. The average expected life for young birds from first, second, third broods, which survived at least until a given month, was calculated and then such number of months was added to the life of each bird which was for the last time captured in a given month. Nothing of course was added to the duration of life of a bird found dead. In this way, a new assessment of the duration of life of young birds from specified broods in a given year was obtained, from the first November to the end of their life. From these data indices of survival were obtained used for calculating changes in the age-structure of the population. Data for 1961 and 1962, starting from 1,000 young birds from first broods and proportional real values of second and third broods from colonies 1–W and 2–W.

Since there was no survival index for the second and third month of life of young birds, when survival is most probably poorer than in later months, these indices were decreased by 10% as compared with the mean index after moult (November). The degree of loss of young Tree Sparrows in the second and third month after leaving the nest obtained in this way coincides with losses, at the same age, of the House Sparrow (Summers-Smith 1963).

On the average one pair of Tree Sparrows raised in the breeding season 8.7 fledglings: (in 1961 – 8.9, while in 1962 – 8.7, Tab. XX). And so in order to maintain a stable population it would be enough if about 20% of young birds survived to the next breeding season.

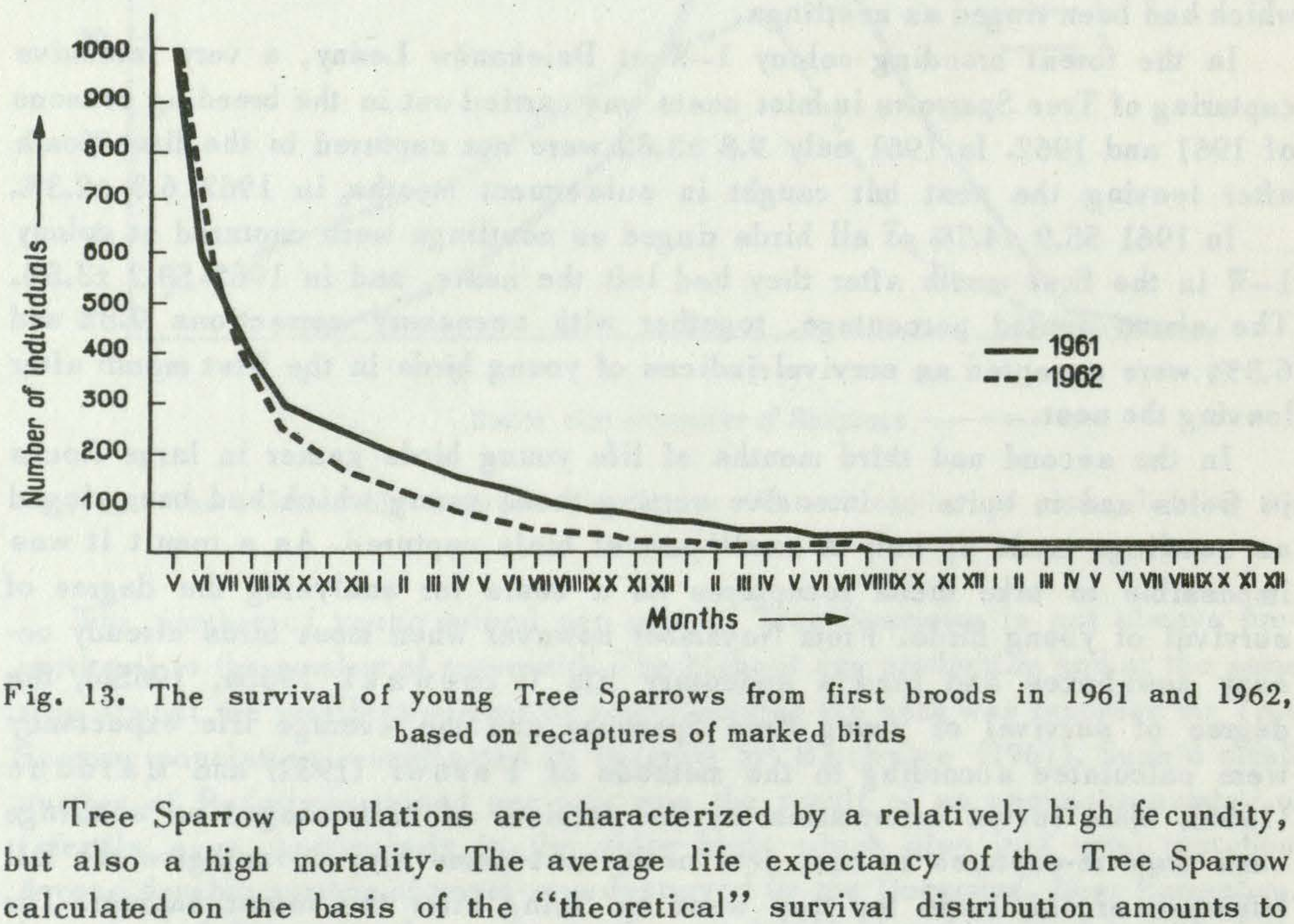

Fig. 13. The survival of young Tree Sparrows from first broods in 1961 and 1962, based on recaptures of marked birds

Tree Sparrow populations are characterized by a relatively high fecundity, but also a high mortality. The average life expectancy of the Tree Sparrow calculated on the basis of the "theoretical" survival distribution amounts to about 6 months. (First brood: 1961 – 5.5, 1962 – 4.0; second brood: 1961 – 6.5, 1962 – 6.4; third brood: 1961 – 6.7, 1962 – 4.6). The average expected duration of life of young birds which just left the nest is probably even shorter than the duration of life of those individuals which survive to the November increases to a year or more and this affects the average expected life of the whole population (Fig. 13, Tab. XXI). According to the "theoretical" distribution about 15–20% of young birds survive to the first breeding season, 3–6% to the second breeding season, 1–2% to the third, and only fractions of per cent to further breeding seasons (Tab. XXII, Fig. 14). These data are in line with data on the age of Tree Sparrows in the study area obtained from recaptures. Out

Average life expectancy (in months) for young birds from their first November

Tab. XXI

Brood		1951	1962
I	m_1	5.6	3.2
	m_2	9.9	6.3
II	m_1	8.0	5.1
	m_2	14.5	11.8
III	m_1	10.0	3.9
	m_2	13.6	7.9

m_1 — average life expectancy for the real distribution,
m_2 — average life expectancy for the theoretical distribution.

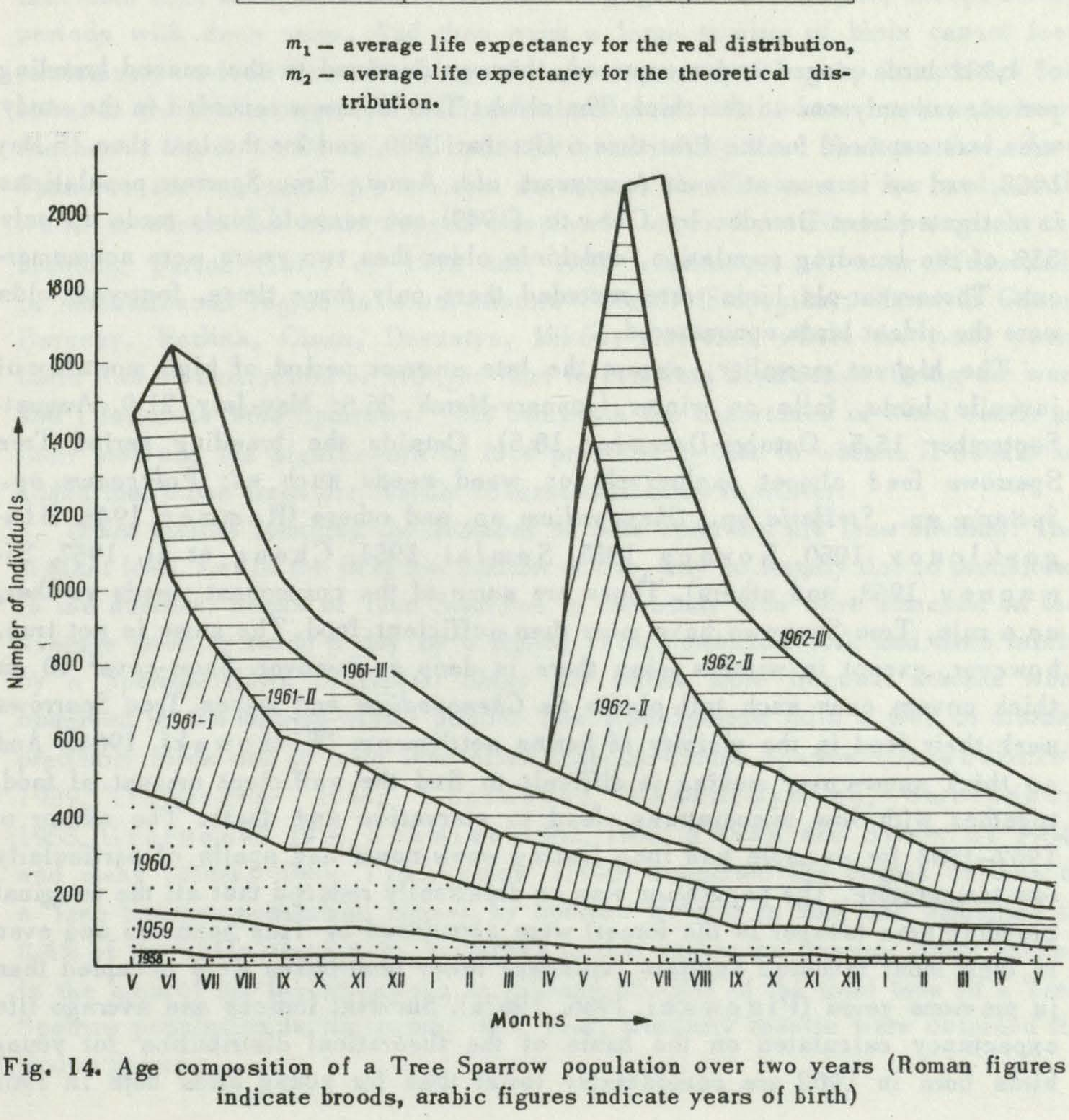

Fig. 14. Age composition of a Tree Sparrow population over two years (Roman figures indicate broods, arabic figures indicate years of birth)

Per cent of young Tree Sparrows surviving to May of the first, second, third, fourth and fifth breeding season of their life according to the "theoretical" distribution (for further details, see text)

Tab. XXII

Year of birth	1961	1962
Breeding season	Per cent	
I	17.9	13.8
II	6.2	3.6
III	2.2	1.2
IV	0.8	0.3
V	0.2	0.1

of 1,382 birds ringed and recaptured, thirteen survived to the second breeding period, and only one to the third. The oldest Tree Sparrow recorded in the study area was captured for the first time 6 October 1960, and for the last time 15 May 1963, and so it was at least four years old. Among Tree Sparrow populations investigated near Dresden by Creutz (1949) one-year-old birds made up only 55% of the breeding population, and birds older than two years were not numerous. Three-year-old birds were recorded there only three times, four-year olds were the oldest birds encountered.

The highest mortality, except the late summer period of high mortality of juvenile birds, falls on winter (January-March 26.6; May-July 21.9, August-September 15.5, October-December 18.5). Outside the breeding period Tree Sparrows feed almost exclusively on weed seeds such as: *Polygonum* sp., *Settaria* sp., *Stellaria* sp., *Chenopodium* sp. and others (Hammer 1948, Blagosklonov 1950, Kovacs 1955, Somfai 1954, Cheng et al. 1957, Simeonov 1963, and others). These are some of the commonest weeds so that, as a rule, Tree Sparrows have more than sufficient food. The same is not true, however, except in winters when there is deep snow-cover. Snow-cover 40 cm thick covers even such tall plants as *Chenopodium* and makes Tree Sparrows seek their food in the vicinity of human settlements (Witkowski 1964). And so thick snow-cover making it difficult to find the sufficient amount of food, together with low temperatures, lead to starvation and death. The winter of 1962–1963 for example had long lasting snow-cover and spells of particularly low temperature. The population was so drastically reduced that all the marginal breeding area (deeper in the forest) were abandoned by Tree Sparrows and even in their most favoured habitats (villages) fewer nest-boxes were occupied than in previous years (Pinowski 1966, 1967a). Survival indices and average life expectancy calculated on the basis of the theoretical distribution for young birds born in 1962 are considerably lower than for young birds born in 1961

(Fig. 13, Tab. XXI). It should be stressed that the way of drawing the theoretical distribution (prolonging the line of life by the duration of average expected life) reduced the loss during winter months. In the next year, 1963/1964, the winter was again relatively severe and as a result the Tree Sparrow population maintained its numbers on a rather low level, and even by 1966 it had not reached the 1962 level (Pinowski 1967a). High numbers of Tree Sparrows in the study area were the result of a large number of suitable nesting places (nest-boxes, holes), and easily accessible food in the form of weed seeds. The study area, in the majority, consists mainly of sandy patches of low agricultural value many weeds covering the fields and gardens. According to our calculations, a moderately weeded field of potatoes yields about 20 g of *Chenopodium album* seeds per m^2; i.e. at least 2,000 kg of such seeds per km^2. There is in fact more than enough food for even such a large number of birds, except during periods with deep snow. And then such a large number of birds cannot feed exclusively on food found in farmyards and a catastrophic drop in numbers follows. In the southern part of Poland (submontane areas) where every year snow reaches a depth of 50 cm and lasts for a very long time (3–4 months), Tree Sparrows are comparatively scarce. In autumn the flocks are few and small, while in winter the birds depend completely on food provided by man. In the breeding period (July) of 1962 and 1963 I searched all over Bieszczady (a mountaineous region in south-eastern Poland) (Stuposiany, Ustrzyki Górne, Berechy, Wetlina, Cisna, Duszatyn, Mików, Smolnik), where for many years there was no cultivation or villages (due to complete destruction during the war) and I found no Tree Sparrows. This indicates the importance of weed seeds as their food and the significance of food provided by man in winter. It should be added that those areas are thickly covered with snow in winter.

Other factors reducing the numbers of Tree Sparrows are less obvious. The highest loss, i.e. in the first few months of life, may be largely due to predators. In the summer, flocks of Tree Sparrows in the study area were attacked on the average once or twice a day by a Hobby (*Falco subbuteo* L.), and more rarely by a Sparrow Hawk (*Accipiter nisus* L.) whose more frequent attacks were observed in the autumn-winter period. The Tree Sparrow falls a prey to diurnal predatory birds and to owls less often than the House Sparrow (Uttendorfer 1939, Tinbergen 1946, Czarnecki, Gruszczyńska, Smoleńska 1955, Czarnecki 1956, Schmidt 1962, 1965, Köves and Schmidt 1964, and many others). Only Tinbergen (1946) estimated the degree of loss of a Tree Sparrow population caused by Sparrow Hawks. In May this amounted to 8.4% of the whole population. According to this author the Sparrow Hawk caused in the area of his investigations in Holland 30–50% of the total loss of a Tree Sparrow population in the course of a year, similarly results were obtained for House Sparrow.

In the study area most of the recoveries of ringed birds, which were found dead, concerned birds killed by cars on the motorway running across the area. I frequently observed cars killing several Tree Sparrows at a time when the flock flew across the road. They were usually young birds.

The degree of survival of young birds after leaving the nest, from month to month, is known for only a small number of species of passerine birds. In the House Sparrow mortality of young birds in their first month after leaving the nest in England is nearly the same as in the Tree Sparrow in our area, i.e. about 40%. Also, as in the Tree Sparrow about 20% of young House Sparrows survive to the first breeding period (Summers-Smith 1963). A similar mortality of young Song Sparrows was given by Johnston (1956). There are many more data on the survival of young passerines from leaving the nest to their first breeding period, and they are similar to ones on the Tree Sparrow and amount to about 20% or less (Kluyver 1933, 1951, Nice 1937, Ruiter 1941, Kendeigh and Baldwin 1937, Haartmann 1951, and others). On the other hand the survival of old birds of other species is generally higher than for the investigated population of Tree Sparrows even when calculated on the basis of "theoretical" distribution, and so probably overestimated, it amounted to 38%. It follows from the data summed up by Lack (1954) that most of young passerine birds have a survival index from August to the next breeding season varying between 40–50%. Only the Robin (*Erithacus rubecula* L.) has such a high degree of mortality like the Tree Sparrow in our study area.

Despite a high annual mortality of both young and old birds, there has been an increase in numbers of Tree Sparrow but this has been much slower after a heavy loss than one might expect from such a high number of young raised per pair each year (cf. Tab. XX). In different conditions when most probably the loss of young is smaller the Tree Sparrow may increase a few times its population size in the course of 3–4 years (Eliseeva 1960).

11. BIOMASS AND ENERGY FLOW THROUGH THE TREE SPARROW POPULATION

Production, i.e. formation of new biomass of Tree Sparrows occurs mainly in the breeding season, that is from the end of April to the middle of August when the analysed species raises 2–3 broods (cf. chapter 5.2). Production of Tree Sparrows in the study area may amount to more than 20 kg per km^2 (about 30,000 Kcal) (Tab. XXIII, Pinowski 1967b).

The rotation of biomass in the course of a year calculated according to the formula production/mean biomass (Petrusewicz 1966, 1967) for the whole population amounted in 1961 to 2.8, and in 1962 to 2.6. The same indices calculated for birds older than 6 months, that is for those which already finished their juvenile period characterized by a high degree of mortality amounted in 1961 to 1.9, and in 1962 to 1.7, while for younger birds respectively 3.3 and 3.4.

The flow of energy through the Tree Sparrow population during a year

Tab. XXIII

Year	Energy intake (consumption) Kcal per km²	Energy assimilated (assimilation) Kcal per km²	Production Kcal per km²
1961/1962	3,099,583	2,534,589	31,657
1962/1963	3,401,193	2,753,222	23,616

The rotation of biomass in the Old Field Mouse (*Peromyscus polionotus* Wagner), calculated by an analogous method, varied in different environments from 2.5 to 4.9 (Odum, Connel, Davenport 1962). The indices of rotation calculated from data quoted by Wiegert and Evans (1967) amount to: Deer Mouse (*Peromyscus* sp.) – 3.3, Ground Squirrel (*Citellus* sp.) – 2.2, Old Field Mouse – 6, large herbivorous mammals – 0.2, elephants – 0.04. The Tree Sparrow has the indices of rotation similar to the indices of small mammals (rodents).

Kale II (1965) calculated for the Long-billed Marsh Wren [*Telmatodytes palustris griseus* (Brewster)] the rotation of biomass during a year by dividing the production of the breeding period alone by the biomass of older birds just before the same breeding period. The rotation of biomass in this species amounted in separate years to 1.8, 1.4, 0.5, 1.0. The rotation of biomass for the Tree Sparrow calculated according to this method was much higher and amounted in 1961 to 5.1, and in 1962 to 6.0. The main reasons for such a small biomass rotation in the American species compared to the Tree Sparrow seem to be that the former raises fewer young.

Relatively high indices of the rotation of biomass in the Tree Sparrow were caused both by high production and mortality. The average period of life for the whole population amounts to about 6 months, and the average duration of biomass calculated according to the formula of Ryszkowski (1967) amounted for 1961 to 5.6 month, and for 1962 to 3.3 months.

The method of calculating the numbers and biomass of Tree Sparrow populations per 1 km². In the previous paper (Pinowski 1967b) the method of calculating the number of young birds leaving their nests in a specified area was given. Having the number of fledglings raised by a pair of old birds (cf. Tab. XX) I could calculate the total number of both old and young birds at the end of the breeding season. I multiplied the result, i.e. the number of both old and young birds, by the mortality indices for each age class and month respectively. In this way I obtained the numbers of birds in each month. Multiplying the number of birds by mean body weight of each Tree Sparrow I arrived at the dynamics of the biomass of the Tree Sparrow population.

When calculating the area with which the analysis of Tree Sparrow numbers was concerned i.e. the area of flock A, I did not take into account those areas which were not visited by Tree Sparrows (those deeper in the forest), but I considered fields, farmland and woodland areas in the vicinity of dwellings fre-

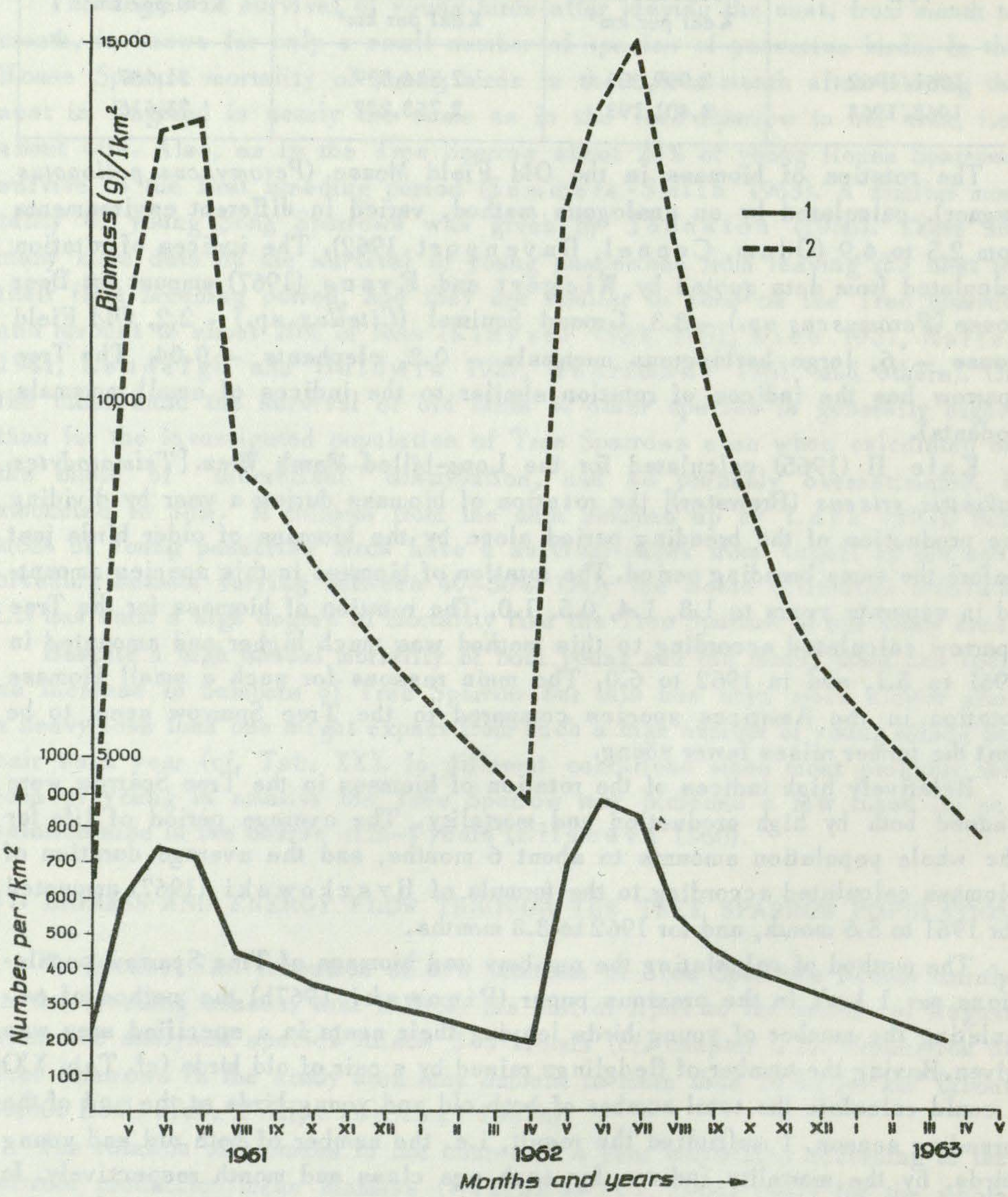

Fig. 15. Changes in numbers (*1*) and biomass (*2*) of a Tree Sparrow population (changes include numbers or biomass both adults, fledglings and nestlings), per 1 km², in the area of flock *A*

quently visited by Tree Sparrows. Numbers and biomass showed a sudden increase in the breeding season and after the leaving of the nest by the last brood an almost equally rapid drop (Fig. 15). It was caused by a high degree of mortality of young birds in the first few months after leaving the nest (cf. Fig. 13).

The flow of energy through a Tree Sparrow population was calculated, in the following way. The energy assimilated by nestlings during their growth was calculated using data from papers by Kendeigh (1939), Dawson and Evans (1957, 1960) on other altricial birds not differing much in size from the Tree Sparrow. Respiration energy, according to these authors, in nestlings from hatching to the fifth day amount to 10–20 cal/g/hour, and after the fifth day from 20 to 40 cal/g/hour. And so I accepted for nestling Tree Sparrows (of 1–5 days old) 15 cal/g/hour, for nestlings 6–10 days old – 30 cal/g/hour, and for nestlings 11–15 days old – 40 cal/g/hour. I multiplied these figures for respiration energy, by the weight of the nestling and the time of its duration ($\bar{B} \times T$) and the result showed that the nestling from hatching to leaving the nest loses in respiration 164.7 Kcal. Multiplying the weight (in grams) in the nestling from hatching to leaving the nest by its caloric value (Pinowski 1967b) and adding the number of calories obtained to the respiration energy, we arrive at the total amount of energy assimilated by a nestling during its development from hatching to leaving the nest. It amounted to 186.7 Kcal.

Throughout the 15-day nestling period, young Tree Sparrows are fed on invertebrates, mainly insects. The digestability of food amounts in birds to about 75% (Kale II 1965). This brings the total energy requirement (energy intake) during the nestling period to about 250 Kcal or about 16.6 Kcal on the average on each day of the nestling period.

I carried out, with W. Tomek, some preliminary investigation on the amount of food required daily by adult Tree Sparrows kept in large cages (105 × 60 × × 52 cm) and at 17°C. The birds were fed on seeds of those weeds which are normally a basic food of Tree Sparrows in nature. The calorific value of seeds of various species of weeds was obtained from Kendeigh and West (1965). Under these conditions Tree Sparrows need 21 Kcal per day or 1.0 Kcal per 1 gram of body-weight. This corresponds exactly to values obtained by Davis Jr. (1955) for the House Sparrow at the same temperature. Because of this the average amount of food taken by the House Sparrow per 1 gram of body-weight/day at various temperatures was considered sufficient to calculate the amount of energy taken by Tree Sparrows at different temperatures during a year. On this basis the flow of energy through a Tree Sparrow population fledglings and old birds was calculated by multiplying the biomass of the Tree Sparrow population by the amount of energy needed according to Davis Jr. (1955) per 1 gram of biomass of the House Sparrow during one month, taking into account the mean temperature of each month. When calculating the energy assimilated by the population the digestive efficiency for the House Sparrow at various temperatures were used (Davis Jr. 1955). In the breeding months, the energy intake by nestlings, was added to energy requirements of old birds and fledglings.

As expected in view of the seasonal changes in numbers and biomass, the energy intake by the Tree Sparrow population increased very rapidly in the breeding season and dropped suddenly just afterwards (Fig. 16). At the beginning of winter (November–December) when numbers of Tree Sparrows are lower there is an increase in the amount of food taken by the population caused by the drop in temperature. However, the increase in the amount of energy assimilated by the population at the same time is proportionatelly much smaller as a result of a drop in the digestability the food. In the following winter months there is a decrease in the energy consumption of the population as a result of a drop in numbers of birds.

With such high numbers of Tree Sparrows in the study area their role in the over all energy-flow through field ecosystems must be quite considerable (Tab. XXIII). Initial investigations carried out by Dr. Z. Wójcik and myself showed that a Tree Sparrow population eats during September and October about 50% of weed seeds from the potato fields under observation which were particularly frequently visited by Tree Sparrows. The problem of the exact role of Tree Sparrows in field ecosystems requires further study.

12. RESULTS AND CONCLUSIONS

1. The date of the onset of first broods and the number of broods started in a given day depends on the mean temperature of the week preceding the laying of the first egg.

2. All Tree Sparrows have two broods in a year and only about 2/3 of pairs have third broods as well. It is those pairs which start their first broods relatively early in the season that raise third broods.

3. The end of the breeding season of the Tree Sparrow is conditioned not by climatic factors or lack of food in the period of incubation and parental care. These affect the period of moult of young birds from late broods and their participation in autumn sexual display. Young birds leaving the nests latest do not finish moult before autumn cold spells and do not take part in autumn sexual display; also they survive less well to the next breeding period than early hatched young. In this way, natural selection would favour the termination of the breeding season before food or climate become unfavourable.

4. Second clutches are the largest in the Tree Sparrow, and third clutches are the smallest. In years with low Tree Sparrow populations the average

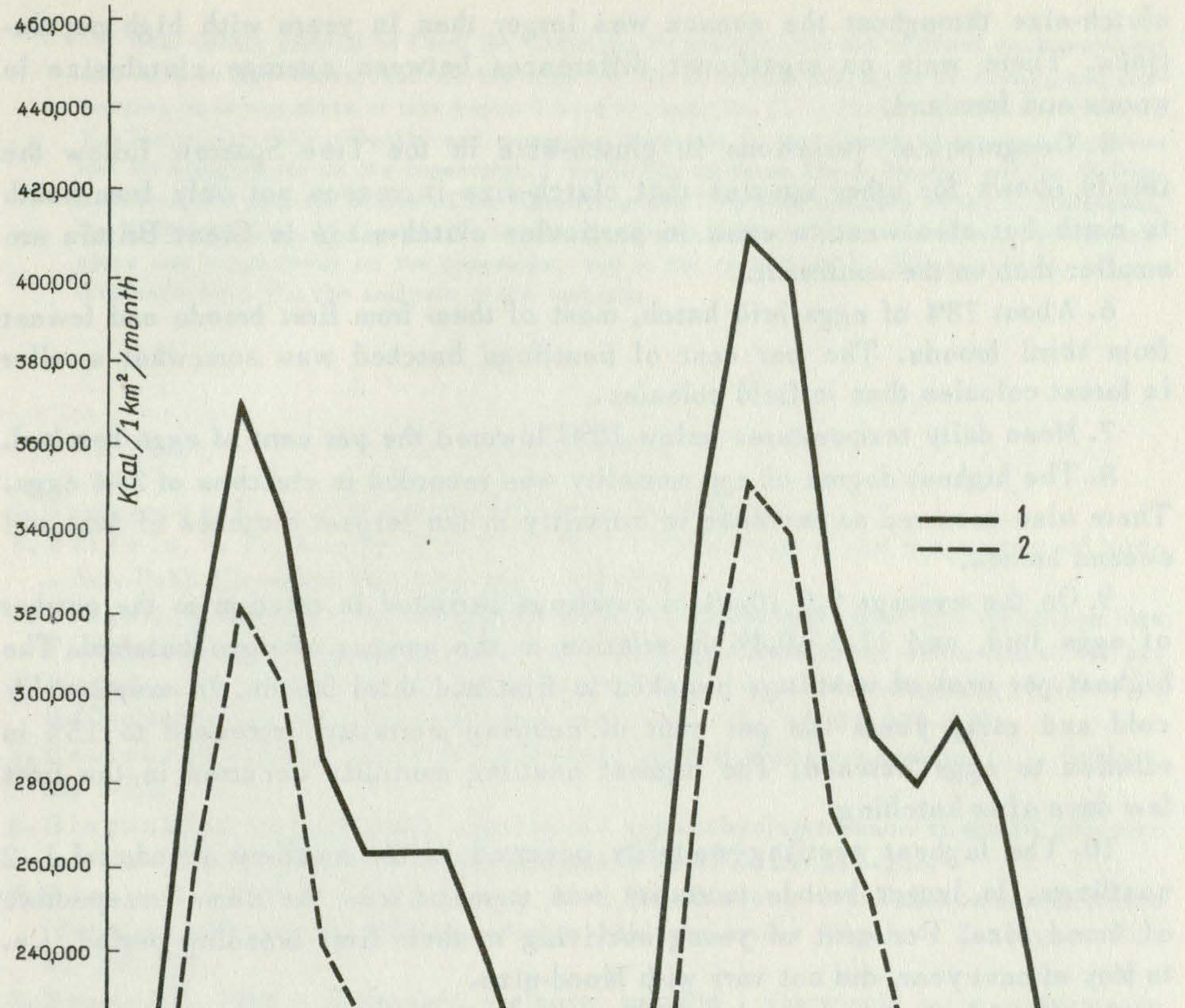

Fig. 16. Energy flow through a Tree Sparrow population per 1 km², in the area of flock *A*

1 – energy intake (food), *2* – energy assimilated clutch-size throughout the season was larger than in years with high populations. There were no significant differences between average clutch-size in woods and farmland.

5. Geographical variations in clutch-size in the Tree Sparrow follow the trends shown for other species that clutch-size increases not only from south to north but also west to east; in particular clutch-sizes in Great Britain are smaller than on the continent.

6. About 78% of eggs laid hatch, most of them from first broods and fewest from third broods. The per cent of nestlings hatched was somewhat smaller in forest colonies than in field colonies.

7. Mean daily temperatures below 12°C lowered the per cent of eggs hatched.

8. The highest degree of egg mortality was recorded in clutches of 3–4 eggs. There also occurred an increase in mortality in the largest clutches of first and second broods.

9. On the average 9.5 ±0.4% of nestlings perished in relation to the number of eggs laid, and 11.2 ±0.4% in relation to the number of eggs hatched. The highest per cent of nestlings perished in first and third broods. In exeptionally cold and rainy years the per cent of nestling mortality increased to 15% in relation to eggs hatched. The highest nestling mortality occurred in the first few days after hatching.

10. The highest nestling mortality occurred in the smallest broods of 1–2 nestlings. In larger broods mortality was more or less the same irrespective of brood size. Per cent of young surviving to their first breeding period, i.e. to May of next year, did not vary with brood-size.

11. On the average one pair of Tree Sparrows laid 13.1 eggs season. This amount depended not only on clutch-size but also to a large extent on the per cent of pairs having third broods.

12. On the average one pair raised 8.7 young able to leave the nest. The number of young raised by one pair depended mainly on egg loss and whether they had a third brood.

13. The highest degree of fledgling mortality occurred in the first month after leaving the nest. About 15–20% of young survive to the first breeding season, while only 3–6% to their second period, and 1–2% to the third.

14. The highest Tree Sparrows mortality outside the juvenile period occurs in the winter months (January–March) with thick snow-cover which makes it difficult for the bird to find food.

15. Population density of Tree Sparrows in the farmland area investigated exceeds 500 birds per 1 km² in the post-breeding period. In view of large annual production of biomass and its considerable rate of turnover (3–5) this species must play a considerable role in the energy flow through field ecosystems from which it mainly draws food in the form of weed seeds.

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PŁODNOŚĆ, ŚMIERTELNOŚĆ, DYNAMIKA LICZEBNOŚCI I BIOMASY POPULACJI MAZURKÓW (*PASSER M. MONTANUS* L.)

Streszczenie

Badania prowadzono na obszarze położonym między korytem Wisły a Puszczą Kampinoską około 15 km na NW od Warszawy (52°20'N, 20°50'E). Na badanym obszarze powieszono w latach 1960–1963 ogółem 616 skrzynek lęgowych Sokołowskiego typu *A*, tworząc 6 kolonii leśnych i 4 kolonie wiejskie. Kolonie 1–*W* i 2–*W* były położone w lesie, ale w sąsiedztwie budynków odpowiednio 800 i 400–800 m od brzegu lasu. Kolonia 4–*W* znajdowała się 100–400 m od brzegu lasu, a kolonia 3–*W* położona była aż 1000 m od brzegu lasu. Kolonia 6–*W* mieściła się w lesie łęgowym między wałami przeciwpowodziowymi Wisły. Tereny między wsiami zajęte były przez pola, na których uprawiano – żyto, pszenicę, owies, ziemniaki, buraki. Kultura rolna, zwłaszcza na uboższych, piaszczystych glebach była bardzo niska i pola były z reguły bardzo zachwaszczone.

W latach 1960–1965 przeglądano w okresie lęgowym co najmniej raz na tydzień wszystkie skrzynki lęgowe. Określano, w których skrzynkach gnieżdżą się mazurki, ile w gnieździe znajduje się jaj, czy jaja są ciepłe i nie nadbite. Jaja, z których pisklęta nie wykluły się, rozbijano, by stwierdzić, czy jest zarodek. Jeżeli w gnieździe były pisklęta, zapisywano ich ilość i wiek. Ogółem skontrolowano skrzynki lęgowe 31 140 razy. Zaobrączkowano w gniazdach 4881 piskląt mazurków. W ciągu całego roku odławiano mazurki w siatki japońskie, a w ciągu zimy raz na miesiąc przeprowadzano nocną kontrolę skrzynek, w czasie której łowiono nocujące tam mazurki.

Zaobrączkowano 8461 mazurków, z tego złowiono powtórnie 1382, przy czym niektóre osobniki łowiono wielokrotnie, tak że ogólna ilość złowień powtórnych wyniosła 3783.

Początek okresu lęgowego u mazurków, to znaczy składanie jaj, zależy w pierwszym rzędzie od temperatury powietrza (fig. 1, 2). Najniższa średnia temperatura tygodnia poprzedzającego zniesienie pierwszego jaja wynosiła 3,3°C. Mazurki mają trzy dobrze wyróżnione lęgi w roku. Lęgi *I* i *II* są najczęściej jednakowo liczne, a lęgów *III* jest

około o 1/3 mniej (tab. I). W lęgach *III* uczestniczą te pary, które najwcześniej zaczęły lęgi *I*. Są to prawdopodobnie ptaki co najmniej dwuletnie. Okres między złożeniem pierwszego jaja lęgu *I*, a złożeniem pierwszego jaja lęgu *II*, wynosił 36,4 ±5,1 dni, a między lęgiem *II* a *III* 38,0 ±5,1 dni. Maksymalna długość okresu lęgowego wynosiła 136 dni, a minimalna 117 dni. Czym później zaczynały się lęgi, tym okres lęgowy był krótszy (tab. III). Termin zakończenia okresu lęgowego uzależniony jest od konieczności wypierzenia się młodych możliwie wcześnie w jesieni. Ptaki młode, późno pierzące się, a tym samym prawie nie biorące udziału w zalotach jesiennych, mają mniejszą szansę dożycia do następnego okresu lęgowego.

Wielkość zniesień waha się u mazurków od 3 do 8 jaj, średnia wielkość zniesienia z 1417 gniazd wynosi 4,97 ±1,0. Największe są zniesienia lęgów *II*, a najmniejsze – ostatnie, to jest *III* (fig. 7, tab. IV, V). W koloniach leśnych zniesienia były nieco większe niż w koloniach wiejskich (fig. 6, 9). W latach o wysokiej liczebności populacji mazurków (1960–1962) zniesienia były mniejsze niż w latach o niskiej liczebności populacji (1963–1965) (fig. 8). Zmienność geograficzna wielkości zniesień u mazurka przedstawia się podobnie jak u innych gatunków ptaków – czym dalej na połnoc i wschód tym lęgi są większe. W Wielkiej Brytanii lęgi są mniejsze niż na kontynencie, a najmniejsze są w tropikach (Singapur) (fig. 10).

Procent jaj, z których wykluwały się pisklęta, wynosił 78,7 ±0,5% w stosunku do ilości zniesionych jaj. Zwykle najwięcej piskląt wykluwało się z jaj lęgów *I*, a najmniej z lęgów *III* (tab. VII). Procent jaj, z których wykluwały się pisklęta, był o 4,5% mniejszy w koloniach leśnych niż polnych. Większość jaj, z których nie wykluły się pisklęta, pochodziła z gniazd, w których wykluło się co najmniej jedno pisklę (tab. VIII, IX). Najwięcej jaj z takich gniazd po prostu znikało (prawdopodobnie wyrzucone przez rodziców), również dużo było jaj niezapłodnionych, zwłaszcza w ostatnich lęgach (tab. IV, IX, X). Z czynników klimatycznych na procent wykluwających się piskląt może mieć istotny wpływ temperatura powietrza wtedy, gdy średnia dzienna temperatura jest niższa niż 12°C (fig. 11). We wszystkich trzech lęgach najwięcej jaj ulegało redukcji w zniesieniach małych, złożonych z 3 lub 4 jaj, w lęgach *I* i *III* zaznaczał się też wzrost redukcji jaj w zniesieniach największych, liczących 7 i 8 jaj. Zniesienia złożone z 5 jaj, spotykane najczęściej we wszystkich lęgach, ulegały najmniejszej redukcji (tab. XI, XII).

W stosunku do ilości złożonych jaj ginęło średnio 8,9 ±0,3 piskląt, a w stosunku do ilości wyklutych 10,5 ±0,4 (tab. XIII). Stopień redukcji piskląt, gdy lato było wyjątkowo chłodne i dżdżyste (1962, 1965), był wyższy i wynosił 15% (tab. XIV). Tak w koloniach leśnych jak i polnych, stopień śmiertelności piskląt był jednakowy. Najwięcej piskląt ginęło w pierwszych 5 dniach życia (63,7 ±2,9), między 6–10 dniem życia 23,9 ±2,7%, a w ostatnich 5 dniach przed wyleceniem 12,4 ±1,8%. Największa redukcja piskląt występowała w małych lęgach złożonych z 1–2 piskląt (tab. XIII, XV, XVI). Wiele lęgów ginęło w całości z powodu zimna i głodu w czasie dni chłodnych i dżdżystych. Stosunkowo niewiele gniazd było zniszczonych przez drapieżców. Wiele piskląt znikało z gniazd, z których szczęśliwie wyleciała reszta piskląt. Były to często pisklęta najmniejsze, a więc najmłodsze lub chore, które były prawdopodobnie wyrzucone przez rodziców z gniazd.

Nie stwierdzono zależności między wielkością lęgu a stopniem przeżycia młodych po wyleceniu z gniazda i to zarówno do wieku 4 miesięcy, jak i do następnego okresu lęgowego (tab. XVII). Dane te są sprzeczne z tezą L a c k a (1954, 1966) o wpływie doboru naturalnego na wielkość lęgów u ptaków.

Z jednego gniazda wylatywały średnio 3,24 młode (tab. XIX). Jedna para mazurków w okresie lęgów znosiła średnio 13,1 jaj i wychowywała szczęśliwie 8,7 młodych (tab. XX). Srednia wielkość zniesień wahała się stosunkowo niewiele, dlatego płodność w danym roku zależy w dużym stopniu od tego, jaki procent par bierze udział w *III* lęgach.

Średnia długość życia mazurka wynosiła około 6 miesięcy, a długość życia osobników młodych, które dożyły do listopada, wzrastała do roku i dłużej (fig. 13, tab. XXI). W pierwszym miesiącu po wyleceniu z gniazd, ponad 40% młodych ginie, a do następnego okresu lęgowego dożywa 15–20% (fig. 13, 14, tab. XXII). Największa śmiertelność, poza okresem wieku młodocianego, występuje w zimie. Mazurki poza okresem lęgowym odżywiają się prawie wyłącznie nasionami kilku gatunków chwastów, tak że pokarm z reguły mają w nadmiarze, z wyjątkiem zimy, gdy pokrywa śnieżna jest gruba. Taka była zima w 1962/1963 r. Śmiertelność mazurków była wtedy o wiele większa niż w innych latach (fig. 13). Z powodu dużej śmiertelności młodych i starych ptaków, wzrost populacji następuje wolniej, niż by to wynikało z tak dużej ilości młodych, produkowanych przez jedną parę w ciągu roku. Również z powodu dużej śmiertelności młodych, tylko w bardzo sprzyjających latach może istnieć związek między ilością młodych, wychowanych przez jedną parę, a poziomem liczebności populacji w następnym okresie lęgowym.

Gwałtowny wzrost liczebności i biomasy populacji mazurków następuje w okresie lęgowym, a po jego zakończeniu, zaraz w następnych tygodniach, gwałtowny spadek (fig. 15). Rotacja biomasy w ciągu roku wynosi 3–5, gęstość populacji mazurków pod koniec okresu lęgowego, tj. w sierpniu, może przekroczyć 500 ptaków na 1 km^2. Z powodu dużej produkcji biomasy na jednostkę powierzchni populacja mazurków odgrywa prawdopodobnie ważną rolę w przepływie energii przez ekosystemy pól. Poznanie tej roli jest celem dalszych badań.

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