

Barbara PINOWSKA

Department of Population, Institute of Ecology, Polish Academy of Sciences,
Dziedkanów Leśny (near Warsaw), 05-150 Łomiński, Poland

THE EFFECT OF ENERGY AND BUILDING RESOURCES
OF FEMALES ON THE PRODUCTION OF HOUSE
SPARROW (*PASSER DOMESTICUS* (L.)) POPULATIONS*

ABSTRACT: The changes of the basic components of the body of females: water, fat, and lean dry weight during the breeding cycle are analysed. On the day of ovulation of the first egg the amounts of these components were greatest. The fat content in the body of female on the day of ovulation of the first egg was proportional to its clutch-size. During incubation period the females restored fat used during laying eggs. The amount of the lean dry weight of female body decreased during successive broods. The amounts of the above components of the body of females exert an influence on number of breeding females, clutch-size and number of broods per female during breeding season.

KEY WORDS: Rural areas, *Passer domesticus* females, body composition, clutch-size, number of broods.

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1. INTRODUCTION

The house sparrow, *Passer domesticus* (L.), is an extremely common species living in or around human settlements throughout Poland. Mixed farms provide particularly favourable conditions for sparrows (Novotný 1970, Pinowska 1975, Pinowska, Chyliński and Gondek 1976, and others). Sparrows readily utilize artificial nest-boxes and if the conditions are suitable they establish breeding colonies. Foraging and nesting sites are often located inside farm buildings. In Poland the house sparrow is not specifically protected.

The "Working Group on Granivorous Birds", which has concentrated its studies on the house sparrow, was initially established under the auspices of the International Biological Programme, but now it has been included in the International Association for Ecology. The basic aim of the studies conducted within the framework of this Group has been to determine the role of sparrows in various habitats. To achieve this it has been necessary to obtain information about factors affecting population numbers, breeding and mortality of sparrows in particular habitats. Although numerous studies on the breeding activities of sparrows have been conducted (Seel 1968a, 1968b, 1969, 1970, Mackowicz, Pinowski and Wieloch 1970, Novotný 1970, Dawson 1972, Mirza 1973, Naik and Mistry 1973, North 1973a, 1973b, Pinowski and Wieloch 1973, Will 1973, Wieloch and Fryska 1975, Wieloch and Strawiński 1976, and many others) the factors determining basic fecundity parameters, such as clutch-size, number of broods per female in a breeding season, number of breeding females (cf. Dyer, Pinowski and Pinowska 1977) have not yet been properly elucidated.

In previous studies of other free-living species of birds, to date only the relationship between body composition of the female and clutch-size has been examined (Payne 1969, Jones and Ward 1976), while no work has yet been published on the relationship between the body composition of the female and the number of clutches she lays and the total number of eggs laid in one breeding season.

The growth and development of the ovaries and oviducts in females makes greater energy demands on the bird than does testicular growth and development in the male. The initial period of development of ovaries, which ends four weeks before the first ovulation, makes relatively small energy demands. Intensive growth of oviducts and yolky follicles takes place only in the last few days preceding the laying of the egg.

The greatest energy requirements in the female take place at the time of egg-laying, and in passerine species amount, on average, to 45% of basal metabolism (King 1973, Ricklefs 1974, Kendeigh, Dolnik and Gavrilov 1977). Therefore, considerable energy demands are associated with the production of eggs. Egg-laying females consume more insects than females which do not participate in breeding activities (Pinowska 1975) which clearly indicates an increase in the demand for protein. These increased energy requirements are covered at least partially by hyperphagia, which can be observed only during this period (El-Wailly 1966).

Clutch-size of sparrows shows variations, not only for separate climatic zones (Dyer, Pinowski and Pinowska 1977), but also within one breeding colony in different years (Mackowicz, Pinowski and Wieloch 1970, Pinowski and Wieloch 1973). The number of clutches that a female lays during a breeding season is also variable (Dyer, Pinowski and Pinowska 1977).

The observations of a rapid replacement of the fat lost during migration (Dolnik 1968, 1975, Kendeigh, Dolnik and Gavrilov 1977) and the replenishment within a few

hours of the fat lost during several hours of fasting at temperatures below 0°C (King 1963, Evans 1969a, 1969b, Pinowski and Myrcha 1970, Dolnik 1973, 1975, Kendeigh, Dolnik and Gavrilov 1977, and others) indicate that changes in fat reserves can occur quite rapidly in birds. Birds also show an increase in their fat reserves and in components for making feathers before the onset of moult (Newton 1968, Myrcha and Pinowski 1970). Migration and moult are two processes which require large energy reserves. Thus it is reasonable to suppose that sufficient levels of energy and building materials are the factors determining the onset of breeding.

However, the reserves of building materials, such as sulphur, have to be gathered over a long period of time to be sufficient to meet daily requirements during moult (Newton 1968). Consequently, doubts arise as to whether hyperphagia during egg-laying is able to entirely satisfy the demand for all the building materials required by the female.

The problem of what factors determine clutch-size in birds has been studied by a large number of workers. General discussions of the problem can be found in Ricklefs (1965, 1970), Cody (1966), Royama (1966), Lack (1968) and Klomp (1970). However, only a few papers have attempted to analyse the relationship between clutch-size and the energy and building material reserves of the female (Payne 1969, Jones and Ward 1976). In the house sparrow the first and second clutches are more numerous than third and fourth clutches (Mackowicz, Pinowski and Wieloch 1970, Pinowski and Wieloch 1973, and others). The number of broods in a breeding season may also be determined by the availability of energy resources and building materials. If these resources can modify the clutch-size and the number of clutches a female lays, as well as the number of breeding females, they would also affect the total production of sparrow populations.

The purposes of the paper are to analyse the following questions:

1. Do breeding and non-breeding females show any differences in basic body components – water, fat and lean dry weight?
2. Is there a relationship between the body composition of females and the number of eggs laid?
3. Are there any variations in body components during the breeding cycle?
4. Does body composition vary between successive broods?
5. Does body composition determine whether the female is going to engage in breeding activities?

2. STUDY AREA

The birds were captured inside 86 large farm buildings and in their vicinity. The study was conducted in the north of Poland in the provinces of Gdańsk and Elbląg. The study areas were located in the delta at the mouth of the Vistula River (25% of the area of the valley is a depression). The soils of the delta belong to the wheat and beetroot complex, and are mostly made up of alluvial soils and peat (Borowik 1964, Laskowski 1969). About half of the area under crop in the delta is in grains, of which wheat constitutes 26%, barley about 5%, oats 6%, and rye 10%. Meadows and pastures account for 25%, and the rest is in root crops, i.e., potatoes and beetroots.

Large-scale agriculture with advanced cattle-breeding predominates in the whole region. Large farm buildings enable sparrows to find good feeding conditions inside the buildings in winter, which is of particular importance during periods of frosty weather (Pinowska,

Chyliński and Gondek 1976). The structure of the buildings provides numerous suitable nest-sites.

The three breeding colonies studied were located on Sobieszewska Island near Gdańsk. The breeding colony located at the Wieniec farm consisted of 93 nest-boxes of which 46 were hung where nests had been placed in holes in the cow-shed walls. The remaining nest-boxes were put up in surrounding trees and on buildings around the farmyard. The breeding colony at Pastwa consisted of 44 nest-boxes distributed similarly as in the colony at Wieniec. At Górkę Wschodnie 25 nest-boxes were placed in the village on buildings and trees. The sparrows had easy access to water both inside the farm buildings (through with water for farm animals) and outside. The birds used for the analyses were captured inside 86 large farm buildings and in their vicinity.

3. MATERIAL AND METHODS

The sparrows were captured in Japanese nets while in flight inside farm building or outside near their feeding sites (Pinowska 1975). Between February 4 and August 20, 1971, 326 female sparrows were captured in nets, while 1179 females were caught between April 8 and September 7, 1972. Females were also captured on their nests at Pastwa in 1972. All females captured were analysed. After capture the birds were killed with ether. No later than five hours after killing the bird's exterior and its brood-patch were examined, and the ovary was removed and weighed to the nearest 2 mg. The crop and stomach contents were also removed. The ovaries were first stored in Bouin's fluid and then dipped several times in 70% alcohol. Next the diameters of yolky follicles were measured and the six largest ones were recorded. The number of follicles equal in diameter to the sixth follicle was recorded which indicated all clutches of more than six eggs. The sizes of post-ovulatory follicles were measured under a stereoscopic microscope.

As a rule house sparrows lay eggs daily until completion of the clutch. A comparison of the sizes of yolky follicles enabled me to determine the day of ovulation and the number of eggs to be laid. The number of post-ovulatory follicles indicated the number of eggs laid, while the size of the post-ovulatory follicle revealed the number of days which had elapsed since the egg was laid. The rate of resorption of the first post-ovulatory follicle is the same as for all subsequent ones (Payne 1966). The size differences of yolky follicles and the changes they undergo on successive days preceding ovulation enabled me to determine clutch-size exactly. To illustrate the method the situation arising in the case of six-egg clutches has been described in detail (Table I). In smaller clutches yolky follicles which are transformed into eggs undergo similar changes. Yolky follicles which later suffer resorption are distinctly smaller.

Analysis of the body composition of the birds was carried out after the ovary and any eggs in the oviduct had been removed, and after the contents of the crop and stomach had been removed to single out changes in the body gross chemical composition as compared with eggs. The bodies were dried to constant weight. A one-gramme representative sample of the ground body was extracted with ether-alcohol to obtain the fat fraction. The method used was after Puzanov which is called the Hannon and Badun's method (Krauze, Bożyk and Piekarski 1966). The water content was arrived at when considering the difference between the weight of fresh birds (after removal of the contents of the crop and stomach) and the dry weight. The lean dry weight was obtained by calculating the difference in weight between the dry mass of the bird and the fat content, which in turn was calculated on the basis

Table I. Differences in the size of yolky follicles (in mm) on the six successive days preceding ovulation (materials presented here refer to six-egg clutches) and differences of post-ovulatory follicles (in mm) on the six successive days after ovulation

Below the line are border values of the diameter of the largest remaining yolky follicle which is to be resorbed

Number of females	Yolky follicles							Post-ovulatory follicles					
	number of days before ovulation							number of days after ovulation					
	6	5	4	3	2	1	0	1	2	3	4	5	6
6	2.0-2.5	2.6-2.9	2.6-3.0	2.8-3.5	5.0-5.8	7.7-8.0	9.0- 9.5						
9		2.0-2.2	2.6-2.8	2.6-3.0	4.8-5.8	6.5-7.7	9.2-10.0	5.0-4.1					
6			2.4-2.8	3.0-3.6	5.0-6.2	6.2-8.3	9.3-10.0	5.0-4.1	4.0-3.1				
12				2.2-2.6	4.3-6.2	6.0-8.4	8.2- 9.5	5.0-4.1	4.0-3.1	3.0-2.6			
4					2.2-2.6	6.0-8.1	8.4- 9.5	5.0-4.1	4.0-3.1	3.0-2.6	2.5-2.1		
5						1.6-2.2	8.0-10.0	5.0-4.1	4.0-3.1	3.0-2.6	2.5-2.1	2.0-1.6	
1							2.0	5.0	4.0	3.0	2.5	2.0	1.5

of the percentage of fat in the sample. The ovary was not included in the components of the body.

In 1971, nests were checked simultaneously in three nesting colonies (Wieniec, Pastwa and Górki Wschodnie), and in 1972 in two colonies (Wieniec and Górki Wschodnie). The progress of breeding in the nesting colonies was followed by checking the nests every four days recording the number of eggs laid and the number of nestlings found in the nest. These data enabled me to determine the day when the broods commenced, the number of eggs laid, the number of eggs lost during incubation, the number of eggs hatched and the nestlings which died in the nest, as well as fledging success.

The average daily temperatures for 1971 and 1972 were obtained from the meteorological station at Górki Wschodnie (near Gdańsk) which was located near the breeding colonies.

4. RESULTS

4.1. STAGES OF THE BREEDING CYCLE

Five days before ovulation commences there is no sign of the brood-patch and consequently the state of preparation of the female for breeding can only be determined on the basis of the weight of the ovaries and the size of yolky follicles. If the ovary is heavier than 100 mg and if the diameter of the largest follicle exceeds 3 mm, our studies indicate that ovulation takes place in four or five days. Two or three days before the onset of egg-laying the brood-patch can be distinguished (S e l a n d e r and Y a n g 1966). Analysis of changes in the size of yolky and post-ovulatory follicles enables one to determine to one day the stage of the breeding cycle (P a y n e 1966). The brood-patch starts disappearing when the eggs hatch. The skin on the abdomen of the female has a characteristic look in the period when nestlings are fed. The softness of the skin, characteristic of the period of a developed brood-patch, is replaced by intensive flaking off of the epidermis. In the final stage of nestling feeding after this flaking off, the epidermis is smooth and may seem somewhat loose. The combined analysis of the development of the brood-patch, morphological changes in the ovary and variations in the weight of the ovary provide a basis for dividing the breeding cycle of the female into six stages:

1. Pre-breeding females – the ovary heavier than 100 mg. This period lasts for five days.
2. Laying females – an egg in the oviduct, or the post-ovulatory follicle not smaller than 4.1 mm. Such females had their cloaca expanded and abdomen swollen. The duration of this stage depends on the number of eggs laid.
3. Females incubating for not longer than five days – at least one stigma on the ovary, the brood-patch either fully or partially developed.
4. Females incubating eggs between six and twelve days – no traces of stigmas, the brood-patch fully developed, the cloaca dry and contracted, the weight of the ovary not exceeding 100 mg.
5. Females feeding young – the brood-patch disappearing, the skin of the abdomen flaking off, the ovary not exceeding 100 mg (however, it can be heavier when the female is preparing for the next brood). This stage lasts for about 14 days.
6. Non-breeding females – the abdomen covered with feathers or undergoing moult, the cloaca contracted, the ovary not exceeding 100 mg in weight. Females with no brood-patch (the abdomen not covered with feathers, the skin flaked off and smooth) but with the ovary

lighter than 30 mg were included in this group. This, however, excluded females in the final stage of feeding young whose ovaries exceeded 30 mg in weight.

4.2. THE PROGRESS OF BREEDING

An increase in the weight of the ovaries was recorded in females captured in February 1971. The period of the growth of the ovaries was taken to be between the day when the weight of the ovary exceeded 30 mg for the first time and the day of laying of the first egg. In 1971 this period was 60 days, and the same duration was obtained in 1972. In 1972 the average temperature of the 60 days preceding the laying of the first egg (4.2°C) was 1.79°C higher ($p < 0.001$) than in 1971 (2.42°C).

In the warmer year (1972) the broods commenced nine days earlier. The average temperature of the week preceding the onset of breeding was 7°C in 1971 and 8.5°C in 1972 which conforms with data obtained by Pinowski (1968), Will (1969) and Mackowicz, Pinowski and Wieloch (1970).

The first clutch in the study area was initiated on April 9 in 1971, and on April 1 in 1972. As the average clutch-size was between four and five eggs, the period of egg-laying was taken to be five days. Incubation lasted twelve days, and the nestlings were fed for fourteen days.

This provided a basis for the assumption that the minimum theoretical period between successive broods would be 31 days and any drop in the number of broods over a period shorter than 31 days was treated as an irregularity in the intensity of egg-laying within one breeding season. The application of the above-outlined analysis led me to conclude that in 1972 there were three broods each of which was divided into two parts (Fig. 1).

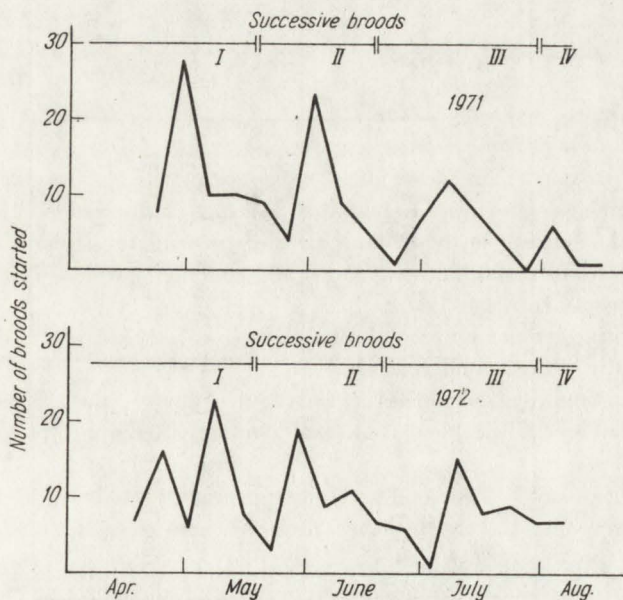


Fig. 1. Number of broods started in successive weeks of the breeding season in the breeding colonies studied

Table II. Duration of the stages of the breeding cycle of successive broods in 1971

Brood	Stages of the breeding cycle					
	preparation for the onset of breeding	egg-laying	first five days of incubation	remaining days of incubation	feeding of nestlings	duration of the period when non-breeding females were captured
	1	2	3	4	5	6
I	by May 14	by May 19	by May 24	by May 31	by June 14	by June 9
II	May 15 – June 13	May 20 – June 18	May 25 – June 23	June 1 – June 30	May 15 – July 14	June 10 – July 9
III	June 14 – July 26	June 19 – July 31	June 24 – Aug. 5	July 1 – Aug. 12	July 15 – Aug. 26	June 10 – Aug. 21
IV	July 27	Aug. 1	Aug. 6	Aug. 13	Aug. 27	

Table III. Duration of the stages of the breeding cycle in successive broods in 1972

Brood	Stages of the breeding cycle					
	preparation for the onset of breeding	egg-laying	first five days of incubation	remaining days of incubation	feeding of nestlings	duration of the period when non-breeding females were captured
	1	2	3	4	5	6
I	by May 14	by May 19	by May 24	by June 1	by June 15	by June 10
II	May 15 – June 15	May 20 – June 20	May 25 – June 25	June 2 – July 2	June 16 – July 16	June 11 – July 11
III	June 16 – July 26	June 21 – July 31	June 26 – Aug. 5	July 3 – Aug. 12	July 17 – Aug. 26	July 12 – Aug. 21
IV	July 27 – Aug. 17	Aug. 1 – Aug. 17	Aug. 6 – Aug. 22	Aug. 13 – Sept. 29	Aug. 27 – Sept. 12	Aug. 22 – Sept. 12

The division of successive broods into two subperiods recorded in 1972 may have been the result of the fact that older females usually commence egg-laying earlier than younger ones (Summers-Smith 1963, Seel 1968a). However, difficulties in aging the females in this study make it impossible to verify this observation with the study material. Young females (i.e., born in the previous year) only participate in egg-laying in the second brood (Summers-Smith 1963, Seel 1968a, Dawson 1972).

Thus, it was concluded that the sparrow population studied had four broods in one breeding season. There is, however, no certainty, in view of the fact that the females were not individually marked, that all the last broods were really the fourth ones for that female. It is possible that they were broods of females which, for unknown reasons, could not have their broods earlier. However, the increase in the number of broods which occurred regularly every 5–6 weeks, indicated some synchrony of breeding. If in the later breeding periods eggs were laid by females breeding for the first time, it would be difficult to distinguish clearly each successive brood.

Consequently, it can be accepted that the successive breeding periods distinguished indicate the number of successive broods which one female has. This is also supported by the "bimodal character" of the intensity of egg-laying in successive broods. If it is assumed that different females were engaged in egg-laying in successive broods, it would be difficult to explain the above-mentioned regularity. Taking into account the intensity of egg-laying (Fig. 1) and the 31-day theoretical period of the breeding cycle, it was considered that the onset of egg-laying in the second brood fell on May 20. As the females laid on average five eggs, then the females which had second broods started incubating their eggs on May 25. The dates of the onset of the remaining stages of the cycle in 1971 were determined on the basis of the information included in Table II. The durations of the various stages of the breeding cycle in successive broods during 1972 were similarly determined (Table III).

In 1971, 168 clutches were started in the three breeding colonies, while in the next year, 203 clutches were started in two breeding colonies. In both these years the per cent of abandoned broods was not statistically different and amounted to 17.8 and 24.8, respectively.

Table IV. The effect of clutch-size on the rates of hatching and fledgling success

Year	Clutch-size	Number of incubated broods	Per cent of nestlings hatched in relation to the number of incubated eggs	Per cent of fledglings in relation to the number of incubated eggs	Per cent of fledglings in relation to the number of nestlings hatched
1971	2	3	83.3	66.7	88.0
	3	9	81.5	70.4	86.4
	4	59	68.1	53.0	77.6
	5	49	73.5	50.6	68.9
	6	17	80.4	39.2	48.8
1972	2	4	75.0	50.0	66.7
	3	9	66.7	51.8	77.8
	4	48	78.6	58.8	74.8
	5	75	70.1	45.9	65.4
	6	16	75.0	35.4	47.2

In 1972 more clutches were started in each colony and in each brood. The two study years had a similar hatching success (73.0 and 73.2%). Clutch-size had no bearing on the hatching success. On the other hand, fledgling success was inversely proportional to clutch-size (Table IV).

4.3. THE BODY COMPOSITION OF FEMALES DURING THE BREEDING CYCLE

The body weight of laying females, excluding the weight of ovaries and eggs in the oviduct was the highest in both study years and throughout the entire breeding season, than the body weight of females in other stages of the breeding cycle. Females feeding their young had the lowest body weight, which did not differ much from that of females not engaged in breeding activities (Fig. 2).

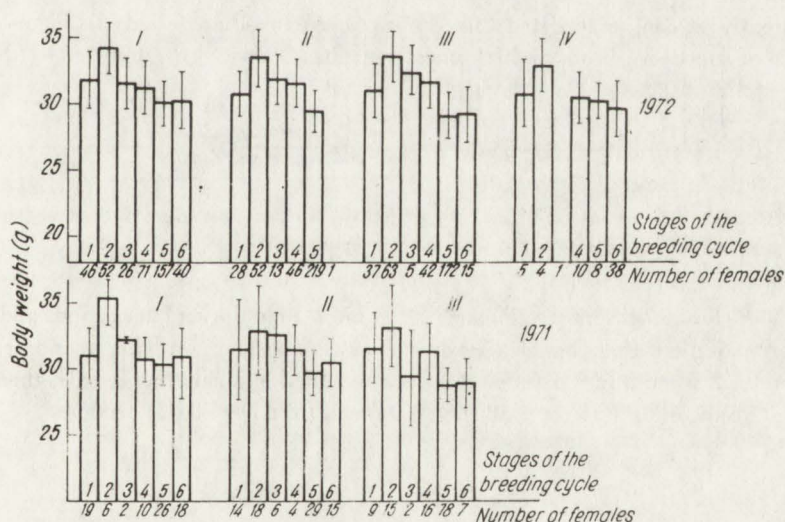


Fig. 2. Changes in the body weight of females in successive stages of the breeding cycle in successive broods (I-IV)

Stages of the breeding cycle: 1 – pre-breeding females – the ovary heavier than 100 mg, 2 – females laying eggs – an egg in the oviduct or post-ovulatory follicle not smaller than 4.1 mm (such females had their cloaca expanded and abdomen swollen), 3 – females incubating for not longer than five days with at least one stigma on the ovary; the brood-patch either fully or partially developed, 4 – females incubating for longer than five days – no traces of stigmas, the brood-patch fully developed, the cloaca dry and contracted, the ovary lighter than 100 mg, 5 – females feeding young – the brood-patch disappearing, the skin of the abdomen flaking off, the ovary not exceeding 100 mg, but it might be heavier when the female is preparing to the next brood, 6 – females not taking part in breeding – the abdomen covered with feathers or in the process of refeathering, the cloaca contracted and the ovary lighter than 100 mg. Females with no traces of a brood-patch (abdomen not covered with feathers, flaked off and smooth) and with the ovary lighter than 30 mg were included in this group. This excluded females which were in the last stage of feeding their young but whose ovary was heavier than 30 mg

Differences in the amount of water in the body of females were similar to differences in their body weights (Fig. 3). Similar amounts of fat were recorded (differences statistically insignificant) in females in different stages of the breeding cycle during the first brood in both

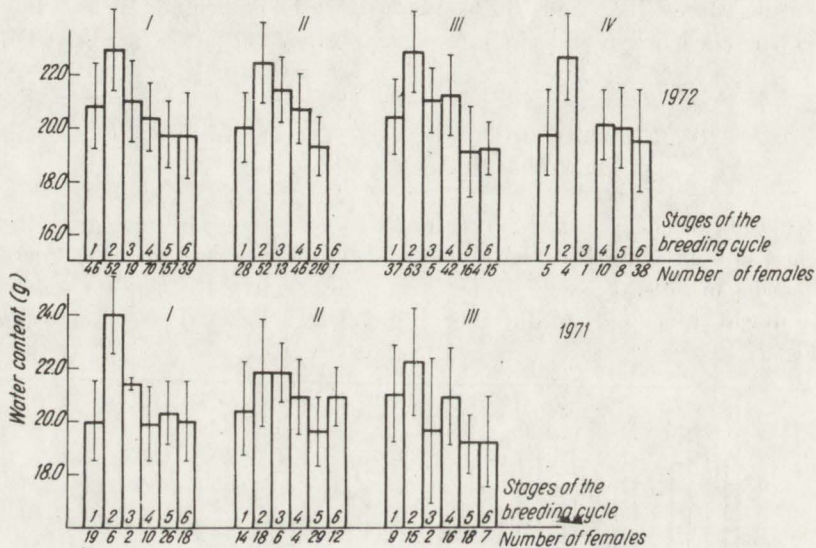


Fig. 3. Changes in the water content in the body of females in successive stages of the breeding cycle (1–6, see Fig. 2) in successive broods (I–IV)

years. Females showed differences in their fat content only during later broods and incubating females had more fat than females feeding their young (Fig. 4). This phenomenon clearly occurred in 1972 when a higher fat content was recorded in incubating females than in females feeding their young in both the second ($p < 0.01$) and third ($p < 0.01$) broods.

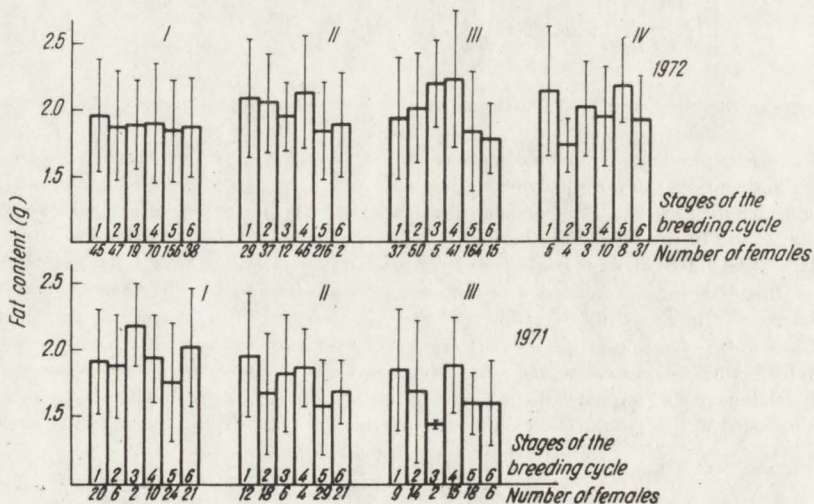


Fig. 4. Changes in the fat content of the body of females in successive stages of the breeding cycle (1–6, see Fig. 2) in successive broods (I–IV)

In view of the paucity of material from 1971 it seemed advisable to combine the data for second and third broods with the result that a statistically significant difference ($p < 0.05$) between the fat content of incubating females and females feeding young was observed. This provides sufficient strong support grounds for the conclusion that there was a similar trend in the variations in the fat contents of females in relation to the stage of the breeding cycle in both years, although the birds were leaner in 1971 than in 1972 (Fig. 5).

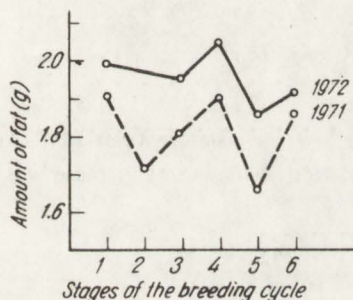


Fig. 5. Amount of fat in the body of females in successive stages of the breeding cycle (1-6, see Fig. 2)

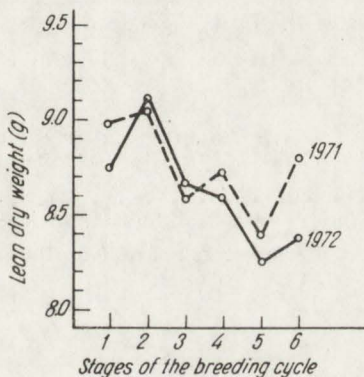


Fig. 6. The lean dry weight of females in successive stages of the breeding cycle (1-6, see Fig. 2)

In the two study years the highest lean dry weight was recorded in females engaged in egg-laying. When laying was terminated their lean dry weight decreased (Fig. 6).

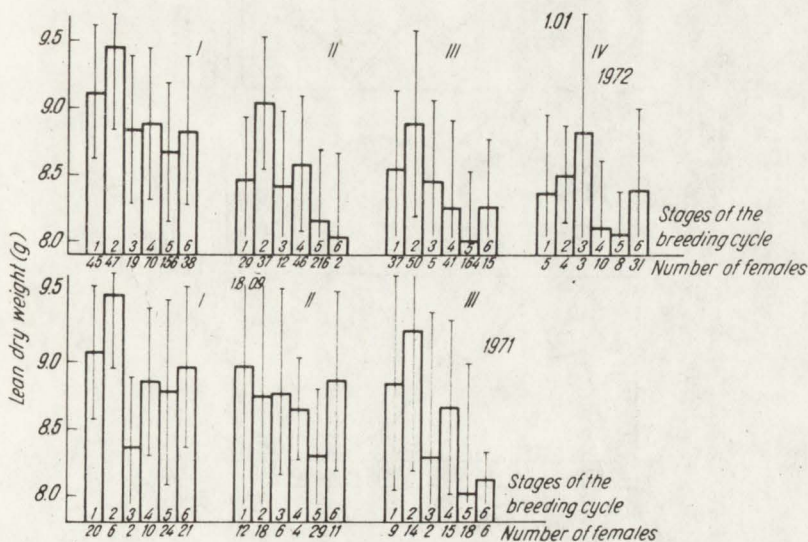


Fig. 7. Changes in the lean dry weight in successive stages of the breeding cycle (1-6, see Fig. 2) in successive broods (I-IV)

Throughout the entire 1972 breeding season incubating females had a lower lean dry weight than females laying eggs ($p < 0.01$). In 1971 the amount of this body component was also smaller in incubating females, but the difference was statistically significant only for the first broods. An analysis of the material from the entire 1971 breeding season revealed that incubating females had a lower lean dry weight than females laying eggs and this difference was statistically significant ($p < 0.05$). In 1972 the lean dry weight of females not engaged in breeding was below that of females laying eggs ($p < 0.01$). Similarly in 1971 a lighter lean dry weight was recorded in non-breeding females than in those laying eggs, but the difference was statistically significant ($p < 0.05$) only for the third broods (Fig. 7).

4.4. THE BODY COMPOSITION OF FEMALES ON SUCCESSIVE DAYS OF EGG LAYING

The body weight of females increased in the last few days before their first ovulation (Fig. 8). Females were heaviest on the first day of ovulation. This weight increase was due to

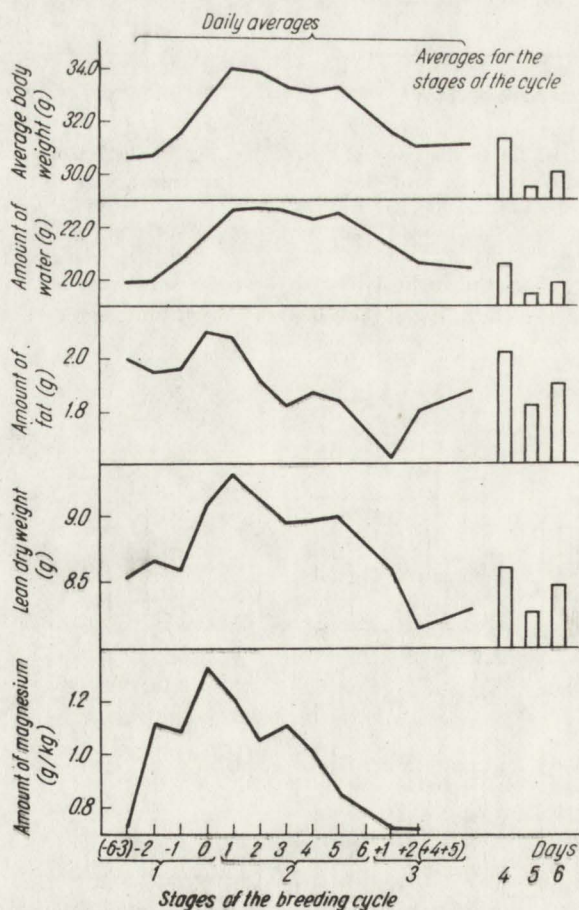


Fig. 8. Changes in the weight of body components in the period of intensive egg production in successive stages of the breeding cycle (1-6, see Fig. 2) (average data covering the two study years)
Amount of magnesium is given according to K. Kraśnicki and B. Pinowska (unpublished data)

increases in the water content (79%), fat content (3%) and lean dry weight (18%). During egg-laying their body weight displayed only small fluctuations, while they clearly lost weight in the two days following the termination of egg-laying. Fluctuations in the water content were similar those in body weight (Fig. 8). During the last few days before the onset of ovulation females contained more fat and the lean dry weight increased. The fat content dropped on successive days of egg-laying, and at the termination of laying it was 73% of the amount recorded on the first day of ovulation. Replenishment of the fat reserves began during the first days of incubation (Fig. 8). Lean dry weight also decreased between the first day of ovulation and the first day of incubation (Fig. 8).

To evaluate the effect of clutch-size on the fluctuations in body weight and other components studied, the material was divided into clutch-size classes. A clear-cut drop in the fat content of the female on successive days of ovulation was recorded only in six-egg clutches (Fig. 9). This

problem will be discussed in the following section on clutch-size. No relationship was observed between clutch-size and fluctuations in the remaining body components.

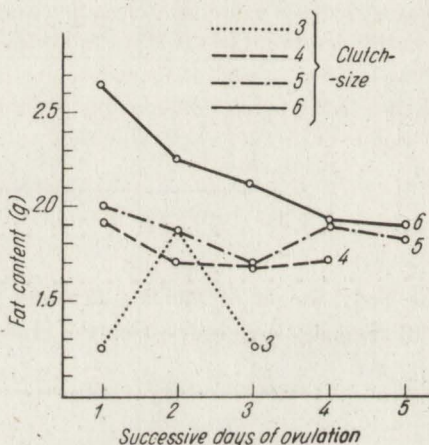


Fig. 9. Changes in the fat content on successive days of ovulation

4.5. CLUTCH-SIZE

In 1971 there were 11.3% of the clutches contained one or two eggs, and exactly the same percentage (11.3%) was recorded in 1972. In 34 of the 41 cases of one- and two-egg clutches in 1971 the birds abandoned the nest. On the other hand, when the clutch-size was estimated by the method described above (see Section 3), only 0.5% of females captured at the various sites had one- and two-egg clutches. This suggests that checking of the nests was one of the causes of abandonment of broods by females. This problem had been analysed by Pinowski, Pinowska and Truszkowski (1973). Taking into account this abandonment of small clutches by females, with possibly a diversity of causes, in the present analysis, the number of incubated eggs has been taken as the clutch-size. This definition is important to correctly analyse the fluctuations in the successive stages of the breeding cycle. The fluctuations in the body components of females discussed in the previous section, for this reason, concerned larger than two-egg clutches. The percentage of deserted broods decreased for successive broods (Table V).

It was found that the average size of the incubated clutch was largest for the second brood and decreased considerably for ensuing broods. This conclusion was supported by both data derived from observations of nests and the analysis of the reproductive organs of captured females (Fig. 10). The modal clutch-size of the first three broods in both years was five eggs. In fourth broods the modal clutch-size dropped to four eggs.

The trends in clutch-size estimated on the basis of nest observations and on the analysis of breeding organs concurred (Fig. 11).

Table V. Number of broods started and percentage of deserted clutches in successive broods

Year	Brood	Colony						Per cent of deserted broods in all colonies
		Wieniec		Górki Wschodnie		Pastwa		
		number of broods started	per cent of deserted broods	number of broods started	per cent of deserted broods	number of broods started	per cent of deserted broods	
1971	I	47	23.4	15	26.6	14	21.4	23.7
	II	35	17.1	7	14.3	7	14.3	16.3
	III	28	7.1	4	0	6	16.7	7.9
	IV	5	20.0	0	0	0	0	20.0
	total	115	17.4	26	19.2	27	18.3	17.8
1972	I	61	31.1	16	31.2			31.1
	II	59	18.6	14	28.5			20.0
	III	42	19.0	6	0			16.6
	IV	5	60.0	0	0			60.0
	total	167	24.5	36	25.0			24.6

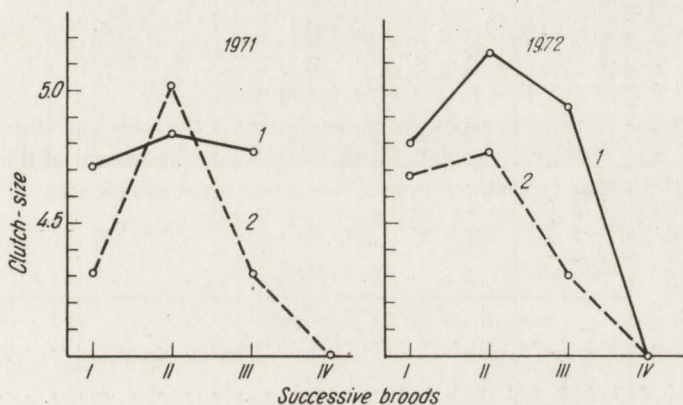


Fig. 10. Average clutch-size calculated on the basis of the analysis of ovaries and observation of nests in colonies
1 – ovaries, 2 – nests

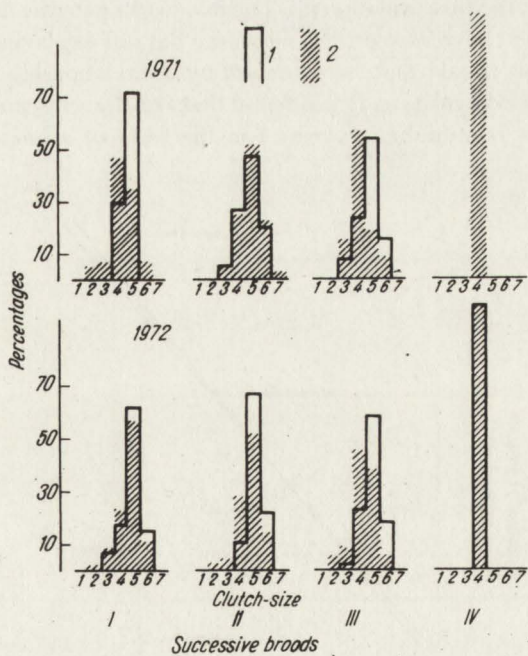


Fig. 11. Percentages of different clutch-sizes in successive broods
1 – from the analysis of ovaries, 2 – from nests. For brood IV, 1971, ovaries were not analysed. Results of the two methods completely overlap for brood IV, 1972

A combined analysis of the entire material collected in the two study years revealed that heavier females had larger clutches. This relationship is described by the following linear regression equation:

$$y = 3.008 + 0.0563 x \quad (1)$$

$$r = 0.200, \quad p < 0.05, \quad n = 211$$

where: y = clutch-size, x = weight of female in grammes.

No relationship was observed between the water content in the body and clutch-size.

Clutch-size was also positively correlated with the absolute fat content of the female during egg-laying. The 1971 material gave the following linear regression equation:

$$y = 4.4044 + 0.2507 x \quad (2)$$

$$r = 0.4045, \quad p < 0.02, \quad n = 36$$

where: y = clutch-size, x = amount of fat in grammes.

On the other hand, the 1972 material yielded the following equation:

$$y = 4.4514 + 0.2065 x \quad (3)$$

$$r = 0.3829, \quad p < 0.01, \quad n = 138$$

where: y = clutch-size, x = amount of fat in grammes.

The difference between these two equations is not statistically significant.

The highest fat content in the body of females was recorded on the day preceding the first ovulation. On the day of the first ovulation it is possible to estimate the number of eggs laid by the female. As fat content decreased on the successive days of egg-laying, the dependence of clutch-size on fat content should best be expressed by the relationship between the features calculated on the first day of ovulation. It was found that females with more fat on that day lay more eggs (Fig. 12). This relationship, expressed in the form of a linear regression equation

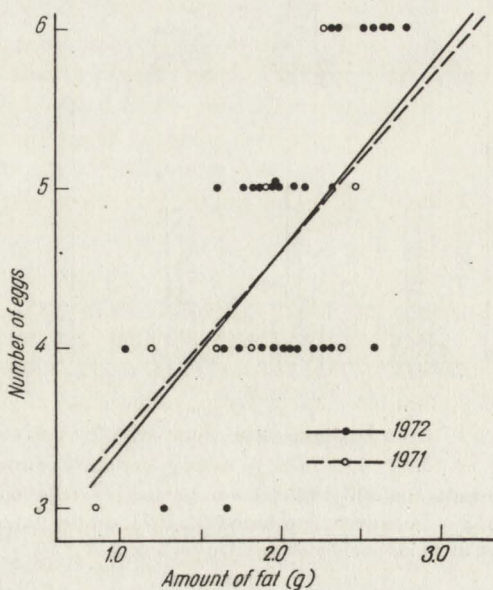


Fig. 12. Dependence of the number of eggs laid on the amount of fat accumulated to the first day of ovulation in 1971 and 1972

between clutch-size and the fat content on the first day of ovulation, was as follows for the 1971 material:

$$\begin{aligned} y &= 2.314 + 1.131 x \\ r &= 0.7173, \quad p < 0.05, \quad n = 8 \end{aligned} \quad (4)$$

where: y = clutch-size, x = amount of fat in grammes.

In 1972 the equation had the following form:

$$\begin{aligned} y &= 2.1561 + 1.2205 x \\ r &= 0.6425, \quad p < 0.01, \quad n = 32 \end{aligned} \quad (5)$$

where: y = clutch-size, x = fat content in grammes.

The difference between these two equations is not statistically significant. The regression equation for the two years combined is:

$$\begin{aligned} y &= 2.1967 + 1.2007 x \\ r &= 0.6683, \quad p < 0.01, \quad n = 40 \end{aligned} \quad (6)$$

where: y = clutch-size, x = fat content in grammes.

According to equations (4)–(6) an increase in clutch-size by one egg was associated with an increase in the fat content of 0.884 g in 1971 and of 0.819 g in 1972, and on average in the two years of 0.833 g. At the same time the average fat content of females on the first day of ovulation in 1971 was 14% lower than that of females captured in 1972. Consequently it can be said that in a year when females had a lower fat content in their bodies the energy costs (amount of fat) for the production of one egg were higher.

Females which were to lay six eggs had the highest fat content on the first day of ovulation. On successive days of egg-laying the fat losses suffered by females laying six eggs were greater than in females laying fewer eggs. The fat content of females which have just terminated laying of six-egg clutches was similar to that of females which have laid smaller clutches (Fig. 9). The large fat losses suffered by females laying six-egg clutches indicate the higher energy requirement of females which have large broods. Only 13% of the females in 1971 and 18% in 1972 had six-egg clutches. A higher percentage of six-egg clutches was recorded in 1972 when females were able to have a higher fat content as demonstrated by the analysis described above.

The water content in the bodies of all females and the lean dry weight showed no correlation with clutch-size.

4.6. CHANGES IN THE BODY COMPOSITION OF FEMALES DURING SUCCESSIVE BROODS

So far we have analysed changes in various body components of females throughout the breeding cycle. It still remains to be analysed how these selected body components of females at a particular stage of the breeding cycle change during successive broods. The lower average fat content of females recorded in 1971 allows me to assume that the trophic conditions in that year were less favourable than in 1972 (Fig. 5). Thus it would be expected that the seasonal changes in the energy components of the body would be different for the two study years, while the body components less directly dependent on energy would show similar changes.

The water content of females in the two study years did not show any directional variations (Fig. 3). A comparison of the fat content of the body of females in relation to stages of the

breeding cycle in successive broods in 1971 revealed that beginning with the second brood the amount of fat decreased, while the situation was reversed in 1972 (Fig. 4). As a result of a cyclic recovery of the initial fat content before each successive brood is initiated, the level of fat reserves in females about to commence egg-laying was relatively even between successive broods in 1971, while in 1972 it displayed considerable and irregular fluctuations. It was, however, at a level higher in 1972 than in the corresponding stage of the breeding cycle in 1971.

Clearly different tendencies in the variations in fat content occurred in females engaged in egg-laying, the stage of the cycle which has the highest energy requirements associated with breeding, and also in females during the first few days of incubation when the process of fat regeneration is not yet in full swing. The differences in the fat content between the two study years referred to above probably account for the smaller proportion of six-egg clutches, as well as for the lower mean clutch-size, in 1971 as compared with 1972 (Fig. 10). They also seem to indicate that breeding in 1971 was carried on under conditions of greater energy shortage.

The increase in the fat content of females engaged in fourth broods (Fig. 4) is associated with the approach of the period when females embark on the recovery of their fat losses which occurs during the autumnal moult (Myrcha and Pinowski 1970).

In 1972 females commencing their second broods had a lower lean dry weight than females laying first clutches ($p < 0.01$, $t = 55.34$) (Fig. 7).

Females engaged in incubation and feeding young also had a lower lean dry weight during second broods than first ones ($p < 0.01$, $t = 3.08$ for females in the fourth and fifth stages of the breeding cycle). Only those females participating in third and fourth broods in 1972 had similar lean dry weight to females captured during second broods. A decrease in lean dry weight was also recorded in 1971, both in females engaged in egg-laying and in those feeding their young, when second broods were compared with first broods ($p < 0.01$, $t = 2.67$).

These data indicate that before they initiate another brood females either do not recover their lean dry weight which declined during egg-laying, or the recovery is only partial. Successive broods are initiated only by those females which have enough body components for egg production. The drop in lean dry weight in females not engaged in breeding recorded in the two study years between successive broods is probably due to the fact that some of these females participated in previous broods. My analysis leads to the conclusion that the breeding activities of females are determined both by their lean dry weight and their fat content. However, the seasonal changes in these two body components are different. Lean dry weight decreases over the entire breeding period and when it drops below a critical level the female is unable to start another brood in that breeding season. Fat is cyclically rebuilt as is indicated by the fact that the highest fat content is found in females just beginning ovulation in successive broods. The fat content affects both the ability of the female to participate in breeding and the clutch-size.

4.7. NUMBER OF BREEDING FEMALES

Higher number of breeding females in the study area was recorded in 1972. This conclusion is derived both from the number of nests occupied in the two study years and the percentage of non-breeding females captured. The number of occupied nests increased in 1972 in the Wieniec and Górkki Wschodnie breeding colonies although the number of nest-boxes was the same in the two study years. The percentage of non-breeding females captured in 1971 was higher than in 1972 (Table VI).

Table VI. Number of occupied nests and percentage of non-breeding females

Differences in per cent between years in successive broods:

I 1971 and I 1972	$p < 0.01$	$z = 2.82$	$n = 466$
II 1971 and II 1972	$p < 0.01$	$z = 8.16$	$n = 446$
III 1971 and III 1972	$p < 0.05$	$z = 2.39$	$n = 401$

Year	Brood	Number of occupied nests in colonies		Per cent of non-breeding females
		Wieniec	Górki Wschodnie	
1971	I	47	15	22.22
	II	35	7	17.24
	III	28	4	10.54
	IV	5	0	
1972	I	61	16	10.20
	II	59	14	0.003
	III	42	6	4.49
	IV	5	0	

Not all of the females in the population participated in breeding even at the time of the most strongly represented brood. In 1971 during the first brood 22% of females captured were non-breeding, while in 1972 only 10%. During second broods the percentage of non-breeding females decreased. This, however, did not lead to more nest-boxes being occupied by sparrows (Table VI).

4.8. AVERAGE EGG AND NESTLING PRODUCTION PER FEMALE PER BREEDING SEASON

Biomass production of the population is determined by the number of breeding females, egg losses and nestling mortality. The number of eggs laid per breeding season is determined by the clutch-size and number of broods per female.

The mean clutch-size was similar for the two study years (Table VII).

It has been assumed, after Lack and Schifferli (1948) and after Pinowski (1968), that the maximum number of females participating in one brood, usually the first, is equivalent to the number of breeding females in the area. The average number of broods raised by one female in the study population was estimated by dividing the number of all broods in the breeding season by the number of breeding females participating in the best represented brood. In this study this was the first brood (cf. Pinowski 1968, Mackowicz, Pinowski and Wieloch 1970, Pinowski and Wieloch 1973).

The average number of broods per female calculated according to this principle was 19% higher in 1972 than in 1971 (Table VIII). Because of the larger number of broods per female in 1972, the number of eggs laid was also higher. Density dependent factors with the larger number of nestlings hatched in 1972 contributed to a higher nestling mortality which resulted in the number of young leaving the nest being only 10% higher than in 1971.

The increase in biomass production in 1972 was due mainly to the increase in number of broods raised per female, because the production of eggs and nestlings in one brood was similar for the two study years (Table VIII). This increase in production was recorded in the year when birds had a higher fat content (cf. Fig. 5).

Table VII. Average egg and nestling production of one pair in one clutch

Year	Total number of ^a		Eggs laid		Eggs lost		Nestlings which perished		Fledglings	
	females	clutches	number	weight (g)	number	weight (g)	number	weight (g)	number	weight (g)
1971	76	168	4.17	11.7	1.46	4.1*	0.89	15.4**	1.82	43.5
1972	77	203	4.21	11.8	1.67	4.7*	0.86	15.5**	1.68	40.1

*Weight of egg 2.8 g (after Pinowski and Myrcha 1977).

**Average weight of 0–5-day-old nestlings was taken as 8.35 g, of 6–10-day-old nestlings as 20.96 g, and older ones – 23.45 g (after J. Pinowski – unpublished data).

Table VIII. Average number of eggs laid and nestlings raised per one female per breeding season

Year	Number of females	Average number of broods per female	Eggs laid		Eggs lost		Nestlings which perished		Fledglings		Total biomass production (g)
			number	weight (g)	number	weight (g)	number	weight (g)	number	weight (g)	
1971	76	2.21	9.22	25.8	3.89	10.9*	1.96	34.0**	4.02	96.1	141.0
1972	77	2.64	11.10	31.1	4.40	12.3*	2.26	40.8**	4.44	106.1	159.2

*See Table VII.

**See Table VII.

5. DISCUSSION

It is well known that an increasing photoperiod (length of day) stimulates the growth of gonads. This process has been studied in a number of bird species, including the house sparrow (Riley and Witschi 1938, Bartholomew 1949). However, when air temperatures are too low energy losses associated with thermoregulation delay the progress of breeding. That is why air temperature is such an important factor determining the date of laying of eggs. In Poland egg-laying begins when the average air temperature in the week preceding the onset of laying reaches 7–10°C (Mackowicz, Pinowski and Wieloch 1970). The other important factor affecting the date of the onset of egg-laying is the availability of food resources. Before the onset of egg-laying birds have to gather sufficient amounts of nutrients and energy, which is reflected in the hyperphagia observed at this time (Elliott 1966).

Sparrows nesting in warmer places (e.g., in lighted and heated animal sheds) start their broods earlier and have a larger number of broods during a breeding season than those nesting in the open (Will 1969, Novotný 1970, Il'enko 1976). Sparrows living in sheds for farm animals have easy access to protein-rich food which may serve as a substitute for animal food, or they may feed on invertebrate animals found in manure. These habitat conditions enable sparrows to move the onset of breeding forward when they live inside farm buildings. Thus it is not surprising that in the study area females nesting inside buildings with farm animals started their broods earlier than females occupying the nest-boxes in the colonies under observation. An analysis of the gonads of a large number of females captured throughout the study area enabled me to record the differences in the date of laying the eggs for the entire population. On this basis it was possible to conclude that broods were, in fact, commenced about two weeks earlier than it would seem from observation of nests in the breeding colonies (nest-boxes).

The method of estimating the average number of broods per female per breeding season widely used by ornithologists is based on the assumption that the total number of females capable of breeding determines the brood in which the largest number of females participates. In other less well-represented broods only part of females is engaged in breeding. The results obtained with this method can be treated as an estimate of the theoretical number of broods raised by each female (Lack and Schifferli 1948, Pinowski 1968, Mackowicz, Pinowski and Wieloch 1970, Pinowski and Wieloch 1973, and others).

The data obtained in the present study (cf. Tables VI, VIII) showed that in a year when there were more breeding females there were also more broods per female. A comparison of the number of broods per female from available data using the above method revealed considerable variations in the feature within the geographical range of the house sparrow. The number of broods raised per female varies not only throughout the range of the species (Table IX), but it also varies from year to year in a given area (Table X). This parameter varies from 1.6 broods, recorded on the northern border of the range, to 4.3 in the equatorial zone. The number of broods raised by the population inhabiting the area around Dziekanów Leśny near Warsaw, and studied over a number of years, varied from 2.0 to 2.6. In study area near Gdańsk, 2.2 broods per female were recorded in 1971, and 2.6 broods per female in 1972.

The breeding activities of the female are associated with the condition of the bird determined by changes in body weight, and in particular such components as fat content and lean dry weight.

An increase in the body weight of females in the period of egg-laying has been recorded in the dunlin (*Calidris alpina* (L.)) (Holmes 1966), and in the bullfinch (*Pyrrhula pyrrhula* (L.))

Table IX. Average number of broods in one breeding season

Locality	Latitude	Average number of broods	Author
Baroda, India	22°18' N	4.3	Naik (1974)
Lahore, Pakistan	31°30' N	2.1	Mirza (1973)
Oktibbeha Co., Mississippi, USA	33°28' N	2.8	Sappington (1977)
Plainview, Texas, USA	34°10' N	3.9	Mitchell et al. (1973)
Portage des Sioux, Missouri, USA	38°55' N	2.5	Anderson (1973)
McLeansboro, Illinois, USA	38°07' N	2.2	Will (1969)
Whitewater, Wisconsin, USA	42°50' N	1.5	North (1973a)
Slezké Rudoltice, Czechoslovakia	50°13' N	2.6	Novotný (1970)
Kraków, Poland	50°04' N	2.0	Pinowski and Wieloch (1973)
Oxford, England	51°46' N	2.1	Seel (1968a)
Dziekanów Leśny, Poland	52°20' N	2.3	Pinowska and Pinowski (1977)
Gdańsk, Poland	54°20' N	1.7	Strawiński and Wieloch (1972)
Kangasala, Finland	61°27' N	1.6	P. Rassi (unpublished data)
Oulu, Finland	65°00' N	2.0	Alatalo (1975)

(Newton 1966). Yourbrough (1970) recorded variations in the percentage of fat in the dry weight in *Calidris alpina* and *C. minutilla* (Vieillot) during one breeding season. An increase in the fat content of birds was also recorded during incubation (Redfield 1973) with a subsequent decrease in this component when feeding of the young began (Nice 1937, Newton 1966, Payne 1969, Thoresen 1969, Yourbrough 1970). The general tendencies of the variations at different stages of the breeding cycle in body composition of female house sparrows and females of the above-mentioned species are, generally, in agreement.

In the papers not dealing with sparrows the changes in body composition were studied without going into a detailed analysis on successive days of egg production. For this reason it is also difficult to compare the results of the present study with the results of studies of the body composition of sparrows carried out by Barnett (1970), Blém (1973) and Dolnik and Gavrilov (1975). Rapid changes in the body composition observed during the period a few days preceding the onset of ovulation, as well as during egg-laying, indicate how intensive the process of metabolism can be. However, detailed study of these processes has so far been carried out only for domestic fowl (hens). These studies revealed that in the period preceding ovulation the amount of phospholipoproteins in the blood increases, and new phosphoproteins which are incorporated in the yolk can be detected (Vanstone, Maw and Common 1955, McIndoe 1959). At the same time the amount of free fatty acids of phospholipids in the blood increases as well, only to drop drastically as soon as the first egg is laid (Held and Badman 1963, Held et al. 1964). When the amount of fat in the body of females increases, increase can be recorded in the liver, which in turn is dependent on the free fatty acids in the blood (Hawkins and Held 1966). These results indicate the rapid changes in the metabolism of hens. It can be assumed that similar phenomena also occur in other bird species, including sparrows.

Table X. Average number of broods per female per breeding season in different localities and years

Locality	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	Author
Dzieskanów Leśny (52°20' N, 20°50' E)	2.3	2.5	2.6	2.3	2.5	2.4	2.3	2.5	2.2	2.0	2.3	2.0	2.4	2.1	Pinowska and Pinowski (1977)
Rzepin (52°21' N, 14°51' E)								1.9	1.8						Mackowicz, Pinowski and Wieloch (1970)
Kraków (50°04' N, 19°57' E)								2.0	1.6						Mackowicz, Pinowski and Wieloch (1970)
Slezké Rudoltice (50°13' N, 17°43' E)				2.9	2.8	2.4									Novotný (1970)
Portage des Sioux (38°55' N, 90°22' W)										2.08	2.04	2.09	2.35		Anderson (1973)
McLeansboro (38°07' N, 88°32' W)							2.44	2.25	2.18						Will (1973)

The analysis of changes in the body composition on successive days of egg production in the present study enabled me to describe the variations in fat content and lean dry weight (Fig. 8).

The number of yolky follicles up to the first day of ovulation is correlated with the amount of fat accumulated in the body of the females. Consequently, the amount of energy accumulated by females in the form of fat affects the number of eggs laid (Fig. 12). A similar dependence was recorded by Jones and Ward (1976) in the dioch (*Quelea quelea* L.) although they failed to attach any particular significance to their finding. These authors considered that the clutch-size was mainly determined by the protein resources in the body of females, and in particular the opportunity of replenishing these resources from the daily food rations. It has been found that clutch-size depends on the availability and quality of food in a number of bird species (Moreau 1944, Pitelka, Tomich and Treichel 1955, MacArthur 1958, Breitenbach, Nagra and Meyer 1963, Mebs 1964, Cave 1968, Anderson 1977, and others). Ashmole (1971) suggested that clutch-size in tropical birds is regulated by the energy reserves of the female.

The analysis of the study material revealed not only that clutch-size increased when the fat reserves increased on the first day of ovulation, but also that the lean dry weight of females decreased when the brood was terminated, and especially when all the eggs were laid (Fig. 6). In later broods (i.e., third and fourth) females preparing to breed had a similar lean dry weight as those laying eggs in the second brood. In other words, only females having a sufficiently high lean dry weight are prepared for participation in later broods. It is possible that those females had higher lean dry weight during the first brood than the average for the population. On the other hand, females with lower lean dry weights are unable to take part in the subsequent broods. The failure to differentiate between the various components of the lean dry weight in my analysis makes it impossible to determine whether a shortage of protein resources or various mineral compounds is the limiting factor here, especially as variations in the amount of magnesium and lean dry weight are similar (Fig. 8).

The results of my analysis suggest that clutch-size is determined by fat reserves while the number of broods raised by one female in a given breeding season is limited by the lean dry weight and the level of replenished fat reserve. These data contradict the conclusions of Läck (1954, 1968) who claimed that clutch-size is determined by the number of nestlings the female is capable of feeding, or in other words that clutch-size is regulated by the situation which will arise after the eggs have been laid. This theory is contradicted by the relationship, observed in the present study, between clutch-size and fat content in the body of females and the changes in lean dry weight, which suggests that clutch-size is determined by the condition of the female during the period of egg-production, and not by the possibility of feeding a given number of nestlings.

The body weights of sparrows are higher in the northern parts of their range (Danilov et al. 1969, Pinowski and Myrcha 1977). The fat contents of bird species, including house sparrows, are also higher in the north (Dolnik 1968, Blem 1973, Postnikov 1975). At the same time clutch-size is larger at more northerly latitudes (Dyer, Pinowski and Pinowska 1977). The increase in the fat contents in the north is undoubtedly the result of adaptation enabling the birds to live at lower temperatures and to survive long nights. It can be assumed that the acquired physiological ability to accumulate large fat reserves to survive the winter period makes it easier for birds to do likewise during the breeding season, and this probably explains the larger clutch-size in the north.

If the increase in fat content affects the clutch-size and also the total number of broods in one breeding season, one would expect to find a correlation between the mean clutch-size and

the mean number of broods per female in a given year and area. Data obtained during long-term studies of house sparrow populations at Dziekanów Leśny near Warsaw in which the author participated enabled me to support this conclusion. The mean annual clutch-size and the mean number of broods raised per female in a given year were calculated. Data covering a seven-year period showed a positive correlation between the number of broods per female and mean clutch-size (Fig. 13).

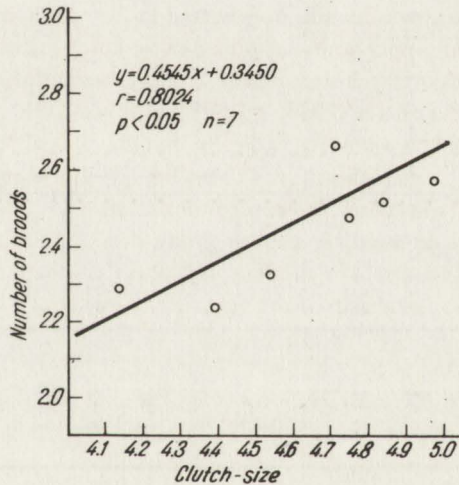


Fig. 13. Dependence of the average number of broods per female on average clutch-size

Over the geographical range of the house sparrow there is an inverse relationship between clutch-size and the number of broods per female. Clutch-size increases when we move north while the number of broods raised per female decreases (Dyer, Pinowski and Pinowska 1977). This is the result of the shorter breeding season in the north which is determined by the climatic factors, while the increase in clutch-size in the north is associated (as discussed above) with the ability to accumulate larger fat reserves.

These relationships between the fat reserves and clutch-size and the number of breeding females enable me to connect the production of the population with the condition of the females, and through this to the trophic conditions of the habitat. The size of population production is a reflection of the trophic conditions where the population lives.

By adding new data to that collected by Dyer, Pinowski and Pinowska (1977) on the production of eggs and nestlings throughout the entire breeding season, it has been possible to compare the results of the present study with the range of variations in these parameters recorded throughout the whole geographical range of the species (Table XI). The number of eggs laid ($CV = 28\%$) and the number of nestlings leaving the nest ($CV = 27\%$) are much less variable than the number of eggs lost ($CV = 46\%$) and the number of nestlings which perished ($CV = 58\%$).

No relationship was observed between the number of eggs laid and the fledgling success due to varying intensities in egg losses and nestling mortality. Of the highest number of eggs laid per female in the breeding season, which amounts to 18.49 eggs (in India), only 4.7 sparrows leave the nest as fledglings, while of the smallest number of eggs laid, i.e., 8.40 eggs (in England),

Table XI. Egg and nestling production per female over the entire breeding season

Locality	Number of eggs laid	Number of eggs lost	Number of nestlings which perished	Number of fledglings	Author
Baroda, India (22°18' N, 73°13' E)	18.49	7.03	6.76	4.7	Naik (1974)
Oktibbeha Co., Mississippi, USA (33°28' N, 88°48' W)	11.93	2.04	2.28	7.61	Sappington (1977)
Plainview, Texas, USA (34°10' N, 101°43' W)	16.38	7.04	6.72	2.62	Mitchell et al. (1973)
Cloverlake Dairy, Plainview, Texas, USA (34°10' N, 101°43' W)	12.6	4.91	2.54	5.15	Mitchell et al. (1973)
McLeansboro, Illinois, USA (38°07' N, 88°32' W)	10.12	3.44	3.14	3.54	Will (1969)
Portage des Sioux, Missouri, USA (38°55' N, 90°22' W)	10.8	3.88	2.35	4.57	Anderson (1973)
Whitewater, Wisconsin, USA (43°50' N, 88°32' W)	7.35	3.60	—	—	North (1973a)
Kraków, Poland (50°04' N, 19°57' E)	9.6	3.74	2.28	3.58	Pinowski and Wieloch (1973)
Slezké Rudoltice, Czechoslovakia (50°13' N, 17°43' E)	11.18	2.12	1.36	7.7	Novotný (1970)
Oxford, England (51°46' N, 01°15' W)	8.4	1.26	3.92	3.22	Dawson (1972)
Dziekanów Leśny, Poland (52°20' N, 20°50' E)	9.87	4.44	1.14	4.29	Pinowska and Pinowski (1977)
Gdańsk, Poland (54°20' N, 18°56' E)	7.31	1.97	1.55	3.79	Strawiński and Wieloch (1972)
Gdańsk (Wieniec, Pastwa), Poland (54°20' N, 18°56' E)	9.22	3.89	1.96	4.02 (1971)	data collected in the present study
	11.10	4.40	2.26	4.44 (1972)	
Kangasala, Finland (61°20' N, 24°03' E)	8.96	1.34	3.50	4.12	P. Rassi (unpublished data)
Average	10.81±3.08	3.79±1.73	3.04±1.75	4.29±1.17	

3.2 young leave the nest successfully (Table XI). This explains why the production of nestling sparrows is proportional to the number of females and can, with some approximation, be estimated by multiplying the recorded number of breeding females by 4.3 (average number of nestlings raised to fledging per season by one female). The estimated range of variation of this parameter does not exceed 30%. Taking into account the possibility of considerable inaccuracy in the estimation of these biological parameters this seems to be fairly accurate. This enables me to assume that the number of breeding females is the main factor determining production. As has been demonstrated above, the number of females participating in breeding activities is determined by their physical condition, and fat metabolism is of prime importance.

6. CONCLUSIONS

1. The occurrence of four broods was recorded on the basis of the number of clutches started.

2. An analysis of the size of the ovaries and the growth of the brood-patch enabled me to identify the stages in the breeding cycle of females. The day of ovulation and the day on which egg-laying was terminated were determined on the basis of variations in the size of yolky follicles and post-ovulatory follicles in the ovary. Identification of the stages of the breeding cycle of females captured enabled the author to analyse changes in the body composition of females during the breeding cycle.

3. Water, fat content and lean dry weight were found to increase before the onset of ovulation. They then decreased on successive days of egg-laying.

4. Fat reserves were regularly rebuilt in successive broods while the lean dry weight decreased in successive broods.

5. Heavier females had larger clutches. This relationship is expressed by the linear regression equation: $y = 3.008 + 0.0563 x$.

6. Fat content on the first day of ovulation was correlated with clutch-size. This relationship is expressed by the equation: $y = 2.1967 + 1.2007 x$.

7. A decrease in lean dry weight may be one of the factors eliminating females from initiating breeding activities. In the third brood fewer females lay eggs, and only very few go on to have fourth broods. The lean dry weight of females raising third and fourth broods was similar to that for those raising second broods.

8. The period of feeding young, similar to that of egg-laying, was characterized by a drop in the fat content of the females.

9. In the year when birds had more fat in their bodies, more females were engaged in breeding activities, which indicates that fat shortages not only lead to smaller clutches but can also eliminate females from further breeding.

10. Smaller fat reserves and lower lean dry weights were recorded for non-breeding females than for those on the first day of ovulation.

11. An increase in fat reserves of female house sparrows contributes to an increase in the population production by enabling more females to breed and raise more broods. The increase in clutch-size due to larger fat reserves was offset by a higher nestling mortality in nests where larger clutches were laid.

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7. SUMMARY

During 1971 and 1972, 1505 female house sparrows were captured in and around 86 large farm buildings in the province of Gdańsk and Elbląg. An analysis of the ovaries and the rate of development of brood-patches made it possible to separate the females into six groups with respect to the stage of the breeding cycle (Table I). Changes in the weight of the body of females were recorded in relation to the stage of the breeding cycle (Fig. 2, 8). These changes were associated with changes in the amount of water, fat, and lean dry weight.

The amounts of these three components were greatest on the day of the ovulation of the first egg. With the laying of successive eggs the amount of fat and lean dry weight decreased. The amount of water in the body of the female decreased especially after the laying of the last egg (Fig. 8). During incubation the amount of fat increased, to again be used during feeding of the nestlings (Figs. 4, 8). After egg-laying the amount of the lean dry weight increased to a small degree (Fig. 8).

Larger clutch-sizes were recorded in females with a greater fat content (Fig. 12). A larger number of the nest-boxes was occupied in the breeding colonies during the breeding season of 1972 in which the fat content of the females was greater (Fig. 5, Table VI).

Four broods were recorded on the study area (Fig. 1). The amount of lean dry weight in the body of the females decreased during successive broods (Fig. 7). Females preparing for third and fourth broods, however, had a similar amount of lean dry weight compared with females captured during the second brood. The number of breeding females also decreased with successive broods (Table VI).

The material presented in this paper indicates that decreases in fat content and lean dry weight in the body of the female can be factors in the cessation of breeding of females. Non-breeding females have a lower fat content and lean dry weight than laying females (Figs. 4, 7). An increase in the fat content of female house sparrows results in greater production by increasing the number of broods per female per breeding season. The increase in clutch-size associated with greater fat content of females was somewhat offset by increased mortality of nestlings in nests with a larger clutch-size (Tables VII, VIII).

8. POLISH SUMMARY

Wróble domowe odławiano na terenie zabudowań gospodarskich w 86 punktach woj. gdańskiego i elbląskiego. W czasie 2 lat badań odłowiono 1505 samic.

Analiza jajników (tab. I) i stopnia rozwoju płamy lęgowej umożliwiła podział samic na 6 grup w zależności od etapu cyklu rozrodczego. Stwierdzono zmienność ciężaru ciała samic w zależności od etapu tego cyklu (rys. 2, 8). Zmiany tej cechy związane były ze zmianami ilości wody, tłuszczu i składników suchej masy beztłuszczowej.

Ilość każdego z analizowanych składników była najwyższa w dniu pierwszej owulacji. W czasie składania kolejnych jaj obniżała się ilość tłuszczu i suchej masy beztłuszczowej. Ilość wody w ciele samic obniżała się przede wszystkim po złożeniu ostatniego jaja (rys. 8). W okresie inkubacji samice ponownie zgromadziły tłuszcz, a następnie zużyły go w czasie karmienia piskląt (rys. 4, 8). Po złożeniu jaj ilość suchej masy beztłuszczowej wzrastała w niewielkim stopniu (rys. 8).

Stwierdzono wyższe zniesienia u samic bardziej otłuszczonych (rys. 12). W sezonie lęgowym, w czasie którego stwierdzono wyższe otłuszczenie samic, była też wyższa liczba zajętych gniazd w koloniach lęgowych (rys. 5, tab. VI).

Na badanym terenie stwierdzono występowanie 4 lęgów (rys. 1). W ciele samic, w czasie kolejno następujących po sobie lęgów, stwierdzono obniżanie się zawartości suchej masy beztłuszczowej (rys. 7). Samice przygotowujące się do trzecich i czwartych lęgów miały jednak podobną ilość tego składnika do samic odłowionych w czasie drugiego lęgu. W czasie kolejnych lęgów zmniejsza się również liczba samic uczestniczących w rozrodzie (tab. VI).

Dane uzyskane w tej pracy wskazują, że zarówno obniżanie się zawartości tłuszczu w ciele samicy jak i zawartość składników suchej masy beztłuszczowej mogą być czynnikami eliminującymi samice z rozrodu. Samice nie biorące udziału w rozrodzie miały niższą zawartość tłuszczu i składników suchej masy beztłuszczowej w porównaniu z samicami składającymi jaja (rys. 4, 7). Wzrost otłuszczenia samic wróbla domowych powoduje wzrost wielkości produkcji poprzez zwiększenie liczby legów odbywanych przez samice. Wzrost wielkości zniesienia wywołany wyższym otłuszczeniem niwelowany był wyższą śmiertelnością piskląt w gniazdach o większych zniesieniach (tab. VII, VIII).

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