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Studies on the Activity of Starlings *Sturnus vulgaris* LINNAEUS, 1758, in the Breeding Season

[Pp. 97—122 and 11 text-figs]

Badania nad aktywnością szpaków *Sturnus vulgaris* LINNAEUS, 1758, w okresie lęgowym

Исследования над активностью скворцов *Sturnus vulgaris* LINNAEUS, 1758, в выводковом периоде

Abstract. The results of four years' study on the activity of Starlings in three main periods of breeding, i. e., those of egg laying, incubation, and nestling feeding are presented. The investigation was carried out under natural conditions. Endogenic agents have a decisive effect on the course of activity in particular stages of breeding, whereas the exogenic ones (chiefly weather) determine the behaviour of Starlings at different times of day. Their behaviour varies considerably from pair to pair. In general, the share of both parents in the feeding of the young is more or less the same, but fairly big differences are observed between individual pairs.

CONTENTS

I. INTRODUCTION

Most investigations of the activity of birds published so far were carried out under laboratory conditions. A few studies made under natural conditions dealt with the behaviour of single pairs of birds only and in this case the time of observation was usually short.

To be sure, my investigation concerns the species whose activity at the nest has already been studied by several authors (KLUIJVER, 1933; PROMPTOV, 1940; KEIL, 1963, and others); however, these studies were mostly pretty fragmentary and they covered chiefly the intensity of feeding. DELVINGT (1963a) was the only worker who wrote about the activity of Starlings in the period of incubation, and I failed to find any publications on their activity in the period of egg laying. Having at my disposal fairly ample material, collected for several years, I attempted to give special attention to the differences in the behaviour of Starlings in three main periods of breeding, i. e., those of egg laying, incubation, and feeding of the young. The elaboration of such material allows a description of the essential features of the activity course and the determination of the range of influence of the endo- and exogenic agents on the course of activity throughout the breeding season.

II. MATERIAL AND METHOD

Observations on the activity of Starlings were carried out in the nesting seasons of 1960—1963 and 1966. The Starlings observed nested in a small breeding colony (some dozen nests) in the Wielkopolski National Park at Puszczykowo near Poznań (58°18'N, 16°52'E). All of them nested in wooden nesting boxes.

The frequency at which adult Starlings passed through the entrance of the nest-box has been taken as an index of their activity in the breeding season.

Each nest-box was equipped with a switch with a lever, which partly covered the entrance of the box, so as to facilitate the determination of the number of entries and exits of the birds. Entering the box, the Starlings raised the lever, which caused the switch contacts to touch each other. The switch was connected to a counter, such as is used to count telephone calls, and this recorded each closing of electric circuit. A 6V storage battery was used as the source of energy. The battery and counters were placed in a closed room. The connection of all these elements is shown in the diagram in Fig. 1. An improvement made in the construction of the switches in the second year of investigation made it possible to eliminate the repetitive closing of circuit (up to 3 times) during one and the same passage of a bird. I divided the total of passages (entries and exits) recorded by the counter by two to obtain the number of arrivals of a pair of birds in the nest. The counters were read every two hours from 6 a. m. to 8 p. m. (Central European Time). The last reading, at 8 p. m., presented the result for the whole past 24-hour period. No readings were taken at night, since the Starling reveals no activity then. The switches were fitted on as early as a few to more than ten days before egg laying so as to let the birds get used to the equipment, which besides took them hardly a few hours.

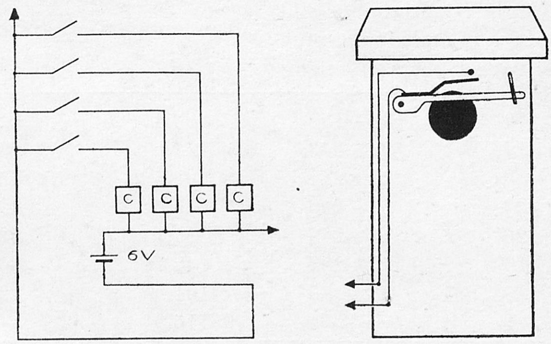

Fig. 1. A connection diagram showing the switches, counters (C) and current generator and a sketch of the front wall of a nesting box with a switch

In 1960 and 1961 five nests were connected to this automatic equipment (actometer) at the same time, in 1962 nine nests, and in 1963 six ones. A total of 25 nests in 4 successive breeding seasons were covered by observations. The relatively uniform distribution of observation material in the period of four years has the virtue of eliminating, to a great extent, the influence of external factors, e. g., weather conditions, on the pattern of activity in the recapitulation of results. The discordance between the dates of commencement of the breeding season in particular pairs still more neutralizes the effect of exogenic agents. The pattern of activity thus obtained will depend nearly exclusively on the endogenic agents, inherent to the behaviour of the species examined.

The numerical data were worked out by the simplest statistical methods. In addition to arithmetic means ($\bar{x}$), I also calculated the standard deviations ($\pm$ s) for them and the coefficient of variation.

In 1966 additional direct observations were made using 10×40 field-glasses to determine the share of particular parents in the incubation of eggs and feeding of the young. Out of the 29 hours of observation, 8 were given to incubation and 21 to feeding of the young. Statlings were watched in 4 nests, their sex (the birds were marked), the hours of arrivals and the time of stay in the nest being noted. With these data I constructed actograms, which are a graphic representation of the intensity of incubation and feeding of the young by both parents.

III. ACTIVITY OF STARLINGS IN THREE MAIN PERIODS OF BREEDING

The course of activity of adult birds is not uniform throughout the breeding season. The number of entries into the nest is quite different in particular periods (egg laying, incubation, feeding of the young) and for this reason the

Table I

The number of entries of both adult Starlings into the nest on particular days of three basic periods of breeding. A — egg-laying, B — incubation, C — nestling-feeding

Period	Day of period	Number of days of observation	Minimum and maximum numbers of entries	Mean number of entries	Standard deviation s	Coefficient of variation V
A	0	12	39—159	96,4	32,5	33,7
	1	17	50—343	144,0	75,6	52,3
	2	19	28—241	98,6	55,6	56,4
	3	20	88—266	156,3	49,3	31,5
	4	20	14—266	119,1	62,7	52,7
	5	16	73—289	142,7	66,7	46,7
	6	5	63—180	101,0	42,3	41,9
	7	1	—	115,0	—	—
	1—7	98	—	130,0	—	—
B	1	21	66—286	121,6	51,4	42,3
	2	19	59—203	107,9	44,9	41,6
	3	22	58—205	87,9	34,3	40,2
	4	21	46—157	94,2	29,0	30,8
	5	20	58—230	97,3	35,2	36,2
	6	22	38—189	90,3	36,9	40,8
	7	23	32—297	101,2	50,1	49,6
	8	23	42—259	120,1	57,1	47,6
	9	19	45—247	127,8	46,2	36,1
	10	19	60—358	144,5	60,3	41,7
	11	21	71—262	145,4	50,4	34,6
	12	22	69—360	161,6	62,4	38,6
	13	11	103—285	180,4	55,6	30,8
	14	3	140—162	144,7	—	—
	1—14	266	32—360	119,3	—	—
C	1	21	99—285	176,3	44,7	25,3
	2	20	126—273	201,5	38,1	18,9
	3	20	146—316	218,4	42,3	19,4
	4	20	152—392	249,3	74,4	29,8
	5	18	150—528	269,3	103,4	38,4
	6	18	51—513	278,8	111,5	40,0
	7	19	126—640	324,1	128,2	39,5
	8	19	142—714	349,4	160,3	49,9
	9	18	55—800	351,9	209,7	59,6
	10	17	88—963	367,6	222,3	60,5
	11	19	54—891	328,6	195,8	59,6
	12	20	134—645	297,3	156,2	52,5
	13	17	144—604	295,5	152,6	51,6
	1—13	246	51—963	282,7	—	—

course of activity should be discussed separately for each of the three main stages of breeding. The graphs presented in Figs. 2 and 5 and Tables I and II provide the best outlook on the range and nature of these differences.

1. Egg Laying

Towards the end of April, when Starlings' nests are nearly completed and only lack a feather lining, the females begin laying eggs. During my four-year observations the laying of the first egg fell on the average on 24 April, ranging from 20 to 26 April. The female as a rule laid one egg each day, mostly in morning hours (before 8 a. m.). The number of eggs found in the nests fluctuated from 3 to 7, but it usually amounted to 5, and the first period of breeding, discussed in this section, lasted as many days.

The most distinctive feature of activity in the period of egg laying is its evident regularity (Fig. 2A), which can be described by the following formula: the numbers of entries into the nest on the days of laying the first, third and fifth egg (odd days) are larger than those on the days of laying the second, fourth and eventually sixth egg (even days). Naturally, this regularity is not equally distinct in all the pairs of Starlings observed; in some of them it is scarcely marked, being conspicuous in others. In two cases I observed a slight deviation from the scheme. One of them is shown in the graph in Fig. 3.

The causes of such a pattern of activity should be sought rather among the endogenic than exogenic factors, especially in the physiology of the process of egg production and the psychical state of birds involved in it. It is hard to draw any far-reaching conclusions as long as the share of either parent in the formation of this pattern of activity is not known. It seems, however, that it is the female which is responsible for the activity pattern, whereas the male, accompanying it, only increases the number of entries into the nest, without affecting the pattern essentially. That the main part is played by the female would be indicated by the fact that the characteristic zigzag line of activity is closely connected with the sequence of egg laying. For this very reason the primary causes of the regularity in the numbers of entries into the nest in the period of egg laying should be referred to the process of egg production.

In the reproductive organs of the female Starling eggs are probably formed two at a time, one of them being naturally always better developed. On the day preceding the laying of the first egg the birds, at least the female, spend most time in the feeding ground, where the female prepares for laying the first two eggs by feeding intensely. On the day of the laying of the first egg the other one is nearly completely formed and the birds can give much more time to the finishing of the nest. On the next day, however, immediately after laying the second egg, the female again must spend much time foraging so as to be able to prepare the next two eggs; as a result, the birds stay much longer out of the breeding colony.

I have no proofs to support this hypothesis directly. Nevertheless, I observed several phenomena which confirm it indirectly. In the evening of 25 April there were no eggs in nest No. 5/62. At the noon of the next day there was already one egg in this nest, and another one was found in it in the evening of the same day. Thus the female laid two eggs on the first day of laying, one in the morning and one in the evening. The next egg was not added until the morning hours of the third day. The further eggs were laid at normal times. This observation indicated that on the day of laying of the first egg the female had already another entirely formed egg in the oviduct or funnel, and it had to lay this egg a few hours later on the same day. The third and fourth eggs

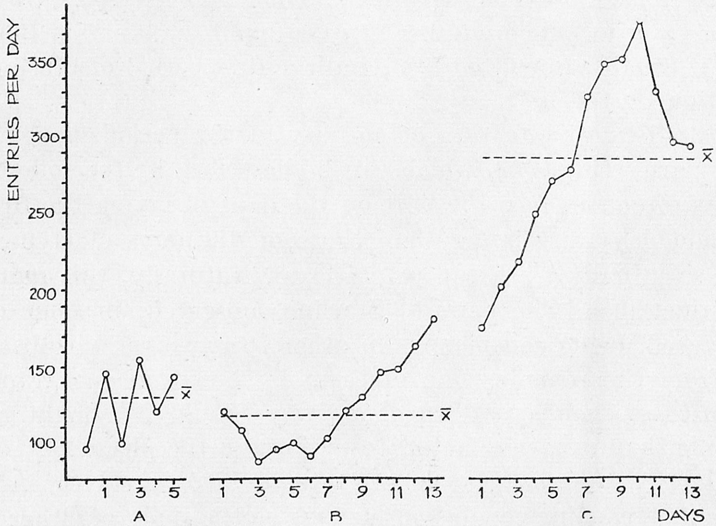

Fig. 2. Activity course of the Starling in three basic periods of breeding (mean from 25 nests). A — egg-laying, B — egg incubation, C — nestling feeding. $\bar{x}$ — arithmetic mean for given period

were at a normal stage of development and they were laid on the third and fourth days. I fairly often found a whole Starling egg lying on the ground in the area of the breeding colony or in its close vicinity. At the same time a break in the laying of eggs was noted in one of the nests. The finding of whole Starling eggs lying on the ground is a relatively common incident and they may be supposed to be just those too early formed eggs, which females, as if "taken by surprise", were forced to lay out of the nest.

The activity curves of some pairs of birds have a zigzag course for the initial period of incubation. Delvingt (1963a) describes the behaviour of the activity index for one of the pairs observed by him; on the fourth, sixth, eighth and tenth days of incubation the index was higher than on the odd days.

In the period of egg laying Starlings sleep outside the colony. The birds of the colony examined roosted at a distance of about 1 km., in the reeds overgrowing an old riverbed among meadows. The arrival of the first birds in the colony was obseved unvariably after sunrise, most commonly about 20 minutes after it or approximately at 4.35 a. m. Delvingt (1963b) writes that in the last decade of April the Starlings left their roosts 25—38 minutes before the sunrise. They do not come to the breeding colony until about half an hour later, though. In the colony they show very much agility at first (they enter the nest on the average every 3 minutes); they complete the building of the nests or mend them,

Table II

The frequency of entries of both adult Starlings into the nest in various times of day. The symbols as in Table I

Period	Hours of day-time	Number of one-hour observations	Mean number of entries	Mean number of entries per hour
A	before 6	23	29,1	20,5
	6— 8	21	17,0	8,5
	8—10	21	20,8	10,4
	10—12	20	20,5	10,2
	12—14	20	15,2	7,6
	14—16	24	20,3	10,1
	16—18	23	14,9	7,4
	after 18	23	2,6	5,1
	4.35—18.30	175	140,4	10,1
B	before 6	68	20,3	11,1
	6— 8	68	16,7	8,4
	8—10	68	18,0	9,0
	10—12	66	16,7	8,4
	12—14	66	17,2	8,6
	14—16	66	17,1	8,6
	16—18	68	17,0	8,5
	after 18	70	5,0	7,6
	4.10—18.40	540	128,2	8,8
C	before 6	138	55,7	27,9
	6— 8	129	48,8	24,4
	8—10	145	41,8	20,9
	10—12	150	37,1	18,6
	12—14	155	35,5	17,8
	14—16	147	32,3	16,1
	16—18	147	30,3	15,2
	after 18	155	10,4	9,7
	4.00—19.05	1166	292,1	18,8

the males sing intensely and the females lay eggs. About 8 a. m. the activity subsides in the colony, because the birds leave it for their feeding grounds, but it augments again as early as 10 a. m. The birds bustle about near the nests and are busy completing the lining of the nest-cup. At noon the entries into the nest occur approximately every 6 minutes. Early in the afternoon the activity in the colony decreases again, but about 3—4 p. m. its third peak can be observed. After 4 p. m. the frequency of entries into the nest decreases rapidly, on the average to one every 8 minutes, and after 6 p. m. the activity of the colony dies out nearly completely. Starlings leave for their roosts approximately at 6.30 p. m., or about 25 minutes before sunset. After 6 p. m. they call at their nests only 2 or 3 times and next all of them leave the colony.

2. Incubation Period

In Starlings, egg incubation begins on the day of laying of the last egg of the clutch. It is difficult to determine the moment at which they take to incubating their eggs and for this reason I regard the same day as the last day of the period of egg laying and the first day of incubation. In the nests observed incubation took 12 to 14 days, averaging 12.6 days.

In the incubation period the mean number of entries into the nest is lower than it is in the other two stages of breeding. This is so because the parents spend much more time in the nest when incubating than they do in the period of egg laying and especially that of feeding the young. The numbers of entries in particular days of incubation are not equal throughout this period and the shape of the activity curve is very characteristic (Fig. 2 B).

During the first three days of incubation the daily number of entries into the nest decreases to remain next at a more or less uniform but very low level up to the 6th day. This evident fall in activity of Starlings is connected with an increase in the number of hours of effective incubation. A continuous increase in the number of entries begins about the 7th day of incubation, and about the 8th day this number approximates to that on the first day of incubation. From this day onwards it is always larger than the mean calculated for the whole period of breeding. The greatest activity of Starlings observed in the last days of incubation indicates a relatively less intense warming of eggs in the sense of shorter total times of warming per day.

During the whole period of incubation the daily time of egg warming is far steadier (80 and 85% of day) than the number of entries into the nest. This may be due to the fact that towards the end of incubation the birds often leave the nest and also much more often change over in sitting on the eggs. On the last day the number of entries approximates to the number of feedings in the first days of life of the young.

The coefficient of variation (Table I), which characterizes the differentiation of behaviour of the pairs on particular days of this period, is the lowest on the fourth and last days of incubation. These relatively low values indicate that on the days mentioned the numbers of entries into the nests were least differentiated or that the fall in the number of entries about the 3rd-5th day and the marked rise in the last days are features characteristic of the course of activity in all the pairs of Starlings examined.

The findings concerning activity at different times of day are given in TableII. Females, which spend nights in the nests, become active about 10 minutes after sunrise (sunrise about 4 a. m.). I watched the females wake up from 5 minutes before to 20 minutes after sunrise. The morning increase in activity is connected with the replacement of females, incubating at night, by males. The further course of activity shows hardly any major differences. Being even, it gives evidence not so much of similar behaviour of particular pairs but rather of the fact that the periods of maximum and minimum activity occur at any time of day. Most of the main peaks of activity in the pairs studied were noted between 10 a. m. and 4 p. m. This is the time of particularly intense insolation and Starlings cannot stay quietly for a long time in their greatly heated nest-boxes. The incubating birds very often come out of the boxes to return to them in a few seconds. A continuous drop in the frequency of entries into the nest begins after 4 p. m., and the activity ends in the colony about 25 minutes before sunset (sunset about 7.05 p. m.).

Eight-hour direct observations show that the Starlings warmed eggs on the average 28 minutes per hour (Fig. 10). Out of the 14.4 hours of daily activity they spent about 7 hors warming the eggs, to which we must add 9.5 night hours to receive a total of 16 hours of incubation per day.

A pair of Starlings observed by Delvingt (1963a) warmed the eggs most intensely on the third (according to the criteria adopted by me, the fourth) day of incubation. On that day the birds remained in the nest for 1235 minutes (635 in the daytime and 600 minutes at night), that is, more than 85% of the day. Observations presented by Delvingt (1963a) refer to the second brood and, according to him, the first brood is incubated much more intensely, the duration of night sitting being more or less the same, whereas in the daytime these birds warmed the eggs 2—3 hours longer. On the 11th (12th) day of incubation the Starlings sat on the nest for 1163 minutes or nearly 80% of the day. This pair started daily activity from 0 to 60 minutes after sunrise and ended it from 0 to 100 minutes after sunset.

The course of activity during the period of incubation seems to be dependent on the developmental stage of the embryo enclosed in the egg heated. At the beginning of the second day the heart of the embryo begings to pulsate and some changes, particularly important to the developing organism and leading to the formation of buds of different organs, occur from the 2nd to about the 6th day (Shmidt, 1953). At approximately the same time the parents warmed the eggs most intensely and, consequently, left the nest most rarely (the smallest number of entries). About the eighth day the embryo already resembles a chick and from about that time onwards the adult birds more and more frequently break incubation. Bones and the first down develop at the same time and on the 10th—11th day of development the embryo hardly differs from a one-day-old chick (Portmann, 1950; Fig. 373). Just before hatching the organism develops a tendency to homoiothermism and this is probably why the parents cannot leave the nest for rather a long time without harm to the chicks enclosed in the eggs.

3. Feeding of the Young

The young hatch on the average after 13 days of incubation. They do not hatch all at the same time; one or sometimes even two of them emerge a day later. The last day of incubation therefore coincides with the first day of feeding and for this reason I include it in both these periods of breeding. The feeding of the young went on for about 21 days. My observations on the intensity of feeding however covered only the first 13 days of their life, because 2-week-old nestlings, leaning out of the entrance of the nest-box, jostled against the switch-lever and thus caused a remarkable increase in the records.

The nursing period is characterized, above all, by an evident rise in the activity of the adults. The males, which still in the previous period sang in the vicinity of the nest, are completely silent now. The birds are busy feeding the young all day long, from dawn till dusk. The mean number of entries into the nest, being 283 per day, is considerably higher than in the other periods of breeding, but, as in those periods, the number of entries per day is not the same for all the successive days of the feeding period. The course of the activity curve for this period is shown in the graph in Fig. 2 C.

In the first 2—3 days of life of the young the frequency of feeding is not great and approximates to the number of entries into the nest in the last days of incubation. A gentle passage from the period of incubation to that of feeding can well be seen in particular pairs of Starlings (Fig. 4). The low initial fre-

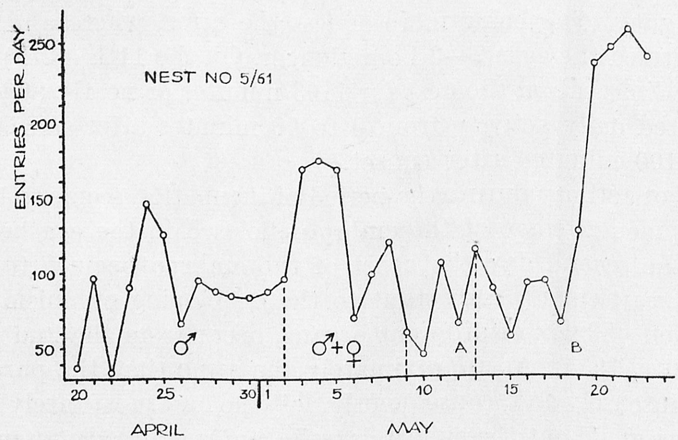

Fig. 3. An instance of the activity course in one of the Starling pairs observed. For explanation see Fig. 2

quency of feeding is probably caused by the fact that one- or even two-day-old Starlings take very little food, as they still avail themselves of the supplies stored in the yolk sac. After 3—4 days of life of the young the frequency of feeding begins to increase, which is due to their intensifying hunger caused for the most part by the exhaustion of the yolk supplies, the growth of body and the development of plumage. The greatest absolute increase in the body weight of nestlings was recorded between the 5th and 9th day. From about the 7th day onwards the female does not warm the young at night.

A peak of intensity of feeding occurs about the 10th day of life of the young ($s = \pm 2.15$ days) and is followed by a decrease in the activity of the parents. This decrease need not imply a reduction in the total amount of food brought to the nest, because now the large nestlings can swallow much bigger morsels. Nevertheless, the fact is that the frequency of feeding is evidently lower.

The intensity of feeding of the young depends not only on their age but also on the size of the brood. There is a visible regularity: the more nestlings in the nest the larger is the total number of feedings (Table III). However, the rise

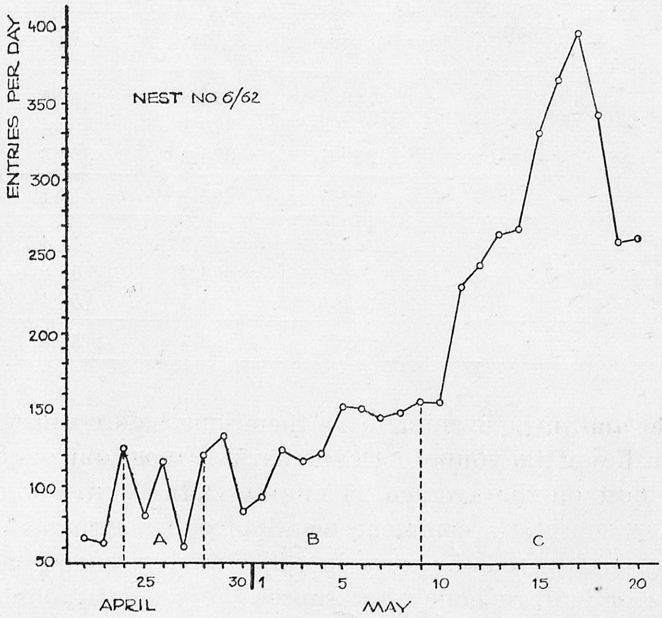

Fig. 4. An instance of the activity course in one of the Starling pairs observed. For explanation see Fig. 2

in the number of feedings is not directly proportional to the number of nestlings in the nest. If we analyse the number of feedings falling to one nestling, it naturally appears larger in a small brood than in a large one. In this case the number of feedings per nestling is inversely proportional to the production of heat by the nestling; in small broods this production is considerably greater than it is in very large broods (MERTENS, 1969). In broods composed of 4 and 5 young Starlings the difference in the number of feedings per nestling is far smaller than that in broods of 5 and 6. This seems to confirm the generally accepted opinion that in our environmental conditions the optimum size of Starling broods is 4 or 5 chicks.

In the period of feeding of the young, Starlings are active on the average for 15 hours per day. This is a mean value calculated for the first 15 days of nursing. During the first 7—8 days of life of the young the daily time of feeding exceeds the mean. This is so, because the one which begins and ends the daily nursing activity is the female, which remains in the nest for the night. At that time the feeding of the young begins more or less at sunrise and ends just before sunset. The males, which roost out of the breeding colony, come to the nests

Table III

The number of feedings per day for the whole brood (a) and that calculated for one nestling (b) relative to the age and number of nestlings in the nest

	Day of feeding	Number of feedings per day		
		4 juv.	5 juv.	6 juv.
a	1— 5	186,4	226,3	248,5
	6— 9	275,1	340,7	364,4
	10—13	290,5	326,6	332,3
	1—13	250,7	297,7	315,1
b	1— 5	46,6	45,3	41,4
	6— 9	68,8	68,2	60,8
	10—13	72,8	65,3	55,4
	1—13	62,7	59,5	52,5

somewhat later and in the evening leave them long before sunset. From about the 8th day of life of the young both the parents roost out of the colony and appear at the nest on the average 20 minutes after sunrise and end feeding 25 minutes before sunset, the commencement of feeding occurring more regularly than its ending. I observed the cases in which feeding ended even more than an hour before or half an hour after sunset. Very similar observations have been published by Kluijver (1933), and Keil (1963) writes that he incomparably more often saw the first feeding occurring before sunrise (58% of observations) than after it (2%), the number of the first feedings coinciding with sunrise forming 40%.

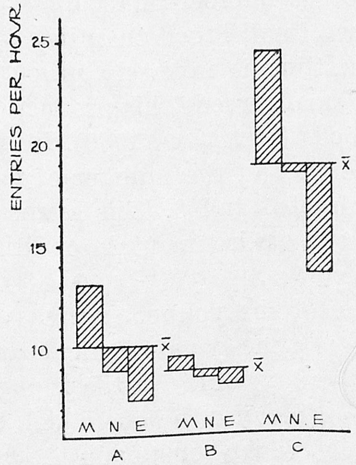

Fig. 5. Frequency of entries into the nest in three main parts of the daytime. M — from dawn to 10 a. m., N — from 10 a. m. to 2 p. m., E — after 2 p. m. For other explanation see Fig. 2

As in the period of incubation, the frequency of entries into the nest is marked by a constant fall with time. The fall is steepest after 6 p. m. (Table II), when the breaks in feeding become longer and longer. In the morning hours the intensity of feeding is highest, the number of feedings per hour exceeding the daily mean (Fig. 5).

Observations show that, though each pair of birds behaves differently, most of them feed much more intensely in the morning, and the highest intensity of feeding generally occurs in the early morning hours.

The changes in the intensity of feeding of the young in the successive days of their stay in the nest may be connected with the development of homoiothermism. Homoiothermism is still poorly developed in 2—3-day-old nestlings of passerines (KENDEIGH and BALDWIN, 1928; NEKRASOW, 1966), their power of temperature regulation being very little. In the first four days of life the body temperature of nestlings fluctuates within a range of 6°C according to air temperature (NEKRASOV, 1966). The nestlings receive the amount of heat necessary for life mainly from their parents, especially the female, which keep warming them fairly persistently (hence a small number of entries) and, consequently, both the yolk and food brought by the adult birds are almost completely used for body building. Thus, in spite of the relatively low intensity of feeding and at the same time the small amount of food given to the nestlings, their body weight increased by nearly 53% within the first three days of life (BOGUCKI, in prep.). According to NEKRASOV (1966), about the 5th ot 6th day of life the body temperature becomes settled about 40°C and the fluctuations range only between 0.3 and 1.1°C both ways. From about the 8th-9th day of life the nestlings of passerines have their temperature regulation completely stabilized and their organs and feathers well developed; then, while the body ceases growing, the food brought to the nest and ingested by the young is used for the most part to meet the energy requirements and only to a small extent to develop the organs. I found a loss in the body weight of nestlings before their departure from the nest (BOGUCKI, in prep.) and it seemed to be related to the lowering frequency of feeding. A decrease in the number of feedings towards the end of the stay of Starling chicks in the nest was also recorded by KLUIJVER (1933) and PROMPTOV (1940).

The dependence of the intensity of feeding on the number of chicks in the nest has also been confirmed by the results obtained, among other authors, by KLUIJVER (1933), ŁĄCKI (1962) and SEEL (1969).

On the basis of a parallel investigation on the diet of Starling nestlings I have ascertained that the number of feedings is proportional to the volume of food brought to the nest (BOGUCKI, in prep.). Hence, it may be supposed that the nestlings of small broods should be better nourished and, in consequence, grow faster than those of large broods. I have stated above that the greatest intensity of feeding coincides with the cessation of increase in the body weight of nestlings. The nestlings of small broods, being better nourished, should, in theory, attain the moment of cessation of weight increase earlier or the above-mentioned culmination of intensity of feeding should occur here in advance of that in large broods. However, as will be seen from the graph in Fig. 6, in broods of 4 chicks, and so better nourished, this peak occurs later (on the 10th—13th day of feeding) than it does in broods of 6 chicks or worse nourished ones (on the 6th—9th day). The materials illustrating the general development of chicks show no visible differences in development rate between the chicks

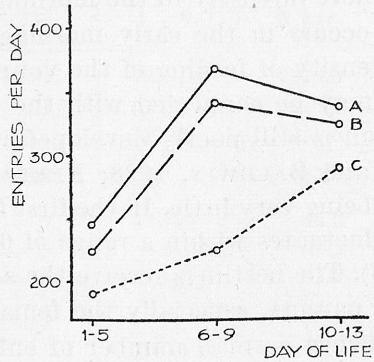

Fig. 6. A general course of nestling feeding in broods of various size. A — 6 nestlings (mean from 4 nests), B — 5 nestlings (10 nests), 6 — 4 nestlings (2 nests)

of the two types of broods. The literature of this subject (e. g., DUNNET, 1955; DELVINGT, 1962) also reflects the general opinion that under favourable nutritional conditions there are no significant differences in weight between the chicks of large and small broods. The nutritional conditions of the Starling colony under study were more or less typical, which is indicated by the quite normal bodily development of the nestlings examined. It is impossible to solve this problem on the basis of the materials that I have collected and research methods that I have had at my disposal and for this reason I leave it without an attempt at explanation.

The causes of the grater intensity of feeding in the morning than in the afternoon are in some measure elucidated by the fact described by KLUIJVER (1933). He observed the greatest afternoon fall of activity (from 22 to 9 feedings per hour) in a nest with 2 chicks. This pronounced decrease in the intensity of feeding was probably connected with the satiation of the young. Many a time in the afternoon I saw old birds carry food that they had brought before out of the nest and eat it up, this being particularly often observed at nests with small numbers of chicks. Apparently the young had already been satiated and refused to receive food. Afterwards the old birds did not feed them for a fairly long time. This shows that the intensity of feeding of the young is also dependent on the degree of their satiation and is regulated by the nestlings themselves. The young birds are hungriest after the night and it is then that they receive largest amounts of food. In the evening, after more or less intense daylong feeding, the chicks are satiated, demand food much less importunately and the old birds bring it to the nest at much longer intervals.

4. Discussion

The values of standard deviation and coefficient of variation, presented in Table I, are so great that they virtually disqualify the mean numbers of entries into the nest from the standpoint of statistics. The same is also reflected by the maximum and minimum values given in this table. For example, on the day of laying of the fourth egg the minimum number of entries recorded was 14 and the maximum one as many as 226. Hardly 20 data are contained within this range, which fact is responsible for so great a standard deviation and coefficient of variation. The means, however, despite the above-mentioned inaccuracy, truthfully render the general nature of the activity course in particular periods and days of breeding. In spite of the marked standard deviation the shape of the curve representing the mean numbers of entries is, in general, consistent with the tendencies recorded for particular pairs of Starlings, which is best illustrated by two instances of activity course observed in two chosen pairs of Starlings (Figs. 3 and 4).

The coefficient of variation calculated for the 24-hour cycle is, like that for periodical activity, very high and ranges between 30 and 40%. The maxima and minima of daily activity and also the complete lack of entries into the nest occur at any times of day and for this reason they have not been included in Table II. The means cannot therefore be treated as absolute values representative of all the pairs of Starlings, because these values may fluctuate within limits of 30—40%.

The results of the studies on the intensity of feeding of the Starling young carried out so far are listed in Table IV. There are great differences between the results obtained by the quoted authors.

The average number of feedings calculated from 246 records, covering all day each, amounts to 283 and lies within the limits given in literature (118—350), although it is somewhat higher than the mean calculated on the basis of different reports. The same value calculated in another way, as the sum of the average numbers of feedings in 2-hour periods, is 292 entries per day (Table II). The difference of 9 antries forms hardly 3% of the values presented and practically these two values little differ from each other. If it is besides taken into consideration that either of them has been calculated from entirely different data, the result obtained, in spite of the differences mentioned, should be regarded as compatible.

The mean number of feedings per hour (calculated on the basis of 1166 observations) is 18.8, in approximation, 19. This means that a bird flew to the nest with food every 3.1 minutes. This is an average frequency for the first two weeks of life of the young and, as will be seen from the graph (Fig. 2) illustrating the activity course in this period, in the first two days of life of the young it is much lower than about the 10th day of feeding, when in turn it is higher than the average.

Keil (1963) considers 13 entries per hour to be the maximum frequency

Table IV

Comparison of the numbers of feedings per Starling pair per day

Author	Number of nests examined	Duration of observations	Day of life of nestlings	Mean number of entries into nest
Author's own investigation	25	246 days	1—13	283
KALAMBACH, GABRIELSON (1921)	?	?	?	118
PFEIFER, KEIL (1962)	1	?	?	133
KEIL (1963)	3	3 days	?	136*
PROMTOW (1940)	1	8 days	9—16	155*
KALMBACH (1928)	?	?	1—20(?)	156*
NEWSTEAD (1908)	1	17 h	?	169
HASSEL (1961)	1	5,5 h	?	219*
BUSSMANN (1929)	1	1 day	3	242
KLUIJVER (1933)	3	52 days	1—21	320*
SOKOŁOWSKI (1953)	1	1 day (?)	?	332
COLLINGE (1908)	?	?	?	350
Mean (excluding own results)				218 (118—350)

* converted by the author

of feeding in Starlings, the average value being 8 feedings per hour. According to him, feedings normally occur one every 5 to 10 minutes. It is not given in the paper in what period of life of the young his investigation was carried out, but judging by the small values generally offered by him, it must have covered the first days of feeding, when, as I have mentioned above, the lowest frequency of arrivals of birds carrying food was observed.

SZIJJ (1957) states that a Starling nestling is fed 6.4 times per hour in the morning, 9 times at noon, and every 20 minutes in the evening.

The best example of differences in behaviour between individual pairs of Starlings is the juxtaposition of their activites recorded in different nests on the same day (Fig. 7). For this comparison I chose a day (12 May 1962) with average weather conditions of the feeding period of Starlings in the Poznań region (mean air temperature — 13.3°C, rainfall — 6 mm., insolation — 7.5 hours). In some pairs the maximum frequency of entries fell in the morning (nests Nos. 3 and 4), in others in noon hours (Nos. 2 and 7) or even just before sunset (No. 9). Differences in the behaviour of the pairs observed at the same time and therefore under the same weather conditions indicate the lack of a definite response to average weather conditions (moderate rainfall, small cloudiness, average temperature) or individual responses of each pair to these factors.

No strictly fixed activity rhythm is observed in particular pairs. The same pair of Starlings shows completely different daily rhythms on particular days. Examples of activity of one and the same pair of Starlings on four days chosen at random are presented in the graphs of Fig. 8. These examples indicate lack of a fixed internal rhythm, at least as regards the daily activity course, in a Starling pair.

Attempts to classify activity types are often met with in literature. Aschoff 1957), for instance, writes about bi- and tripartite activity. However, as will

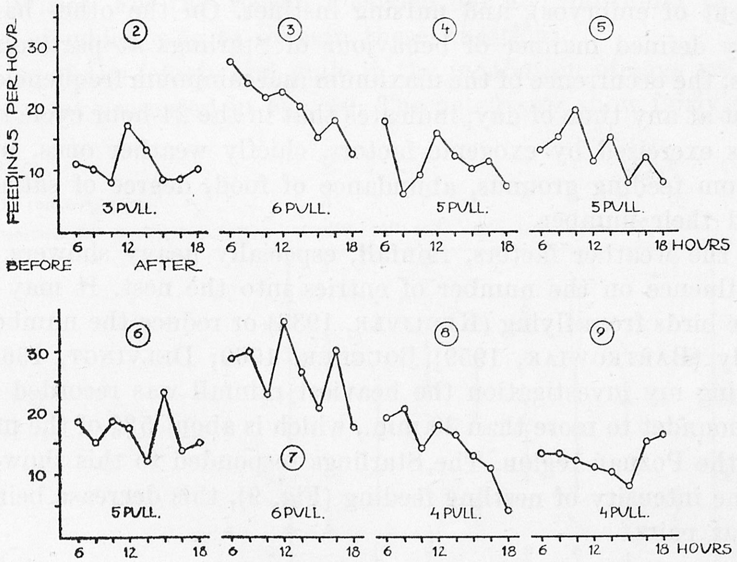

Fig. 7. Intensity of nestling feeding in 8 nests on 12 May 1962

be seen from the foregoing considerations, this classification can be applied only to interpret the activity course in individual specimens or pairs. If a copious material of data concerning even the same population has been summed up,

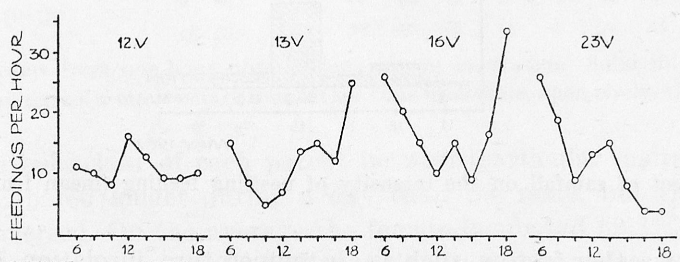

Fig. 8. Intensity of nestling feeding in nest No. 2 on four days chosen at random in 1962

the individual differences will completely or nearly completely neutralize each other and the curve representing such activity will be void of any major swings. The addition of the data allows a more general approach to this phenomenon and, above all, either the elimination of the influence of exogenic factors or the determination of their influence range.

The fact that the activity course in the three stages of breeding is more or less identical in individual pairs of Starlings, although it differs in absolute values, suggests that the decisive factors inducing a given activity are endogenic factors, mainly the psychic and physical conditions of birds — already mentioned before — associated with the production and laying of eggs, their incubation (development of embryos), and nursing instinct. On the other hand, lack of any strictly defined manner of behaviour of Starlings at particular times of day, that is, the occurrence of the maximum and minimum frequencies of entries nto the nest at any time of day, indicates that in the 24-hour cycle the decisive influence is exercised by exogenic factors, chiefly weather ones, but also the distance from feeding grounds, abundance of food, degree of satiation of the young, and their number.

Out of the weather factors, rainfall, especially heavy showers, exerts the greatest influence on the number of entries into the nest. It may completely prevent the birds from flying (Kluijver, 1933) or reduce the number of flights considerably (Bartkowiak, 1959; Boucher, 1960; Delvingt, 1963a; Łącki, 1962). During my investigation the heaviest rainfall was recorded on 14 May 1962. It amoundet to more than 30 mm., which is about 5% of the mean annual rainfall of the Poznań region. The Starlings responded to this shower by a decrease in the intensity of nestling feeding (Fig. 9), this decrease being different in particular pairs.

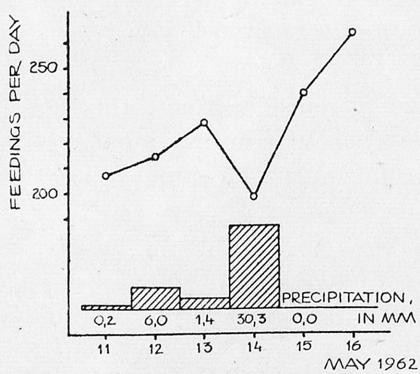

Fig. 9. Effect of rainfall on the intensity of nestling feeding (mean from 9 nests)

The other weather factors, such as air temperature, insolation, athmospheric pressure and winds, have only a slight effect on the rhythm of entries into the nest. In the period of egg incubation and in the first days feeding of the joung only a rather marked fall in air temperature may make adult birds warm their eggs or nestlings more intensely and, in consequence, reduce the number of entries per day (Delvingt, 1963a; Bartkowiak, 1959). Falls in temperature stop being bad for nestlings from about 6th—7th day of life and only in the case of exceptionally late spring ground frost the mortality of broods may be up te 75% (Mierzwiński, 1955).

IV. SHARE OF EACH PARENT IN THE INCUBATION OF EGGS AND FEEDING OF THE YOUNG

The results obtained with the use of mechanical counters of entries into the nest do not allow any conclusions as to the shares of the male and female in given activities. For this reason I carried out an additional investigation, the purpose of which was to explain these questions.

The shares of the female and male in the incubation of eggs are illustrated by the actograms presented in Fig. 10. The actograms show fairly great diffe-

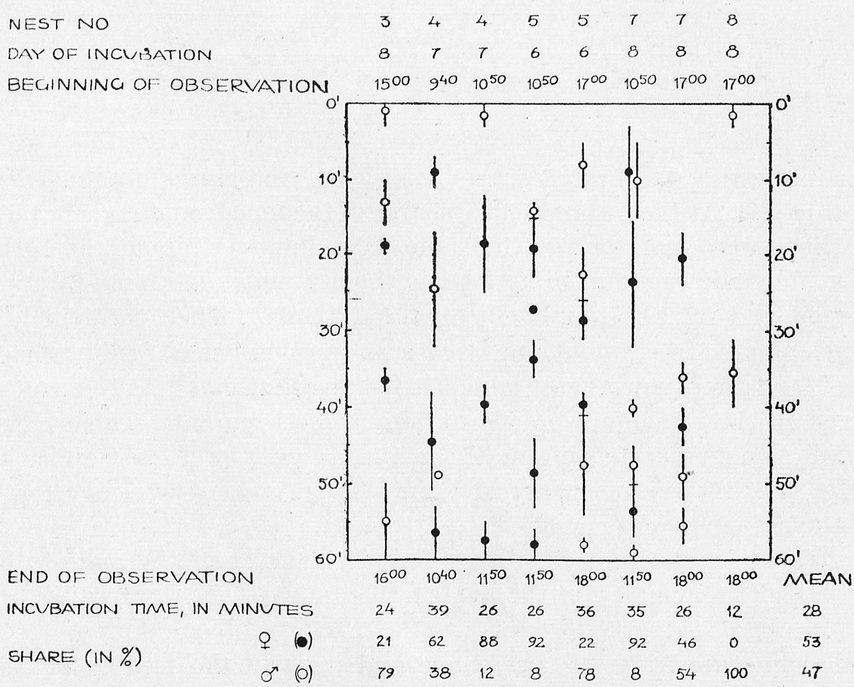

Fig. 10. Actograms from one-hour observations of egg incubation. Solid lines represent the time of egg warming, solid circles mark incubation done by female, open circles that done by male

rences in the behaviour of each parent between particular pairs. The female generally incubated longer during a day than the male, but the situation is sometimes reversed. On the average the female incubated 52.8% and the male 47.2% of the eight-hour period of observation in the day-time. At night (about 9.5 hours) eggs are warmed exclusively by the female, which therefore does 80% of incubation in all. Males incubate most zealously early in the morning and in the evening, females at night and partly in the middle of day. This is so because females forage most intensely in the morning (after night) and towards the evening (before night) and then they must be replaced by the males.

In the period of nestling feeding the distribution of activities according to sex is somewhat similar. The 21-hour direct observation of the Starling nests showed that nearly 55% of the feeding was done by the females and about 45% by the males (Table V). Excluding an extreme case of abandonment of the nest by the male, it may be assumed that the share of either parent in the feeding of the young is approximately equal in Starlings, though the female feeds more regularly and persistently than the male.

Table V

Shares of female and male in the feeding of young Starlings

Number of feedings	Female		Male	
Mean	8,3	54,9%	6,8	45,1%
Minimum	3	30,4%	0	0,0%
Maximum	14	100,0%	16	69,6%

An interesting example is presented by the actograms obtained from nest No. 3 (Fig. 11). At the beginning the shares of the female and male in the feeding of nestlings were more or less the same, later however (about the 10th day of feeding) the male began to bring food to the nest more and more rarely to leave the brood and female completely on the 12th day. Then the female fed the nestlings alone. Moreover, it appeared that the number of feedings had hardly changed and the frequency at which it fed the nestlings was the same as that observed in the remaining broods nursed by both parents. This suggests that the adult birds, when feeding nestlings, do not use the utmost effort but have a fairly great reserve of energy and time left, which is necessary for them to meet their own requirements.

In another nest (No. 8) I always found the share of the male to be larger than that of the female (on the average 66 and 34% of the feedings, respectively).

Although the shares of the female and male in the feeding of the young are nearly the same, the time either of them stays in the nest, while feeding the nestlings, is different. The feeding female stays in the nest on the average 22.6 sec. (mean from 314 measurements), the male only 16.4 sec. As the nestlings grow up, the time of the parents' stay in the nest becomes evidently shorter and shorter (Table VI). In the first 5 days of feeding the female stays in the nest on the average 2.5 times as long as the male does, but as early as the following 4 days this difference decreases visibly, and about the 10th day it practically disappears altogether (male — 11.6 sec., female — 12.1 sec.). The reduction in the time of stay in the nest is therefore far more distinct in the female (from 66.1 to 12.1 sec.) than in the male (from 25.9 to 11.6 sec.). This is due to the fact that the female warms the nestlings, cleans their feathers and removes faeces, and is generally in charge of them — especially in the first days of their life — more often than the male is.

The results of observations concerning the behaviour of males and females separately are too scanty to allow any far-reaching conclusions as to their shares

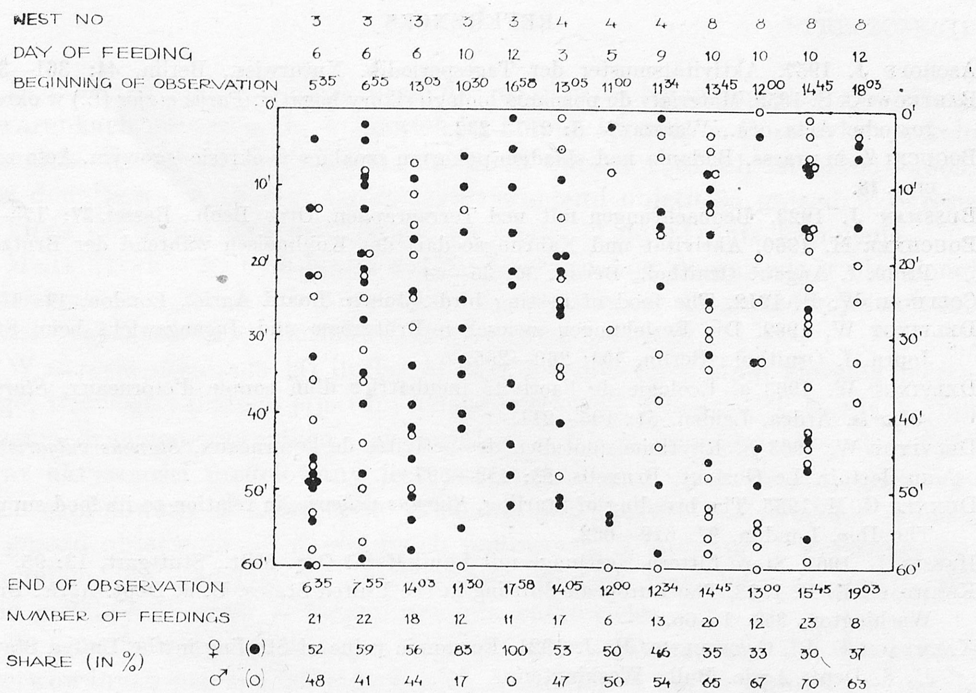

Fig. 11. Instances of actograms from one-hour observations of nestling feeding. Solid circle — feeding done by female, open circle — feeding done by male

Table VI

Time of stay of an adult Starling in the nest during a single feeding of nestlings

Day of life of nestlings	Number of measurements	Time of stay in nest, in sec.		
		Male	Female	Parents
1— 5	64	25,9	66,1	45,4
6— 9	132	15,2	26,0	21,2
10—12	118	11,6	12,1	11,9
1—12	314	16,4	27,8	22,6

in the rearing of nestlings. However, there are rather great differences also in this respect between individual pairs, just as they occur between the joint activities of these pairs.

Differences in behaviour between the Starlings observed by me as well as great divergencies of the observations made by other authors indicate that the question of the share of either sex in the feeding of nestlings needs elaboration of large series of observations.

Translated into English
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STRESZCZENIE

Badania nad aktywnością szpaków w okresie lęgowym przeprowadzono w warunkach naturalnych, w niewielkiej kolonii lęgowej w Puszczykowie koło Poznania. Badania terenowe prowadzono w okresie czterech lat (1960—1963) oraz dodatkowo w 1966 r. Ogółem obserwacjami objęto 25 gniazd w okresie od kilku dni przed złożeniem pierwszego jaja aż do 14 dnia karmienia.

Miarą aktywności była liczba wlotów pary szpaków do gniazda w określonej jednostce czasu (dzień lub 2 godziny). Liczbę wlotów do gniazd rejestrowano mechanicznie używając liczników elektromagnetycznych.

W okresie składania jaj liczba wlotów do gniazda w dniu złożenia pierwszego, trzeciego i piątego jaja (dni nieparzyste) była zawsze większa niż w dniu złożenia drugiego, czwartego i ewentualnie szóstego jaja (dni parzyste). Taki obraz aktywności modelowany jest prawdopodobnie przez samicę, gdyż jest ściśle skorelowany z kolejnością składania jaj. Największe nasilenie wlotów do gniazd obserwuje się w godzinach porannych, w południe i wczesnym popołudniem. Po godzinie 16 częstotliwość wlotów raptownie zmniejsza się, a po godzinie 18 ruch w kolonii zamiera całkowicie.

W okresie wysiadywania jaj daje się zauważyć wspólny dla wszystkich obserwowanych par spadek aktywności. Najmniejszą liczbę wlotów zarejestrowano od 3 do 6 dnia wysiadywania, a więc wtedy, kiedy w zarodku formują się szczególnie ważne narządy. Po tym spadku następuje stały wzrost liczby wlotów do gniazda. Aktywność dzienną rozpoczynają samice około 10 minut po wschodzie słońca. W okresie wysiadywania nie obserwuje się znaczniejszych szczytów aktywności związanych z określonymi porami dnia. Najwięcej indywidualnych dla każdej pary szczytów aktywności zanotowano w godzinach południowych (silna insolacja rozgrzewa skrzynki i ptaki nieustannie z niej wychodzą). Ruch w kolonii ustawał około 25 minut przed zachodem słońca.

Okres karmienia piskląt charakteryzuje przede wszystkim wyraźnie zwiększona aktywność dorosłych ptaków. Przeciętna wlotów do gniazda wynosi 283. Częstotliwość wlotów jest w pierwszych dniach życia piskląt najmniejsza, następnie mniej więcej do 10 dnia wzrasta, a potem nieznacznie lecz stale maleje. Średnia ilość wlotów do gniazda przypadająca na jedno pisklę jest odwrotnie proporcjonalna do liczby piskląt. Częstotliwość wlotów do gniazda w ciągu dnia charakteryzuje się stałym spadkiem w miarę upływu godzin karmienia. Największą intensywność karmienia obserwuje się przed południem, chociaż niektóre pary najczęściej karmiły wieczorem. Intensywność karmienia w znacznym stopniu zależy od nasycenia piskląt.

Obliczone wartości standardowego odchylenia i współczynnika zmienności są duże, wskazują na to, że istnieje bardzo duże zróżnicowanie w zachowaniu się poszczególnych par. Nie można więc obserwacji jednej pary uogólniać jako reguły dla całego gatunku.

W tym samym dniu różne pary szpaków karmiły z różną intensywnością, a szczyty aktywności nie przypadały w tych samych porach dnia. Z drugiej

strony jedna i ta sama para szpaków w kilku kolejnych dniach nie wykazywała jakiegoś utartego wzoru aktywności. Można stąd wnioskować, że przebieg aktywności w poszczególnych porach dnia zależny jest przede wszystkim od czynników egzogenicznych (np. opadów deszczu), natomiast liczba wlotów w ciągu całego dnia i przebieg aktywności w poszczególnych wyróżnionych okresach lęgu zależeć będzie głównie od czynników endogenicznych.

Udział samca i samicy w wysiadywaniu jaj w ciągu dnia jest mniej więcej jednakowy, lecz w nocy wysiaduje wyłącznie samica. Udział obu partnerów w karmieniu piskląt jest również mniej więcej jednakowy, jednakże samica karmi bardziej równomiernie i wytrwalej niż samiec. Jeden z lęgów był karmiony tylko przez samicę; okazało się, że liczba wlotów do gniazda nie odbiegała tu od przeciętnej dla całego materiału. Dość znaczne różnice obserwuje się w czasie pozostawania ptaków w gnieździe podczas jednorazowego karmienia. Daje się zauważyć znaczne skrócenie czasu pobytu rodziców w gnieździe w miarę rozwoju piskląt. Skrócenie czasu przebywania w gnieździe jest znacznie wyraźniejsze u samicy (z 66 sek. do 12 sek.) niż u samca (z 26 sek. do 12 sek.). Udział samca i samicy w wysiadywaniu jaj i karmieniu piskląt podlega równie dużej zmienności indywidualnej jak aktywność.

РЕЗЮМЕ

Исследования активности скворцов в гнездовой период проведено в естественных условиях, в небольшой выводковой колонии в Пущикове около Познани. Полевые исследования проведено в период с 1960—1963 и добавочно в 1966 гг. Наблюдениями охвачено 25 гнёзд в периоде от нескольких дней перед откладкой первого яйца до 14 дня кормления.

Мерой активности было количество влётов пары скворцов до гнезда в определённый период времени (один день или 2 часа). Количество влётов регистрировано механически, применяя при этом электромагнетических счётчиков.

В период откладки яиц количество влётов до гнезда в день откладки первого, третьего и пятого яйца (нечётные дни) было всегда большее, чем в день откладки второго, четвёртого и иногда шестого яйца (чётные дни). Такая картина активности, по всей вероятности, была моделирована самкой, так как она тесно коррелирует с последовательностью откладки яиц. Наибольшая интенсивность влётов наблюдалась в утренние часы, во время обеденных и в начальный период послеобеденных часов. После 16 часов частота влётов резко уменьшается, а после 18 часов движение в колонии совсем замирает.

В период высиживания можно заметить, общее для всех наблюдаемых пар, падение активности. Наименьшее количество влётов зарегистрировано с 3 по 6 день высиживания, то есть тогда, когда в зародыше формируются особенно важные органы. Дневную активность начинают самки около 10 минут после восхода солнца.

В период высиживания не наблюдается более значительных увеличений активности, связанных с определённым временем дня. Наибольшее количество индивидуальных для каждой пары пиковых активностей отмечено в обеденные часы (сильная инсоляция разогревает скворечники и птицы постоянно из них выходят). Движение в колонии останавливается около 25 минут до заката солнца.

Период кормления птенцов характеризуется прежде всего увеличенной активностью взрослых птиц. Среднее количество влётов составляет 283. Частота влётов наблюдалась в первые дни жизни птенцов небольшой, затем более менее возрастала до 10 дня, а затем незначительно но постоянно уменьшается. Среднее количество влётов на одного птенца обратно пропорционально количеству птенцов. Частота влётов до гнезда характеризуется постоянным падением, по мере истечения времени кормления. Наибольшую интенсивность кормления наблюдали перед обедом, хотя некоторые пары наиболее часто кормили вечером. Интенсивность кормления в значительной степени зависит от насыщения птенцов.

Подсчитанные значения стандартного отклонения и коэфициента изменчивости довольно большие, указывают на то, что существует очень большая дифференциация в поведении отдельных пар. Нельзя наблюдения за одной парой обобщить как правило для всего вида.

В один и тот же день, различные пары скворцов кормили с различной интенсивностью, а пики активности не совпадали по времени. С другой стороны, одна и та же пара скворцов в несколько последовательных днях не обнаруживала постоянного образца активности. Отсюда следует, что течение активности на протяжении дня зависит прежде всего от экзогенических факторов (нпр. атмосферных осадков), зато количество влётов в течени целого дня и ход активности в отдельные периоды высиживания зависит от эндогенных факторов.

Удел самца в высиживании яиц в течении дня почти одинаковый, но ночью сидит только самка. Как самец, так и самка кормят почти в одинаковой степени, но самка кормит более равномерно, чем самец. В одном случае кормление производилось только самкой. Оказалось, что количество влётов до гнезда не отличалось от среднего для всего материала. Довольно значительные разницы наблюдались во время пребывания птиц в гнезде во время одноразового кормления.

Можно заметить значительное сокращение времени пребывания родителей в гнезде по мере развития птенцов. Сокращение времени пребывания в гнезде более заметно у самки (с 66 сек. до 12 сек.), чем у самца (с 26 сек. до 12 сек.). Участие самца и самки в высиживании яиц и кормлении птенцов также подлежит большой индивидуальной изменчивости, как и активность.

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