
NESTING BIOLOGY AND ONTOGENESIS OF URBAN SWALLOWS
IN THE NORTH OF THE RANGE (KAMA FOREURALS)

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ABSTRACT: The relevance of the research is related to the lack of studies on the breeding characteristics of birds nesting at the boundaries of the range and the early stages of the ontogenesis of chicks. The study of the nesting biology and early ontogenesis of urban swallows in the Kama Foreurals (the north of the range). The rate of oviposition was studied with the help of dated clutches, the stage of the development of embryos was determined by A.I. Shurakova's method for passerine birds and the stage of the brood patch was identified according to D.S. Lyuleeva. The authors obtained materials on the phenology of the reproduction of urban swallows; morphology; the dynamics of the development of the brood patch; the rate of embryonic development, and the age difference of the embryos in the period of oviposition. Urban swallows fly to the north of the range in late May and early June. The mass nest building begins in early June. Oviposition takes place within a short period. The dimensions of the eggs in the clutches increase by the middle of the cycle and decrease reliably at the end. Intermittent breeding leads to the heterochronicity of embryonic development. The age difference of embryos ranges from 1.0 to 2.5 days. The development rate of embryos from eggs of lower temporal levels is slowed down, which is related to the behaviour of birds on the nest, as well as structural changes in the brood patch.

KEYWORDS: Urban swallow; reproduction; early ontogenesis; heterochronicity; age difference in embryos; north of range

INTRODUCTION

The problems related to the reproduction of birds remain quite relevant in modern ornithology. Fragmentary studies are devoted to the peculiarities of the reproduction and early stages of the ontogenesis of chicks, semi-chicks, and semi-breeding chicks, as well as the breeding of birds nesting at the boundaries of the range. There is no experimental data on the possibilities of normal development of

embryos for a wide range of mean daily temperatures^{7,13,16,20,23,29}.

There are few publications on the double and second oviposition of birds in the development cycle, and there are no detailed studies on the rate of embryonic development during egg-laying and in the subsequent stages of incubation, on its variability, as well as the value of age difference in chick^{4,6} emphasize a number of unresolved problems related to the reproduction and

early ontogenesis of birds.

All the materials on the phenology of the arrival, nest-building, oomorfology, main and doubleoviposition of urban swallows were obtained for this region for the first time. In the general biological aspect, the novelty of the research is related to the data on the study of the age difference and the rate of embryonic development in urban swallows as a closed-breeding bird at the northern boundary of the range within the Kama Foreurals.

The object of the research is the urban swallow (*Delichonurbica*) inhabiting the northern border of the range (Kama Foreurals).

The research questionis related to the nesting biology and early ontogenesis of urban swallows in the north of the range.

The purpose of the research was to study the nesting biology and early ontogenesis of urban swallows at the northern boundary of distribution in the Kama Foreurals.

Research aims: 1) to study the phenology of the arrival, nest-building, and oviposition of urban swallows; 2) to identify the characteristics of the reproductive period and the oomorphological characteristics of eggs depending on their temporal rank, as well as the size of the main and double clutches; 3) to trace the dynamics of the

development of a brood patch in an urban swallow depending on the stage of the nesting cycle; 4) to study the rate of embryogenesis and the age difference of the embryos of urban swallows during the period of oviposition.

The works of a number of domestic and foreign scientists are related to fundamental studies of biology, ecology, and the early ontogenesis of swallow-birds. D.S. Lyuleeva (1974)¹¹ studied the ecology of urban swallows nesting in the Curonian Spit. The mass ringing of birds of this species showed that about 38% of old

specimens live in their microcolony (at 100-300 m from their old nest), 11% settle in 500-1000 m from their former microcolony, and 5% occupy the same nest as in the previous year. The percentage of young birds that return to their nesting sites was 9%, which is higher than in other species (the percentage of return rarely exceeds 5% of the total number of birds).

Among foreign researchers who studied the biology of swallows, are Peterson in the USA, Lind in Finland, Gunten and Sieber in Switzerland, Vietinghott-Riesch and Menzel in Germany, as well as Bryant and Turner in the UK.

Working with urban swallows in Switzerland, Gunten came to the conclusion that on the average, the

nesting colony of funnels included 55% local birds and 45% birds that flew from outside. According to Gunten, almost half of young urban swallows breed away from the maternal colony, and there is a significant exchange between the settlements in the neighbouring villages. Swallows of different populations especially mix in the post-nesting period when a wide movement of birds begins.

The size of clutches of urban swallows ranges from 3 to 5 in different parts of the range. The eggs are predominantly white. For urban swallows, one cycle of reproduction is common in the reproductive period.

Many researchers who studied the behaviour of birds during breeding noted the participation of males in the process of incubating eggs and heating hatched chicks. Lind points out that male and female urban swallows take equal part in egg hatching. According to D.S. Lyuleeva¹¹, male funnels are distinguished by their big attachment to their nest. In the period of incubation, they stay in their nests day and night just like females do. The frequent interchange of family partners allows maintaining the optimal temperature regime, eating, and protecting the nest.

Urban swallows' egg hatching starts with the first laid egg^{4,11}. A number of authors note the dependence of the duration of egg hatching on

weather conditions. According to Lind, daily incubation in urban swallows is 79-82.4% time of the day in cold summer and 89.4-98.6% in warm summer.

In her works, D.S. Lyuleeva¹¹ gives detailed characteristics of spring and autumn migration of swallows and shows the difference of spans on the effects of weather conditions (wind force, air temperature, rain, and fog).

It has been revealed that urban swallows are adjusted to rapid accumulation, conservation and economical use of energy resources maintained at a constant high level. In conditions of starvation, swallows use regulable nighttime hypothermia. Besides, swallows are characterized by adaptive behavioural congestion response, which helps to sharply increase energy saving and allows enduring difficult conditions (cold snap, hunger).

The post-embryonic development of urban swallow chicks includes a detailed description of external morphological features, the growth rates of the individual parts of the body, as well as the changes in the weight of chicks. Three stages of the post-embryonic period of chicks' development have been identified. The main peculiarity of the first stage is the poikilothermic type of heat exchange. In the second stage, mechanisms of

chemical thermoregulation step in, intensive differentiation of plumage is observed, and the chicks reach a maximum mass. The third stage implies the preparation of chicks for flight²⁶.

In the literature on the group of swallows, the early ontogenesis is least studied. Besides, there is no data on the rate of the embryonic development during the period of egg-laying and in the subsequent stages of incubation, as well as on its variability and the value of age difference in chicks. The data on the peculiarities of the nesting life of urban swallows breeding in the north of the range is also fragmentary. The materials of this research are devoted to the above-listed issues.

MATERIALS AND METHODS

The data was collected in the Solikamsk (59.5⁰N) Region in the Perm Krai in 2010-2012. The rate of urban swallows' oviposition was studied with the help of dated clutches. The eggs set aside by birds in the order of demolition were labelled with a quick-drying paint. This was how the clutches were dated. The analysis of clutches was carried out taking into account the temporal rank of the eggs. The incubation days were counted from the time the last egg was laid. To study the dynamics of the onset of egg-laying, the authors counted the number of females that laid off their first egg. This method allowed tracing the stability or variability of the initial

stages of reproduction, establishing the length of the oviposition period, as well as revealing the period of the most intensive egg-laying.

The authors of the research collected data at intervals of 1 to 2 days. In their 1st to 12th stages of development, embryos were fixed in a 10% solution of formalin with the addition of glacial acetic acid, then stained with alcoholic boron carmine and placed in glycerin-gelatin. Starting from the third day of incubation, embryos were fixed in 10% formalin. The stages of the embryonic development were determined according to a scale developed for passerine birds⁴.

When analyzing the degrees of embryonic development on the first to the third days of incubation, the authors of the research took into account the value of the primitive streak, the segmentation of the axial mesoderm, and the state of the brain. In order to compare the age difference in clutches having a different number of eggs, the authors calculated the age-difference index as the ratio of the difference between the extreme variants of embryos and the number of eggs in a clutch, introduced by A.I. Shurakov and Y.V. Dyakonov⁴. When describing the stages of the embryonic development of birds, the authors used the terminology of H.A. Schmidt (a stage is a long-established unit of periodization based

on small changes in a body in the process of its development).

To describe and measure the brood patch in urban swallows, the authors of the research systematically caught them during nest-building, egg-laying, and incubation. The stages of the brood patch were determined according to D.S. Lyuleeva¹¹.

In the statistical processing of the data, the differences in the arithmetic mean were considered reliable if $t \geq 2.0$ ($p = 0.05$).

RESULTS AND DISCUSSION

Climatic peculiarities of the research region

The climate of the Perm Region is moderately continental. Seasonal differences in temperature and other climatic factors affect the phenological peculiarities of living and inanimate nature (migration and nesting, hibernation, molting, reproduction of animals, opening and freezing of water, flood, ice-freezing). In particular, with 3-5 daytime snow snaps accompanied by snowfall, swallows and swifts migrate to more southerly areas in late May and early June, while the chicks of other birds sharply slow growth or die.

Long-term phenological observations show that summer weather is established in the Urals from the time of the transition of the average daily temperature through 15°C . On the average, this happens between June 3

and 13, and between June 15-20 in the northern and eastern regions of the area. However, in the month of June, there is a possibility of frosts and a decrease in air temperature from minus 2 to 4°C in the western regions and from minus 5 to 8°C in the eastern mountainous regions. In the north, there is a possibility of frosts until June 10. The optimum timing of the reproduction of urban swallows is confined to the second decade of June after the summer weather is established, and the danger of frosts is eliminated.

The arrival of funnels to the north of the range is noted in the second-third decades of May, which is due to the appearance of flying insects that serve as the main source of food for them during this period.

Arrival, nesting, and egg-laying

In the vicinity of Solikamsk (59.50 N), a colony of urban swallows was found nesting on the wooden building of a floating pier.

According to the observations of the authors of this research, the arrival of funnels to the nesting sites is carried out in several stages. The advanced specimens were marked on May 11-12, while the mass arrival occurred at the end of May and the beginning of June.

Since June 3, birds started intensive mass nest-building, as well as repair and renovation of their last year's

nests. By June 5, the number of residential nests in the colony reached 144. Of these, the percentage of old nests was 57%, 14% of nests were repaired, and 29% were built by birds.

The construction of a new nest took 5-12 days ($\bar{x} = 8.0 \pm 0.67$ days, $n = 17$). The repair of dilapidated nest

shelters lasted from 4 to 9 days ($= 6.0 \pm 0.6$, $n = 12$).

The beginning of egg-laying by female funnels was observed on June 7-9. The bulk of birds began to lay eggs in the period of June 12-22. The peak of egg-laying was recorded on June 17-18, in the period of the actual summer weather in Forekama (Figure 1).

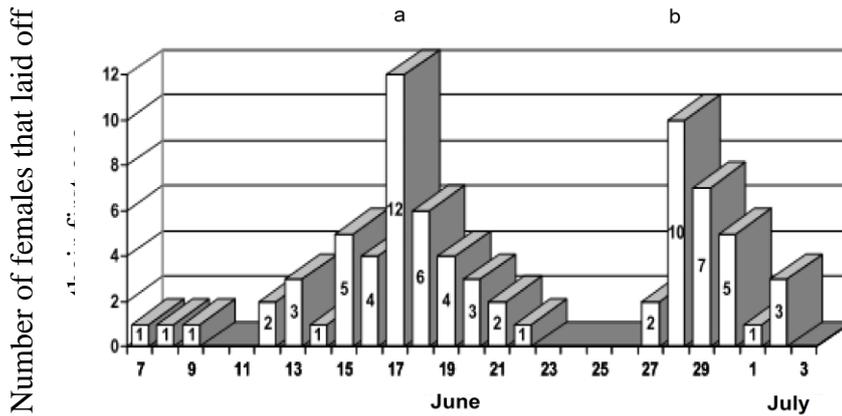


Figure 1. The dynamics of the oviposition beginning in urban swallows during the main (a) and double clutches (b).

Of the surveyed nests, 7.8% of birds had a three-egg clutch, 44.7% had four eggs, and 42.1% had five eggs

(Table 1). Most of the eggs were formed rhythmically.

Table 1. The Size of the Main and Double Clutches of Urban Swallows

| Clutch type | N | $\bar{X} \pm m$ | The number of clutches with the number of eggs, in% | | | | |
|-------------|----|-----------------|---|------|------|------|-----|
| | | | 2 | 3 | 4 | 5 | 6 |
| Main | 38 | 4.3 ± 0.10 | 2.7 | 7.8 | 44.7 | 42.1 | 2.7 |
| Double | 24 | 3.7 ± 0.11 | 4.2 | 25.0 | 70.8 | — | — |

Table 2. The Dynamics of the Mass of Eggs of Urban Swallows Within a Single Clutch

| Clutch type | Number of eggs in a clutch | Egg mass in the order of deposition, mg | | | | |
|-------------|----------------------------|---|------|------|------|------|
| | | 1 | 2 | 3 | 4 | 5 |
| Main | 3 | 1540 | 1690 | 1700 | — | — |
| | 4 | 1620 | 1620 | 1640 | 1610 | — |
| | 5 | 1570 | 1600 | 1630 | 1590 | 1550 |

| | | | | | | |
|---------------|---|------|------|------|------|---|
| Double | 4 | 1750 | 1830 | 1930 | 1510 | – |
|---------------|---|------|------|------|------|---|

The eggs were white. The mass of the eggs fluctuated in the range of 1330 mg to 1970 mg ($\bar{x}=1636 \pm 13.9$ mg, $Cv = 9,1\%$, $n = 112$). At the same time, the mass of the eggs varied within a separate clutch. With the increase in the temporal rank, the mass of the eggs increased from the first laid egg to the third one ($t=1.13$), which was followed by a decrease in their mass with unreliable statistical differences ($t=1.5$) (Table 2).

The length of the eggs varied from 17.8 to 21.3 mm ($\bar{x}=18.7 \pm 0.07$, $Cv = 4.4\%$), and the width varied from 12.4 to 14.0 mm ($\bar{x}= 13.3 \pm 0.03$, $Cv = 2.5$, $n = 112$). According to their form, three groups of eggs were distinguished: rounded (elongation index (EI) from 1.28 to 1.35) that constituted 17%; correct avoid (EI = 1.36 - 1.46) constituting 60.4%, and elongated (EI = 1.47 - 1.63) constituting 22.6%. (Table 3). Based on the above data, the avoid from was dominant.

After the loss of the main clutch, most females started a double clutch.

Characteristically, 54% of the double clutches contained fewer eggs than the main ones. All the five-egg clutches decreased by one or two eggs, while the four-egg clutches turned out to be more stable. Accordingly, the average number of the eggs per clutch decreased too (3.7 ± 0.57). In double clutches, four-egg clutches were dominant (70.8%), while three-egg clutches accounted for 25%, and the percentage of two-egg clutches was 4.2% (Table 1).

In the double clutches, the average mass of the eggs had a larger index than in the main ones (with statistical differences close to reliable $t=1,8$). No significant differences were observed in the length and width of the eggs ($t<1$) (Table 3).

In the Kama Foreurals, urban swallows have a single reproduction cycle in the reproductive period.

Table 3. The mass, length, and width of the eggs of urban swallows in the main and double clutches

| Clutch type | Number of eggs in a clutch | n | Weight of eggs, mg | | | Length of eggs, mm | | | Width of eggs, mm | | |
|-------------------------|----------------------------|-----|--------------------|---------|-----|--------------------|---------|-----|-------------------|---------|-----|
| | | | \bar{X} | $\pm m$ | Cv% | \bar{X} | $\pm m$ | Cv% | \bar{X} | $\pm m$ | Cv% |
| Main | 3 | 12 | 1675 | 33.4 | 7 | 19.3 | 0.20 | 3.9 | 13.1 | 0.08 | 2.1 |
| | 4 | 24 | 1687 | 30.4 | 8.8 | 18.8 | 0.17 | 4.4 | 13.3 | 0.07 | 2.5 |
| | 5 | 30 | 1663 | 17.2 | 5.7 | 18.4 | 0.18 | 5.3 | 12.9 | 0.10 | 4.1 |
| Double | 4 | 16 | 1746 | 28.8 | 6.6 | 19.2 | 0.17 | 3.4 | 13.3 | 0.04 | 1.3 |
| In total for the colony | – | 112 | 1636 | 13.9 | 9.1 | 18.7 | 0.07 | 4.4 | 13.3 | 0.03 | 2.5 |

Change in the brood patch during the breeding period

A brood patch is a useful inflammation of the skin accompanied by a fall of the feather cover, a change in the blood supply, cellular composition, intermediate dermis, and, possibly, a change in lymph circulation. This skin structure facilitates heat exchange between incubating birds and their eggs or chicks. On the example of passerine, D.S. Lyuleeva¹¹ noted a correlation between the stages of the nesting cycle (arrival, nest-building, egg-laying, incubation, etc.) and the stages of the development of a brood patch.

According to the research conducted by the authors of this article, the molting of down feathers in female urban swallows began 3 to 5 days before the first egg was laid. Initially, the area of the liberated part was 0.25 cm², then 1.0 cm², and 7 cm² by the

beginning of oviposition. The skin of the brood patch corresponded to the first stage. It was smooth, glossy and tightly fit the pectoral muscles and the abdomen. In the nests under investigation, the authors of the research observed one nested egg per nest (Table 4). By the middle of oviposition, the brood patch reached the second stage of development (a fine web of blood vessels was clearly visible). By the period of the completion of oviposition, the brood patches of females corresponded to the third stage. Small watery bubbles were visible on the surface, and the skin was embossed. During the actual incubation, the skin of the brood patch was characterized by puffiness. It was easily displaced, i.e. it was in the fourth stage of development. By the time of hatching chicks upon the denudation of the brood patch, a net of blood vessels covering the whole brood patch appeared on the surface of the

patch for a minute. In normal conditions, the skin looked edematous and had deep folds. The onset of the fifth stage in the development of the brood patch contributed to the greatest heat transfer during the incubation of eggs or the heating of immature chicks¹¹.

It is necessary to note that male urban swallows are very attached to their nest, so during the egg-laying and incubation they spend nearly the same time in nests as females. Nevertheless, females play the main role in the heating of eggs, while males maintain a certain temperature in the nest and guard it. It is possible that the degree of the involvement of family partners in incubation condition the difference in

the length of the development of embryos in different nests. When a clutch is lost, funnels resume it, and the subsequent egg-laying and incubation take place when the brood patches of females are already formed and have reached the 3rd or 4th stages of development. As can be seen from Table 5, the value and index of age difference in 0- and 1-day double clutches of urban swallows are lower than in the main ones. The development of embryos from the first eggs still remains slow although, from the time of the laying of the first egg, the brood patches of females had a 3-stage development, and, assumably, the rate of development should have been close to the maximum.

Table 4. The Dynamics of the Development of a Brood Patch in Urban Swallows from the Beginning of Oviposition to the Hatching of Chicks

| Stage of the brood patch | Decades of June, July | | | | Breeding period |
|--------------------------|-----------------------|----|-----|---|---|
| | I | II | III | I | |
| | Number of birds | | | | |
| 1 | 6 | 6 | | | start of oviposition |
| 2 | 3 | 9 | | | middle of oviposition |
| 3 | | 11 | 1 | | completion of oviposition, start of actual incubation |
| 4 | | 4 | 8 | | actual incubation |
| 5 | | | 6 | 6 | Hatching |

Table 5. The value and index of age difference of embryos in the main and double clutches of urban swallows

| Clutch type | Incubation days | Number of eggs | | | | | Value of age difference | Index of age difference |
|-------------|-----------------|--------------------|------|------|----|---|-------------------------|-------------------------|
| | | 1 | 2 | 3 | 4 | 5 | | |
| | | Development stages | | | | | | |
| Main | 0-th | 11 | 9 | 6 | 4 | 1 | 10 | 2 |
| | 1-st | 10 | dead | 5 | 2 | — | 8 | 2 |
| | 10-th | 36 | 35 | | | | 1 | 0.5 |
| Double | 0-th | 7 | 6 | Dead | 1 | | 6 | 1.5 |
| | 1-st | 9 | dead | 5+ | 3 | | 6 | 1.5 |
| | 10-th | 40 | 40 | 39 | 38 | | 2 | 0.5 |

The Development Rate and Age Difference in Chicks in the Period of Oviposition

Urban swallows are characterized by a discontinuous type of incubation. The formation of a brood patch and the

increasing density of incubation leads to an age difference in the embryos. The total preparations of embryos from 0-1-day clutches are a proof of the difference in age (Table 6).

Table 6. The value and index of age difference of embryos on the 0- and 1-day-old clutches of urban swallows

| Type | Time of clutch completion, days | Number of eggs | | | | | Value of age difference | | Index of age difference |
|---------------|---------------------------------|-------------------|------|----|---|---|-------------------------|----------|-------------------------|
| | | Development stage | | | | | in stages | in hours | |
| | | 1 | 2 | 3 | 4 | 5 | | | |
| Urban swallow | 0 | 11 | 9 | 6 | 4 | 1 | 10 | 40-60 | 2,0 |
| | 0 | 11 | dead | 6 | 4 | 1 | 10 | 40-60 | 2,0 |
| | 0 | 10 | 8 | 4 | 1 | | 9 | 36-54 | 2,3 |
| | 0 | 7 | 5 | 1 | | | 6 | 24-36 | 2,0 |
| | 0 | 1 | 1 | 1 | | | | | |
| | 1 | 12 | 10 | 10 | 6 | 2 | 10 | 40-60 | 2,0 |
| | 1 | 10 | dead | 5 | 2 | | 8 | 32-48 | 2,0 |
| | 1 | 12 | dead | 6 | 2 | | 10 | 40-60 | 2,5 |

Table 6 shows that in an urban swallow's one-day clutch consisting of five eggs, the first embryo was in the 12th stage, and its length was 8.8 mm. The size of the vascular area of the yolk

sac was 10-7.5 mm. It was observed that the head part of the embryo started to rotate to the left side. There were 12 pairs of somites.

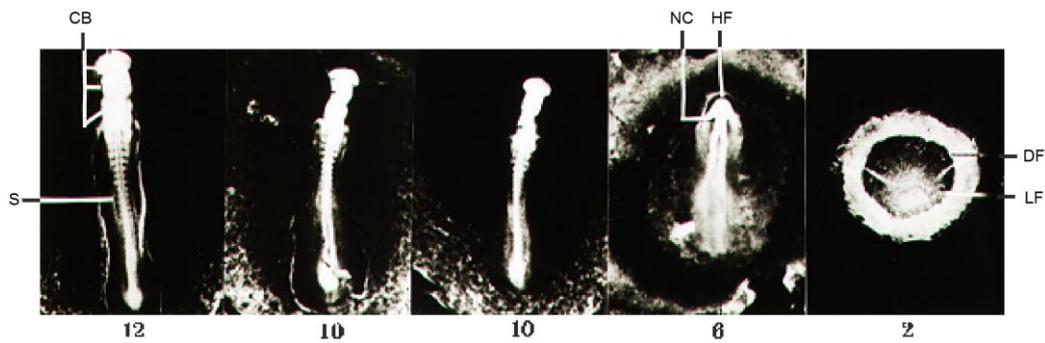


Figure 2. The Age Difference of Embryos of Urban Swallows in a 1-Day Clutch: DF – Dark Field, LF – Light Field of the Blastoderm, HF – Head Fold, NC – Neural Crests, CB – Cerebral Bubbles, S – 12, 10, 10, 6, 2 – Development Stage of Embryos.

The second and third embryos corresponded to the 10th stage of development. They had the same number of somites, in particular, 8 pairs each. However, they somewhat differed in size, in particular, the length of the second was 6.7 mm, while the length of the third embryo was 6.3 mm. The value of the vascular area was different too: 8.8-7.9 mm and 8.5-7.2 mm respectively. The fourth embryo was in the sixth stage, and its length was 4.7 mm. It was possible to observe a formation of short and wide neural crests. There was no division of the mesoderm into somites. The light field had a rounded shape. The last embryo was in the second stage. The light field was round in shape with a diameter of 2.4 mm. The primitive streak was not yet formed. The age difference between the extreme variants was 10 stages. Since it takes 4-6 hours for the passage of one stage on the second day, the size

of the age difference in this clutch was 40-60 hours, or 1.7-2.5 days (2.1 days on average).

In a five-egg clutch set aside on the day the last egg was laid, the embryo from the first laid-off egg was in the 11th stage. The embryos from the second, third, fourth, and fifth eggs were in the 9th, 6th, fourth, and 1st stages of development respectively. The difference between the extreme variants was 10 stages.

The value of age difference varied from 8 to 10 stages, i.e. from 32 to 60 hours (from 1.3 to 2.5 days, an average of 1.9) in 0- and 1-day four-egg clutches and from 24 to 36 hours (1.0-1.3 days, an average of 1.3) in three-egg clutches. The index of age difference varied from 2.0 to 2.5 units. The data obtained during the research indicate that the hatching process takes place individually in each pair, and the pairs that have the same size of clutches in

the period of oviposition spend a different amount of time in the nest.

Thus, the size of the age difference in embryos varied from 10 to 11 stages in five-egg clutches of urban swallows, 8 to 10 stages in four-egg clutches, and was equal to 6 stages in three-egg clutches. In time, the value of this indicator varied from 24 to 60 hours, or from 1.0 to 2.5 days in different clutches. The unequal time spent by family partners in the nest testifies to the individual variability of the incubation processes of each pair. The great variability in the initial hatching period in pairs of funnels is obviously connected with the intermittent incubation of eggs during oviposition.

The further analysis of Table 6 shows that embryos from the first to third eggs (difference in stages 1-2) are closer in the degree of development. The differences in the development between the first and penultimate embryos reached 3-4 stages.

The studies on the rate of the embryogenesis of urban swallows indicate the heterochronicity of the embryonic development since the time of oviposition. For example, in one-day five-egg clutches, the embryos from the first eggs reached only 12-14 stages although the eggs had been in the nests for 6 days and could reach the 25-26th stage with a maximum rate of

embryogenesis, which stands for the development in the last (penultimate) egg. The second and third embryos developed less than expected. Consequently, the rate of the development of the embryos from the first eggs was slow and lower than expected theoretically. In the eggs of a higher temporal rank (fourth, fifth), embryos developed at a maximum rate. In these cases, the authors of the research traced a direct relationship between the time starting from the moment of deposition and the period of incubation. Important factors include the behaviour of hatchers in the nest during the period of oviposition and the degree of the development of the brood patch. In the initial period of oviposition, the hatching density was rather low, and the brood patch was in the first stage of development. By the completion of the latter, the hatching density approached the maximum, and the brood patch reached the third stage of development. Consequently, the eggs that were laid last were incubated at higher temperatures, and the embryos developed at an optimum rate in them.

Urban swallows fly to the north of the range (the Kama Foreurals) at the end of May and the beginning of June. The authors of this research relate the appearance of most birds during this period to a sufficient amount of food, in particular, flying insects. In her

research, D.S. Lyuleeva¹¹ notes the link between the arrival of swallows and the state of the food base. It was revealed that the arrival of urban swallows has a two-wave nature. Swallows arrive at the southern regions of the Perm Krai 7-10 days earlier than to the northern regions. As compared to the Kemerovo Oblast, urban swallows fly to the north of the range 20-35 days later (L.P. Marx). The mass nest-building starts in early June. On the average, the construction of new nest shelters lasts 8 days, while it takes 6 days to repair old dilapidated nests and 4.6 days to renew the old ones. The reduction of the time spent by birds on re-erecting a nest is most likely caused by physiological factors since most females are ready to lay eggs by that time.

Urban swallows start oviposition within a short period and have a single reproduction cycle in the reproductive period. The optimum timing of the reproduction of urban swallows is confined to the second decade of June after the summer weather is established, and the danger of frosts is eliminated.

The north of the range is characterized by later periods of oviposition by females. In comparison with the Altai Reserve (V.D. Stakheev), the dates were displaced for 15-19 days. The total time for the beginning of oviposition was 26 days (taking into account double clutches). D.S. Lyuleeva

notes a large lengthiness of oviposition periods in the Curonian Spit – 57 days.

The initial fecundity of urban swallows in the north of the range was 4.3 ± 0.62 eggs per nest. If the main clutches were lost, they were resumed within a very short time (according to the data of the authors, within 6 days). Double clutches contained fewer eggs, in particular, 2-4 (3.7 ± 0.57). All the five-egg clutches decreased by one or two eggs, while the four-egg clutches turned out to be more stable. The data of the authors of this research are consistent with the data of A.S. Malchevsky and Y.B. Pukinsky, who point out that double clutches were more of the same type since they generally contained four eggs. The size of eggs in the clutches of urban swallows tends to increase by the middle of the cycle and decrease significantly at the end. The eggs in double clutches were larger than in the main ones.

Urban swallows nesting in the Kama Foreursare characterized by a gradual increase in the density of incubation, which results in heterochronic embryonic development. The size of the age difference of embryos is subject to significant fluctuations and can range from 1.0 to 2.5 days, which indicates a large individual variability of the incubation processes of each pair. The rate of

embryonic development at the end of oviposition within a single clutch is not the same. The rate is slow for embryos from eggs of lower temporal ranks, which is related to the behaviour of the hatching (family partners) in the nest and the structural changes that occur in the development of the brood patch.

The results obtained during this research fill only a small gap in the study of problems related to the early ontogenesis of wild birds (from small passerine) that reproduce in the north of the range, and require further continuation.

The results of the research can be used to develop the problems of the evolution of the hatching, incubation, and early ontogenesis of birds, to assess the biological resources of the Middle Urals, to predict the number of eggs, to plan and conduct environmental activities in the region under investigation and other regions with similar ecological conditions.

CONCLUSION

The problem of the embryonic development of birds remains insufficiently studied in modern ornithology. The goal of this research was to study the nesting biology and the early ontogenesis of urban swallows at the northern boundary of distribution in the Kama Foreurals. In this regard, this article analyzes and summarizes data on the phenology of the arrival, nest-

building, and oviposition of urban swallows. The authors of the research identified the peculiarities of the reproductive period, the oomorphologic characteristics of eggs, taking into account their temporal rank, as well as the size of the main and double clutches; traced the dynamics of the development of a brood patch, depending on the stage of the nesting cycle, and studied the rate of embryogenesis and the age difference of the embryos of urban swallows in the period of oviposition.

All the materials presented in this article were obtained for the first time in the region of the Kama Foreurals. In the general biological aspect, the novelty of the research is related to the data on the study of the age difference and the rate of embryonic development in urban swallows as a closed-breeding bird at the northern boundary of the range.

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