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MORPHOLOGICAL DIFFERENTIATION IN NESTLINGS *TURDUS PHILOMELOS* (PASSERIFORMES, TURDIDAE) AND STAGING IN THEIR DEVELOPMENT DURING THE NESTLING PERIOD OF POSTEMBRYOGENESIS

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Morphological Differentiation in Nestlings *Turdus philomelos* (Passeriformes, Turdidae) and Staging in their Development during the Nestling Period of Postembryogenesis. Peskov, V. N., Franchuk, M. V., Atamas, N. S. — The work demonstrates the clear presence of ageing aspects in the postembryonic development of the song thrush in regard to its linear dimensions and body proportions. It is proposed to distinguish the stages of early nesting, mid-nesting and late nesting. At each stage, the mostly developed body parts and organs are those which are needed for the growing organism to provide its best functionality at the current period of its postembryonic development.

Key words: song thrush, nestlings, postembryogenesis, morphological differentiation, development staging.

Introduction

Despite the multitude of works dedicated to studying the postembryonic growth and development in birds, many aspects of the subject still await their accurate analysis and attract much discussion (Jongsomjit et al., 2007; Starck & Ricklefs, 1998). As an example, the rate of growth and differentiation in nestlings, and some other features of their postembryonic development, are species-specific and inherited (Murphy, 1981; Ricklefs, 1975; Starck & Ricklefs, 1998). At the same time, there is evidence that the growth and development rates in nestlings are more often correlated with various environmental factors (predation, food availability, latitude, clutch size, etc.) if compared to hereditary factors, for example, such as body weight of adult birds or phylogenetic proximity of related species (Remeš, Martin, 2002). Therefore, of particular importance is studying the characteristic variability in various traits during post-embryogenesis in closely related species, as well as the identification of developmental patterns in nestlings at different stages of postembryogenesis and finding out whether such stages can be discriminated.

The group of thrushes of the genus *Turdus* is a suitable model object for such studies and, in particular, the song thrush, which is broadly distributed in the area of examination. Many aspects of the post-embryonic growth and development of the song thrush, *Turdus philomelos* C. L. Brehm, 1831, received their description in sufficient detail in special and generalizing works dedicated to the study of the individual development in nestlings (Brovkina, 1959; Mal'chevskiy, 1959; Marisova, 1968; Artamonova, 1970; Poznanin, 1979; Denisova et al., 1986; Gerasimchuk, 2011; Franchuk, 2013; Peskov et al., 2015; Rodimtsev & Yermolaev, 2016). These studies helped establish that the nestling stage of the song thrush's postembryonic development lasts 12–14 days, after which the birds leave the nest (Malchevskiy, 1959; Poznanin, 1979; Franchuk, 2013). L. P. Poznanin (1979) distinguished three developmental periods in nestlings during the postembryonic development of the song thrush. However he himself questioned the possibility of an objective enough periodization of the postembryonic development in birds.

The aim of the current study is to discriminate the peculiarities characteristic for the processes of differentiation of the body parts in the song thrush during its postembryonic period and to find out whether it is possible to distinguish different stages during the growth and development processes on the example of nestlings belonging to this species.

Material and methods

The material had been collected within the period from April till June 2012, on the territory of the reserve object "Razvyilka" (near the town of Sarny, Rivne Region), Rivne Natural Reserve (massifs Beloozersky, Somyne) in the vicinity of Yarynivka village (Sarny District, Rivne Region) and Poliana village (Shepetovsky District, Khmelnytsky Region). The territory of research is situated within the area of the mixed forests in the Western Polissia.

There have been studied 118 nestlings of different age and 15 adult birds. To measure the body weight, the nestlings were weighed daily from the moment of their hatching with the use of the typical equilateral weights, with an accuracy of 0.1 g. The nestlings were also size-measured daily from the first day to the fourteenth, while they were in the nest. To measure the length we used the caliper with an accuracy of 0.1 mm for: 1) body — distance from the tip of the bill (with an elongated neck) to the tailbone without feathers; 2) head — distance from the occiput to the tip of the bill; 3) bill 1 — distance from its tip to the border of the rhamphotheca and the skin of the frontal region; 4) bill 2 — distance from its tip to the nostril; 5) shoulder — distance from the middle of the shoulder joint to the middle of the elbow joint; 6) forearm — distance from the middle of the elbow joint to the middle of the wrist joint; 7) wingtip — distance from the middle of the wrist joint to the distal end of the hand; 8) thigh — distance from the middle of the thigh to the middle of the knee; 9) tibia — distance from the middle of the knee joint to the middle of the intertarsal joint; 10) tarsus — distance from the middle of the intertarsal joint to the toe joint, with bent toes; 11) third toe (the longest one) — distance from the base of the middle toe joint to the beginning of the claw base; 12) first toe (the rear one) — distance from the base of the toe joint to the beginning of the claw base.

Nestlings of different age were compared to each other by the absolute values of the 12 morphometric traits with the use of the hierarchical cluster analysis, calculating Euclidean distance (DE) as an indicator of generalized differences in the linear dimensions of the body. The nestlings' body proportions were compared by means of the Kendall rank correlation coefficient (τ) (Zaytsev, 1984). The traits' absolute values in millimeters were translated into dimensionless numbers via dividing their mean values in nestlings of different age by the means in adult specimens. By doing so, we moved from the traits' absolute values to the indices of their definitiveness, or aging (organ size at certain age, expressed in % of its definitive size).

To identify the structure of the difference matrices for the body's linear dimensions (DE_L) and the matrix of similarity by its proportions (τ_p), we used the factor analysis (the principal component method). Then, the factor loads on the main components reflect the relationship of one or another age group of nestlings to the corresponding PC, which is determined by the entire structure of the similarity-difference relationship among nestlings in their linear dimensions and body proportions.

Statistical calculations for all the variables were done with the use of the statistical analysis applications PAST and Statistica for Windows, v. 6.0.

Results and discussion

Variability in basic dimensions of the body in the postembryonic development of the song thrush is determined primarily by the age and date (order) of hatching, as well as by their individual variability. On the territory of Western Polissia, there is a fairly large type of the song thrush, with the mean body mass equal to 70.9 g, and length — 137.9 mm (table 1). The mean body length of the day-old nestlings ($M = 51.2$ mm) is 37.1 % of that in adult birds, and the mass ($M = 6.2$ g) — 8.8 %. In the process of postembryonic growth, the body length increases by 3.7 times, and the mass — by 11.4. Nestlings, leaving the nest by the 12–14th day, do not still reach the body size of an adult bird in their body length ($M = 109.9$ mm) and mass ($M = 46.1$ g). Their bodies' length and mass during their growth in the nest (nesting stage of postembryogenesis) increase by 2.96 and 7.44 times respectively.

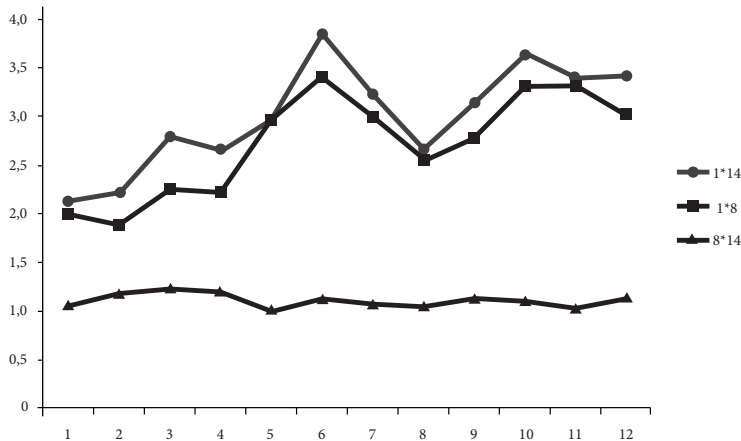
Variability in morphometric traits

The mean values of the 12 morphometric traits in the song thrush nestlings vary from the minimal values in day-old nestlings to the maximum in 13–14 day-old ones that have almost reached their peak development and are ready to leave the nest (table 2).

For the entire nesting period of development, the degree of increase in size of the traits

Table 1. Variability of body length and mass in the three age groups of song thrush

Age	n	Body length, mm		Body mass, g	
		min-max	M	min-max	M
One day	31	46.2–58.5	51.2	4.5–9.5	6.2
12–14 days	27	99.8–17.5	109.9	37.0–53.3	46.1
Adult birds	15	120.0–155.0	137.9	62.0–90.9	70.9

**Fig. 1.** Dynamics of changes in 12 morphometric traits in nestlings during the nesting stage of postembryogenesis (from 1 to 14 days), the stage of fast growth (from 1 to 8 days) and of slow growth (from 8 to 14 days).**Table 2.** Mean values of the 12 morphometric traits in nestlings and adult song thrush specimens

N	Traits, mm	1 day-old	8 day-old	13 day-old	Adults
1	Body length	51.16	102.06	108.80	145.60
2	Head length	17.72	33.28	39.27	45.80
3	Bill length 1	5.68	12.85	15.91	20.00
4	Bill length 2	2.92	6.47	7.79	12.20
5	Shoulder length	8.03	23.79	23.64	32.30
6	Forearm length	8.55	29.23	32.97	33.10
7	Wingtip length	8.84	26.45	28.45	32.10
8	Thigh length	10.25	26.04	27.26	32.20
9	Tibia length	13.55	37.55	42.56	47.00
10	Tarsus length	8.96	29.69	32.67	33.30
11	Third toe length	5.97	19.76	20.32	25.20
12	First toe length	3.89	11.73	13.26	13.20

varies from 2.1 times (body length) to 3.86 (forearm length) (fig. 1). The fastest growth is characteristic for the wing parts (traits 5–7), followed by the hindlimb parts (signs 8–12), and the slowest in growth speed are the body (trait 1), head (2) and bill (traits 3 and 4).

The major increments in size occur within the first eight days of the nestlings' postembryonic development (stage of fast growth). By the end of this stage, the growth is in fact finished for the forearm (trait 5) and almost finished for the third toe (trait 11), thigh (trait 8), and body (trait 1). The rest of the traits, within the next stage of slow growth (8–14 days), receive only a slight increase in size (by 1.1–1.2 times).

Differentiation of nestlings by their body's linear dimensions

Generalized differences, calculated between the nestlings' age groups for the means values of the 12 traits, range from the minimum (DE = 2.0) between the 10 day-old and 11 day-old nestlings to the maximum (DE = 84.5) — between the day-old and 13 day-old ones (table 3).

According to the factor analysis of the DE_L matrix, the first two main components (PC1 and PC2) explain the most part (97.6 %) of the morphological differentiation in body's linear dimensions of the song thrush nestlings (table 4).

Table 3. Comparison of nestlings in their linear dimensions (DE — above the diagonal line) and proportions (τ — under the diagonal line) in reference to their age

Age, days	Nestling age, days												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1	—	9.8	19.2	34.1	43.2	54.8	65.0	73.5	77.6	80.8	81.7	84.6	84.5
2	0.89	—	9.5	24.3	33.4	45.1	55.3	63.8	67.8	71.1	72.0	74.8	74.8
3	0.89	0.91	—	15.2	24.1	36.0	46.3	54.6	58.7	61.9	62.9	65.6	65.6
4	0.63	0.74	0.74	—	9.2	20.9	31.2	39.6	43.7	47.0	48.0	50.7	50.7
5	0.47	0.58	0.58	0.76	—	12.1	22.5	30.7	34.8	38.1	39.1	41.9	41.9
6	0.36	0.47	0.47	0.69	0.76	—	10.7	18.8	23.1	26.4	27.4	30.2	30.2
7	0.36	0.47	0.47	0.65	0.67	0.87	—	9.2	13.0	16.2	17.2	20.3	20.1
8	0.27	0.38	0.38	0.60	0.58	0.82	0.91	—	4.7	8.0	9.1	11.8	12.2
9	0.23	0.34	0.34	0.52	0.58	0.74	0.87	0.82	—	3.5	4.5	7.5	7.8
10	0.23	0.34	0.34	0.52	0.58	0.74	0.87	0.82	0.96	—	2.0	4.4	4.9
11	0.21	0.32	0.32	0.49	0.56	0.67	0.80	0.80	0.93	0.93	—	4.0	4.1
12	0.25	0.36	0.36	0.49	0.52	0.67	0.80	0.80	0.89	0.89	0.96	—	3.5
13	0.30	0.41	0.41	0.49	0.56	0.67	0.76	0.71	0.80	0.80	0.87	0.87	—

Table 4. Results of the factor analysis of the difference matrix for the nestlings' linear dimensions (DE_L) and the similarity matrix for their body proportions (τ_p)

Nestling age, days	PC1	PC2	PC1	PC2
	Body linear size		Body proportion	
1	0.995	-0.013	0.989	-0.083
2	0.988	-0.107	0.982	0.011
3	0.947	-0.273	0.982	0.011
4	0.677	-0.712	0.629	0.684
5	0.255	-0.955	0.035	0.920
6	-0.517	-0.833	-0.727	0.624
7	-0.879	-0.439	-0.932	0.255
8	-0.976	-0.182	-0.938	0.196
9	-0.993	-0.083	-0.990	-0.024
10	-0.997	-0.027	-0.990	-0.024
11	-0.997	-0.015	-0.983	-0.113
12	-0.995	0.009	-0.973	-0.168
13	-0.995	0.008	-0.937	-0.163
Prp. Totl, %	79.47	18.17	79.48	14.49

The PC1, which explains 79.47 % of total variance, marks the one-, two-, and three day-old nestlings by high positive correlation coefficients (0.947–0.995), and the seven- to thirteen day-old nestlings — by high negative ones (–0.879 — –0.997) (table 4). Based on that, one can deduce that the first principal component reflects the generalized differences (DE_L) among the nestlings of these age groups in their body linear dimensions (absolute values of the 14 morphometric traits).

The PC2 (18.17 %) marks the four-, five-, and six day-old nestlings by high negative correlation coefficients (–0.712 — –0.955), denoting their place in the structure of morphological diversity of the song thrush nestlings.

Based on the data, presented above, it seems highly probable that the song thrush nestlings during their nesting development period can be clearly differentiated by their linear dimensions on the stages of early nesting (1–3 days of development), mid-nesting (4–6 days of development) and late nesting (7–13 days of development).

Differentiation of nestlings by their body proportions

It is well known that in young vertebrate animals, including birds, the definitiveness (aging) of most of the body parts and organs during some developmental periods is different, which is determined by the starting point and the speed of morpho- and organogenesis, as well as by the rate of postembryonic growth (Bunak, 1961; Jongsomjit et al., 2007; O'Connor, 1978). The indices of definitiveness or ageing of morphological traits are

Table 5. Mean indices of definitiveness in % and ranks (1–12) of the morphometric traits in the song thrush nestlings

Traits	1 day-old	8 day-old	13 day-old
Body length	35.14 (2)	70.09 (10)	74.72 (10)
Head length	38.70 (1)	72.66 (9)	85.75 (6)
Bill length 1	28.38 (6)	64.23 (11)	79.53 (9)
Bill length 2	23.96 (11)	53.04 (12)	63.84 (12)
Shoulder length	24.86 (10)	73.64 (8)	73.18 (11)
Forearm length	25.83 (9)	88.31 (3)	99.60 (2)
Wingtip length	27.54 (7)	82.39 (4)	88.62 (5)
Thigh length	31.83 (3)	80.85 (5)	84.65 (7)
Tibia length	28.83 (5)	79.90 (6)	90.56 (4)
Tarsus length	26.89 (8)	89.15 (1)	98.10 (3)
Third toe length	23.67 (12)	78.43 (7)	80.63 (8)
First toe length	29.46 (4)	88.85 (2)	100.44 (1)

dimensionless values, which makes it possible to make a comparison among different traits and assign ranks to them depending on these indices (in this case, from rank 1 which is the maximum index of definitiveness to 12 being the minimum one).

In the day-old song thrush nestlings, similar to most nestling birds (Poznanin, 1979), in accordance with their functional meaning at the current moment of organism formation, the most developed are the head length (38.70 %, rank 1) and body length (35.14 %, rank 2), and the least — the bill length from the tip to the nostrils (23.96 %, rank 11) and the third toe of the hindlimb (23.67 %, rank 12) (table 5).

In the eight day-old nestlings, the most developed are the tarsus (89.15 %), the first toe (88.85 %), and the forearm (88.31 %), the least — the body (70.09 %), the bill (64.23 and 53.04 %), which indicates that nestlings are getting ready to leave the nest.

In the thirteen day-old nestlings, the body proportions change insignificantly, which is evident if they are compared with the eight day-olds ($\tau = 0.71$). The leading positions are taken by the first toe (100.44 %), the forearm (99.60 %) and the tarsus (98.10 %); the weakest definitiveness is characteristic for the body (74.72 %), the shoulder (73.18 %), and the bill from the tip to the nostril (63.84 %).

The factor analysis results received for the nestlings' body proportion similarity matrix (table 3) confirm almost completely the differentiation characteristics obtained from studying the linear dimensions of the body (table 4). The only difference is that the group of the mid-nesting chicks differentiates not that distinctly as it was seen for the body linear dimensions. For example, the six day-old nestlings are closer by their body proportions to the group of the late nesting chicks (-0.727) than to the mid-nesting ones (0.624). The correlation (0.684) for the four day-old nestlings with the PC2, which measures the differentiation level of the mid-nesting chicks within the general structure of morphologic diversity in the song thrush nesting chicks by their body proportions, is not high enough.

Conclusion

In the one day-old nestlings, the most mature are the body, head and bill, which is evidence of an earlier development of the body skeleton and the head. In the thirteen day-old nestlings, getting ready to leave the nest, the most developed are the wing (traits 7 and 8) and the hindlimb (traits 9, 10 and 12), i. e., the organs for movement along the ground and air. Adult birds have the proportionally more developed bill and thigh, which corresponds to the properties of their movement in search of food (jumping) and its gathering (loosening the forest litter with the bill) (Baranovsky et al., 2007; O'Connor, 1978). It can be easily seen that at each particular moment of development the most developed are those parts and organs which are most needed for a growing organism for its successful functioning.

During the nesting stage of the song thrush's postembryonic development, there is a well expressed age-related aspect of differentiation in nestlings as to their body linear dimensions and proportions. Within the general structure of morphologic diversity of the song thrush nesting chicks, in reference to their body linear dimensions and proportions, there can be clearly differentiated the groups of early nesting (1–3 days of development), intermediate group of mid-nesting (4–6 days), and the most numerous group of late nesting (7–14 days) chicks. That said, the nesting stage of the song thrush postembryonic development can be divided into three stages of nestlings' development: of early nesting, mid-nesting and late nesting.

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