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Characteristics of Body Mass Growth in Semialtricial and Altricial Bird Species during the Nestling Period

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Abstract—The dynamics of body mass growth were studied in nestlings of 22 semialtricial and altricial bird species based on materials collected in seven regions of Russia in the years 1976–2013. The bird species belong to four orders and 13 families. The results of the study indicate the nonuniform growth of nestlings in different bird species. Of the species investigated, only seven were found to reach or exceed the mass of adult birds. Over the nestling period, the nestlings of open-nesting species, such as the hooded crow (*Corvus cornix*), rook (*Corvus frugilegus*), magpie (*Pica pica*), fieldfare (*Turdus pilaris*), song thrush (*Turdus philomelos*), and goldfinch (*Carduelis carduelis*), do not reach the weight of adult birds and their growth continues after they leave the nest. In closed-nesting species, only the nestlings of the barn swallow (*Hirundo rustica*) reach or exceed the definitive mass, whereas the nestlings of the jackdaw (*Corvus monedula*), starling (*Sturnus vulgaris*), wryneck (*Jynx torquilla*), tree sparrow (*Passer montanus*), and great tit (*Parus major*) continue to grow after leaving the nest. The body mass of birds on the day of their hatching and before their departure from the nests and the mass of adult birds depend on the nesting type, duration of the nestling period, size groups of species, and their definitive size. The average specific growth rate of body mass and its maximum values for different species are also associated with these factors. The maximum specific growth rate in small-sized and medium-sized bird species was observed on the 0–1st days of life; in large bird species, on the 2nd–4th days. The specific growth rate did not depend on the type of nesting, but it was inversely related to the duration of the nestling period and the definitive sizes of birds.

Keywords: postembryogenesis, semialtricial and altricial bird species, open-nesting species, closed-nesting species, specific growth rate, nestling period

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INTRODUCTION

The individual development of organisms is one of the most important aspects of general biological research, which helps us understand issues in the evolution of ontogenesis (Portmann, 1950; Matveev, 1970; Poznanin, 1979). Therefore, study of the early stages of postnatal development of birds has important theoretical and practical significance. The postembryogenesis of birds has been discussed in many papers, but the increase in body weight in the process of growth has been studied only in a small fraction of species (Austin and Ricklefs, 1977; O'Connor, 1984, etc.). It is known that birds are the fastest growing group of vertebrates (Case, 1978; Dolnik, 2006). The growth and development of the nestlings of most species takes place in a short time and is characterized by great species and individual variability. As integrating indicators of the growth of birds, researchers generally use the increase in mass and linear size of the body. One of the methods of comparative analysis of the growth of different species is to determine the specific growth rate for certain periods of postembryogenesis or over the entire time spent by the nestlings in the nest (Schmalhausen, 1935; Zaika, 1970; Mina and Klevezal, 1976).

The growth curves of nestlings of most species of birds have a typical S-shaped form, and are described by the logistic function (Ricklefs, 1968). The dependence between the growth rate of nestlings and the definitive body sizes of birds is accepted by some authors (Ricklefs, 1968; Mukhtarov, 1977; Björnhag, 1979; etc.) and rejected by others (Denisova, 1958; Poznanin, 1979; etc.). However, a clear dependence exists between the growth rate of nestlings and the time spent in the nest. Experimental studies have demonstrated that the postnatal growth also depends on the habitat (Ricklefs and Peters, 1979), climatic fluctuations and food resources (Dunn, 1975; Bryant, 1975; etc.), and the size of the eggs and brood (Lack,

† Deceased.

1954; Parsons, 1970; Schifferli, 1973; Rodimtsev, 1989, etc.).

The objective of this study is to establish certain patterns of growth of semialtricial and altricial species of birds, depending on the type of nesting, duration of stay of nestlings in the nest, and the size groups of species and definitive sizes of birds.

MATERIALS AND METHODS

The growth of 22 bird species belonging to four orders and 13 families (table) was studied. Among the species studied, the semialtricial eco-physiological group of birds included the red-footed falcon, common kestrel, and rock pigeon. Note that we considered the rock pigeon as a semialtricial species based on the data by Kamenskii (1988) about the formation of thermoregulation in the ontogenesis of this species.

Investigations were carried out in different regions of Russia: in the southeastern part of western Siberia (Kemerovo oblast: Belovo district 54°20′ N, 86°42′ E; environs of Novokuznetsk 53°44′ N, 87°7′ E, Mountainous Shoria 53°16′ N, 87°16′ E), in the Altai Republic (51°47′ N, 87°14′ E), in the Bol'shezemel'skaya tundra (67°0′ N, 64°20′ E), on the Curonian Spit (55°5′ N, 20°44′ E), in the Republic of Adygea (45°8′ N, 39°43′ E), and in Tambov (52°53′ N, 40°31′ E) and Rostov (46°28′ N, 42°39′ E) oblasts in the 1976–2013. To identify the nestlings in the nests, one claw of each of them was stained with fast-drying paint. The marked nestlings of known age were weighed in the early morning hours daily or at intervals of 2 days with an accuracy up to 0.1–1.0 g, depending on their size. When calculating the averaged body mass indices, we used the method of "parallel groups" (Mstislavskii, 1938). The nestlings of each species from different nests were pooled into the same age groups over several years, which allowed us to consider their growth and development, regardless of the specific conditions of the individual seasons. Data on the mass of adult birds of the same population were obtained by shooting or capturing them in mist nets. The captured or procured adult birds were not divided by sex. The specific growth rate (C) was calculated using the formula by Schmalhausen (1935). This parameter was calculated using the average mass for each age group. For the nestlings of different species, the nestling periods were conditionally divided into short (8–13 days), medium (14–21 days), and long (22–34 days); the following size groups were distinguished: large nestlings (body mass ≥ 150.0 g), medium nestlings (body mass ≥ 60.0 < 150.0 g), and small nestlings (body mass ≥ 8.0 < 60.0 g), respectively. The names of birds are given according to Stepanyan (2003). Statistical analysis was performed in the Statistica 10.0 program (StatSoft, 2011). The notations used in the text are as follows: sample sizes (n), arithmetic means with the standard error of the mean ($x_m \pm SE$), and the range of values (lim, minimum and maximum). All of the variables had previously been tested in accordance with the normal distribution (Shapiro–Wilk W-test). When analyzing the data, we used the following statistical analysis techniques: the Pearson correlation coefficient (r), analysis of variance (ANOVA), and the Mann–Whitney test (M–W). Statistical hypotheses were rejected at the level of reliability P less than 0.05.

RESULTS AND DISCUSSION

The growth of nestlings of small birds, mainly passerines, was previously studied in detail by Poznanin (1979). Our results on the growth and development of juveniles of larger species, such as falcons, kestrels, rock pigeons, and corvids, revealed largely similar dynamics of development of birds of different sizes and different taxonomic groups. It is known that the initial weight of nestlings of each species is determined by the hereditarily different sizes of eggs at hatching (Mal'chevskii, 1959). The variability of the oologic characteristics depends, for example, on the age, the physiological condition of the females, the cycle and the timing of reproduction, climatic fluctuations, and abundance of food resources in the reproductive period (Myand, 1988; Meijer et al., 1988; Wiebe and Bortolotti, 1995; Christians, 2002; Lebedeva et al., 2011; etc.). We found that over the nestling period the body mass of nestlings increases by different numbers of times: from 10.6 ± 0.4 and 10.8 ± 0.5 in the white wagtail and the pied flycatcher, respectively, to 34.3 ± 0.4 in the hooded crows, which is directly related to the definitive dimensions of birds (table).

An analysis of the data characterizing the growth of nestlings of different species showed that over the nestling period most open-nesting species do not reach the weight of adult birds and their growth continues after leaving their nests (hooded crow: M–W: $z = -3.2$, $P = 0.0014$; rook: M–W: $z = -3.4$, $P = 0.0008$; magpie: M–W: $z = -2.3$, $P = 0.0191$; fieldfare: M–W: $z = -3.7$, $P = 0.0002$; song thrush: M–W: $z = -2.6$, $P = 0.0081$; and European goldfinch: M–W: $z = -2.8$, $P = 0.0051$). Only in the red-footed falcon, kestrel, and western yellow wagtail is the mass of nestlings before leaving their nests slightly greater than the body mass of adult birds, but the difference is not significant. In the postnestling period, their mass decreases.

In terms of the nature of their growth, the closed-nesting species are divided into two groups: in the first group, over the nestling period, the nestlings reach a mass exceeding the definitive one; in the second group, the nestlings continue to grow after departure from the nests. Only the mass of the barn swallow nestlings significantly exceeds that of adult birds before it leaves the nest (M–W: $z = 2.9$, $P = 0.0043$). In most species, growth continues after departure from the nest (jackdaw: M–W: $z = -3.3$, $P = 0.0009$; common starling: M–W: $z = -3.4$, $P = 0.0006$; wryneck: M–W: $z = -2.8$, $P = 0.0058$; tree sparrow: M–W:

Growth parameters of nestlings of some bird species during the nestling period

Species	Duration of nestling period, days	Body mass, g			Increase in body mass of nestlings, times	Specific body mass growth rate of nestlings	
		of nestlings on the day of hatching	of nestlings before leaving the nest	of adult birds		$\frac{\text{maximum}}{\text{period, days}}$	average for the nestling period
Hooded crow (*Corvus cornix* L.) (*1, 1, 0, 2*)	30–32	$10, \frac{13.6 \pm 0.1}{13.0-14.2}$	$10, \frac{465.9 \pm 3.9}{444.0-486.0}$	$6, \frac{522.0 \pm 9.7}{502.0-563.0}$	$10, \frac{34.3 \pm 0.4}{31.9-36.0}$	$\frac{0.415}{2-4}$	$10, \frac{0.114 \pm 0.001}{0.110-0.119}$
Rook (*Corvus frugilegus* L.) (*1, 1, 0, 2*)	31–33	$10, \frac{12.5 \pm 0.1}{12.0-13.2}$	$10, \frac{372.2 \pm 7.0}{320.0-390.2}$	$7, \frac{443.0 \pm 7.3}{415.0-467.0}$	$10, \frac{29.8 \pm 0.8}{24.2-32.5}$	$\frac{0.313}{2-4}$	$10, \frac{0.106 \pm 0.001}{0.097-0.110}$
Rock pigeon (*Columba livia* Gm.) (*0, 0, 0, 2*)	32–36	$10, \frac{12.6 \pm 0.1}{12.0-13.3}$	$10, \frac{333.0 \pm 5.7}{302.0-352.0}$	$10, \frac{324.1 \pm 5.6}{305.0-362.0}$	$10, \frac{26.4 \pm 0.6}{23.6-29.3}$	$\frac{0.386}{2-4}$	$10, \frac{0.096 \pm 0.001}{0.090-0.102}$
Magpie (*Pica pica* L.) (*1, 1, 0, 2*)	26–28	$10, \frac{6.8 \pm 0.1}{6.2-7.2}$	$10, \frac{223.1 \pm 4.0}{205.0-245.0}$	$10, \frac{241.0 \pm 5.0}{215.0-260.0}$	$10, \frac{32.9 \pm 0.9}{28.5-36.8}$	$\frac{0.508}{0-1}$	$10, \frac{0.129 \pm 0.001}{0.121-0.137}$
Jackdaw (*Corvus monedula* L.) (*1, 0, 0, 2*)	29–31	$10, \frac{6.7 \pm 0.1}{6.2-7.4}$	$10, \frac{173.0 \pm 5.5}{142.0-198.0}$	$8, \frac{215.3 \pm 6.4}{191.0-242.0}$	$10, \frac{25.8 \pm 0.6}{21.8-27.8}$	$\frac{0.375}{0-2}$	$10, \frac{0.108 \pm 0.001}{0.103-0.115}$
Common kestrel (*Falco tinnunculus* L.) (*0, 1, 0, 2*)	24–32	$10, \frac{14.6 \pm 0.7}{12.0-19.0}$	$5, \frac{210.8 \pm 7.5}{185.0-230.0}$	$5, \frac{202.5 \pm 12.8}{168.5-234.9}$	$5, \frac{15.0 \pm 0.6}{13.2-16.7}$	$\frac{0.309}{1-2}$	$5, \frac{0.097 \pm 0.002}{0.092-0.100}$
Red-footed falcon (*Falco vespertinus* L.) (*0, 1, 0, 1*)	16–21	$24, \frac{14.0 \pm 0.6}{11.0-20.0}$	$3, \frac{188.3 \pm 32.8}{155.0-254.0}$	$5, \frac{178.5 \pm 8.3}{156.0-196.5}$	$7, \frac{11.7 \pm 1.0}{8.5-15.3}$	$\frac{0.283}{0-1}$	$7, \frac{0.087 \pm 0.003}{0.076-0.097}$
Fieldfare (*Turdus pilaris* L.) (*1, 1, 1, 0*)	12–13	$10, \frac{5.6 \pm 0.1}{5.0-6.1}$	$10, \frac{70.6 \pm 1.1}{66.3-78.0}$	$10, \frac{92.5 \pm 1.3}{87.7-98.8}$	$10, \frac{12.7 \pm 0.4}{10.9-14.8}$	$\frac{0.502}{0-1}$	$10, \frac{0.203 \pm 0.004}{0.187-0.222}$
Common starling (*Sturnus vulgaris* L.) (*1, 0, 1, 1*)	20–22	$10, \frac{5.2 \pm 0.1}{4.8-5.6}$	$10, \frac{65.9 \pm 1.0}{60.7-71.5}$	$10, \frac{72.8 \pm 0.8}{69.7-76.5}$	$10, \frac{12.7 \pm 0.2}{11.6-13.5}$	$\frac{0.429}{1-2}$	$10, \frac{0.121 \pm 0.002}{0.112-0.128}$
Song thrush (*Turdus philomelos* Br.) (*1, 1, 1, 0*)	12–13	$8, \frac{5.1 \pm 0.1}{4.8-5.5}$	$5, \frac{44.0 \pm 1.2}{41.8-48.3}$	$6, \frac{66.2 \pm 1.3}{61.4-70.1}$	$5, \frac{8.5 \pm 0.4}{7.7-9.4}$	$\frac{0.493}{0-1}$	$10, \frac{0.173 \pm 0.006}{0.157-0.187}$
Wryneck (*Jynx torquilla* L.) (*1, 0, 2, 1*)	19–21	$7, \frac{1.9 \pm 0.1}{1.7-2.2}$	$7, \frac{28.6 \pm 1.4}{24.3-33.0}$	$5, \frac{40.4 \pm 1.1}{36.8-43.4}$	$7, \frac{15.2 \pm 1.1}{11.0-19.4}$	$\frac{0.434}{0-2}$	$5, \frac{0.138 \pm 0.004}{0.126-0.148}$
Eurasian tree sparrow (*Passer montanus* L.) (*1, 0, 2, 1*)	15–16	$10, \frac{1.8 \pm 0.1}{1.3-2.1}$	$10, \frac{22.3 \pm 0.5}{19.8-24.6}$	$10, \frac{25.8 \pm 1.0}{21.8-30.1}$	$10, \frac{12.6 \pm 0.6}{10.3-17.1}$	$\frac{0.468}{0-1}$	$10, \frac{0.163 \pm 0.004}{0.148-0.190}$

Table. (Contd.)

Species	Duration of nestling period, days	Body mass, g			Increase in body mass of nestlings, times	Specific body mass growth rate of nestlings	
		of nestlings on the day of hatching	of nestlings before leaving the nest	of adult birds		$\frac{\text{maximum}}{\text{period, days}}$	average for the nestling period
Eurasian nuthatch (*Sitta europaea* L.) (*1, 0, 2, 1*)	20–22	$9, \frac{1.4 \pm 0.1}{1.2-1.7}$	$7, \frac{23.7 \pm 0.5}{21.8-25.2}$	$6, \frac{22.0 \pm 0.8}{20.4-25.6}$	$7, \frac{16.8 \pm 0.9}{14.5-19.9}$	$\frac{0.376}{0-2}$	$7, \frac{0.136 \pm 0.003}{0.122-0.142}$
Common chaffinch (*Fringilla coelebs* L.) (*1, 1, 2, 0*)	12–13	$8, \frac{1.8 \pm 0.1}{1.6-2.1}$	$8, \frac{19.4 \pm 0.7}{17.8-22.5}$	$6, \frac{21.5 \pm 0.9}{19.2-24.4}$	$8, \frac{10.8 \pm 0.3}{9.0-12.3}$	$\frac{0.412}{0-2}$	$8, \frac{0.190 \pm 0.003}{0.180-0.203}$
Great tit (*Parus major* L.) (*1, 0, 2, 0*)	17–19	$10, \frac{1.2 \pm 0.04}{1.0-1.4}$	$10, \frac{16.3 \pm 0.3}{14.8-17.8}$	$10, \frac{19.7 \pm 0.5}{18.1-22.0}$	$10, \frac{13.9 \pm 0.6}{11.0-16.9}$	$\frac{0.485}{0-2}$	$10, \frac{0.145 \pm 0.004}{0.126-0.166}$
White wagtail (*Motacilla alba* L.) (*1, 1, 2, 0*)	11–12	$8, \frac{1.7 \pm 0.1}{1.5-2.0}$	$8, \frac{18.0 \pm 0.4}{16.4-20.3}$	$6, \frac{19.3 \pm 0.5}{18.0-21.3}$	$8, \frac{10.6 \pm 0.4}{9.1-12.7}$	$\frac{0.488}{0-1}$	$8, \frac{0.205 \pm 0.005}{0.193-0.231}$
Goldfinch (*Carduelis carduelis* L.) (*1, 1, 2, 0*)	13–14	$6, \frac{1.3 \pm 0.04}{1.2-1.5}$	$6, \frac{15.1 \pm 0.4}{13.8-16.4}$	$6, \frac{19.1 \pm 0.4}{18.1-20.8}$	$6, \frac{11.4 \pm 0.3}{10.6-12.6}$	$\frac{0.483}{0-1}$	$6, \frac{0.180 \pm 0.003}{0.168-0.191}$
Barn swallow (*Hirundo rustica* L.) (*1, 0, 2, 1*)	18–20	$8, \frac{1.4 \pm 0.1}{1.2-1.7}$	$8, \frac{21.3 \pm 0.6}{19.7-24.5}$	$5, \frac{17.4 \pm 0.2}{16.9-17.8}$	$8, \frac{15.5 \pm 0.9}{11.6-18.2}$	$\frac{0.472}{0-2}$	$8, \frac{0.150 \pm 0.006}{0.132-0.188}$
Yellow wagtail (*Motacilla flava* L.) (*1, 1, 2, 0*)	8–9	$7, \frac{1.6 \pm 0.1}{1.3-1.9}$	$7, \frac{17.4 \pm 0.3}{16.8-19.0}$	$5, \frac{16.5 \pm 0.3}{15.7-17.3}$	$7, \frac{11.0 \pm 0.5}{8.8-13.1}$	$\frac{0.487}{0-1}$	$7, \frac{0.284 \pm 0.008}{0.261-0.312}$
Common redstart (*Phoenicurus phoenicurus* L.) (*1, 0, 2, 1*)	14–16	$10, \frac{1.2 \pm 0.04}{1.0-1.4}$	$10, \frac{14.5 \pm 0.3}{12.7-15.8}$	$8, \frac{15.4 \pm 0.3}{13.7-16.4}$	$10, \frac{12.2 \pm 0.4}{10.3-14.1}$	$\frac{0.465}{0-1}$	$10, \frac{0.140 \pm 0.003}{0.123-0.152}$
Pied flycatcher (*Ficedula hypoleuca* Pall.) (*1, 0, 2, 1*)	14–16	$10, \frac{1.2 \pm 0.1}{1.0-1.5}$	$10, \frac{12.8 \pm 0.3}{11.5-14.4}$	$8, \frac{12.4 \pm 0.3}{10.8-13.5}$	$10, \frac{10.8 \pm 0.5}{8.2-13.1}$	$\frac{0.423}{0-1}$	$10, \frac{0.158 \pm 0.003}{0.146-0.175}$
Coal tit (*Parus ater* L.) (*1, 0, 2, 1*)	17–19	$10, \frac{0.8 \pm 0.04}{0.7-1.0}$	$10, \frac{9.0 \pm 0.3}{8.0-10.6}$	$9, \frac{9.7 \pm 0.3}{8.4-11.2}$	$10, \frac{11.3 \pm 0.5}{8.6-13.2}$	$\frac{0.463}{0-1}$	$10, \frac{0.113 \pm 0.003}{0.099-0.127}$

For each parameter $n, \frac{\bar{x}_m \pm SE}{\lim}$, where *n* is the sample size; x_m is the arithmetic mean; *SE* is the standard error of the mean, and lim is the range of the values: minimum and maximum. The names of bird species are arranged in order of decreasing size of the body mass of adult birds. The following parameters are given in paratheses: the first figure is the type of development of the species: (*0*) semialtricial and (*1*) altricial; the second figure is the type of nesting: (*0*) closed-nesting and (*1*) open-nesting; the third figure designates the size groups of the species: (*0*) large, (*1*) medium, and (*2*) small; and the fourth figure is the duration of the nestling period: (*0*) short, (*1*) medium, and (*2*) long.

$z = -2.3$, $P = 0.0233$; great tit: M–W: $z = -3.7$, $P = 0.0002$). The mass of nestlings of the rock pigeon, nuthatch, and pied flycatcher before their departure from the nests and the mass of adult birds do not differ significantly.

The body mass of nestlings on the day of hatching and before leaving the nests and that of adult birds of all studied species is directly and closely linked to the duration of the nestling period ($r = 0.74$, $P < 0.0001$; $r = 0.86$, $P < 0.0001$; $r = 0.85$, $P < 0.0001$, respectively) and the definitive sizes of birds (nestlings on the day of hatching: $r = 0.87$, $P < 0.0001$; the nestlings before departure from the nests: $r = 0.99$, $P < 0.0001$).

It should be noted that the body mass of nestlings on the day of hatching and before leaving the nests and that of adult birds depends on the type of nesting ($F_{(1;191)} = 38.7$, $P < 0.0001$; $F_{(1;186)} = 25.6$, $P < 0.0001$ and $F_{(1;159)} = 18.8$, $P < 0.0001$, respectively). It is larger in open-nesting species compared with closed-nesting ones in different size groups: 7.2 ± 0.5 g ($n = 89$, lim 1.2–20.0) and 3.3 ± 0.4 g ($n = 104$, lim 0.7–13.3) in small species, 165.5 ± 17.3 g ($n = 86$, lim 13.8–486.0) and 68.7 ± 9.9 g ($n = 102$, lim 8.0–352.0) in medium species, and 171.0 ± 19.7 g ($n = 72$, lim 15.7–563.0) and 77.3 ± 11.2 g ($n = 89$, lim 8.4–362.0) in large species, respectively. In each age group, this index depends on the size of the species ($F_{(2;190)} = 501.9$, $P < 0.0001$; $F_{(2;185)} = 357.7$, $P < 0.0001$ and $F_{(2;158)} = 303.8$, $P < 0.0001$, respectively). It is higher in large species compared with medium and small ones: 11.2 ± 0.4 g ($n = 62$, lim 6.2–20.0), 5.3 ± 0.1 g ($n = 28$, lim 4.8–6.1) and 1.4 ± 0.03 g ($n = 103$, lim 0.7–2.2); 288.0 ± 14.0 g ($n = 62$, lim 136.0–486.0), 63.4 ± 2.1 g ($n = 25$, lim 41.8–78.0) and 17.8 ± 0.5 g ($n = 101$, lim 8.0–33.0); 304.1 ± 16.3 g ($n = 51$, lim 156.0–563.0), 78.9 ± 2.3 g ($n = 26$, lim 61.4–98.8) and 19.4 ± 0.8 g ($n = 84$, lim 8.4–43.4), respectively (Fig. 1).

According to our data, the excess of the definitive mass by nestlings by the end of the nestling period, as well as the reduction in their weight before the departure from nests, was observed in both open-nesting and closed-nesting species. This fact is seen as an adaptation of nestlings to flying out of the nests and active movements, including flight, after leaving the nest (Poznanin 1946, 1979). The most characteristic curves of the change in the mass of nestlings over the nestling period correlated with the relative duration of the nestling period are given in Fig. 2.

The relative body mass of nestlings on the day of hatching and before leaving the nests depends on the type of development ($F_{(1;50)} = 56.1$, $P < 0.0001$). This value is higher in semialtricial birds (rock pigeon, common kestrel, and red-footed falcon) compared with altricial ones (rook, magpie, and jackdaw): for the nestlings on the day of hatching, it is 5.9 ± 0.5% ($n = 22$, lim 3.7–11.2) and 2.9 ± 0.04% ($n = 30$, lim 2.6–3.4); for the nestlings before leaving their nests, it amounts to 99.2 ± 1.9% ($n = 22$, lim 76.2–113.6) and 59.1 ± 7.7% ($n = 30$, lim 0.7–101.7), respectively.

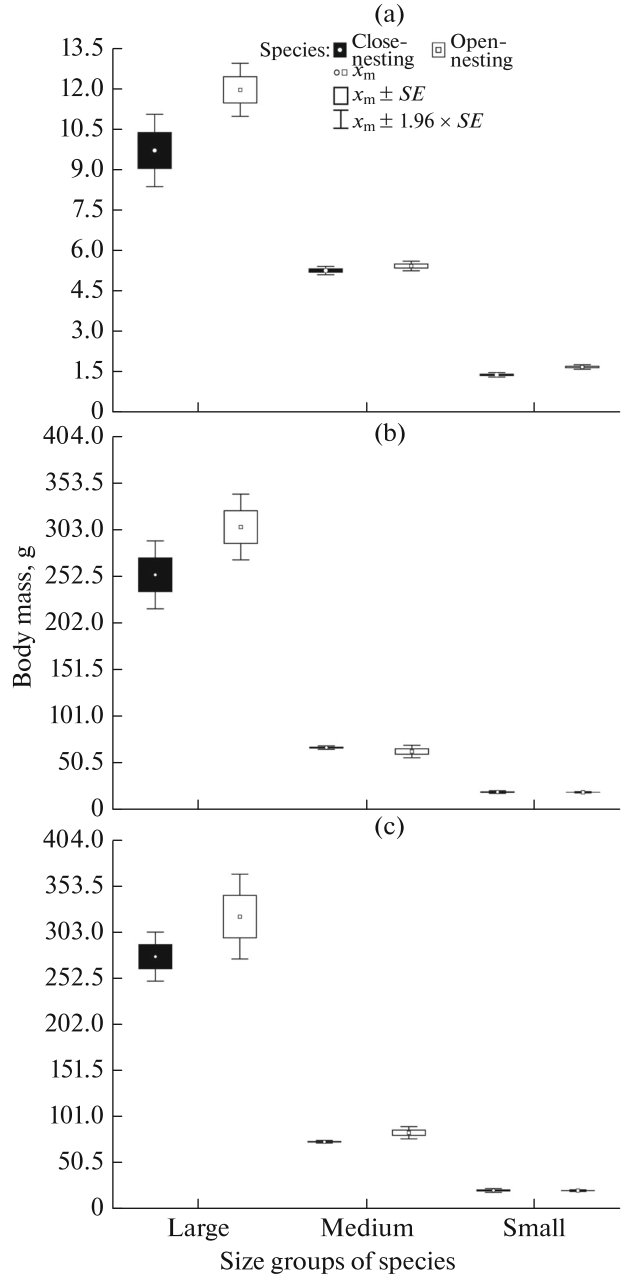

Fig. 1. Distribution of the body mass of nestlings (a) on the day of hatching, (b) before leaving the nest, and (c) in different size groups in closed- and open-nesting species.

In open-nesting and closed-nesting species, the relative body mass of nestlings on the day of hatching does not depend on the type of nesting. In the nestlings before leaving the nests, this parameter depends on this factor ($F_{(1;186)} = 8.0$, $P = 0.0052$). It is higher in the nestlings of closed-nesting species compared to open-nesting ones: 93.7± 1.5% ($n = 102$, lim 60.1–

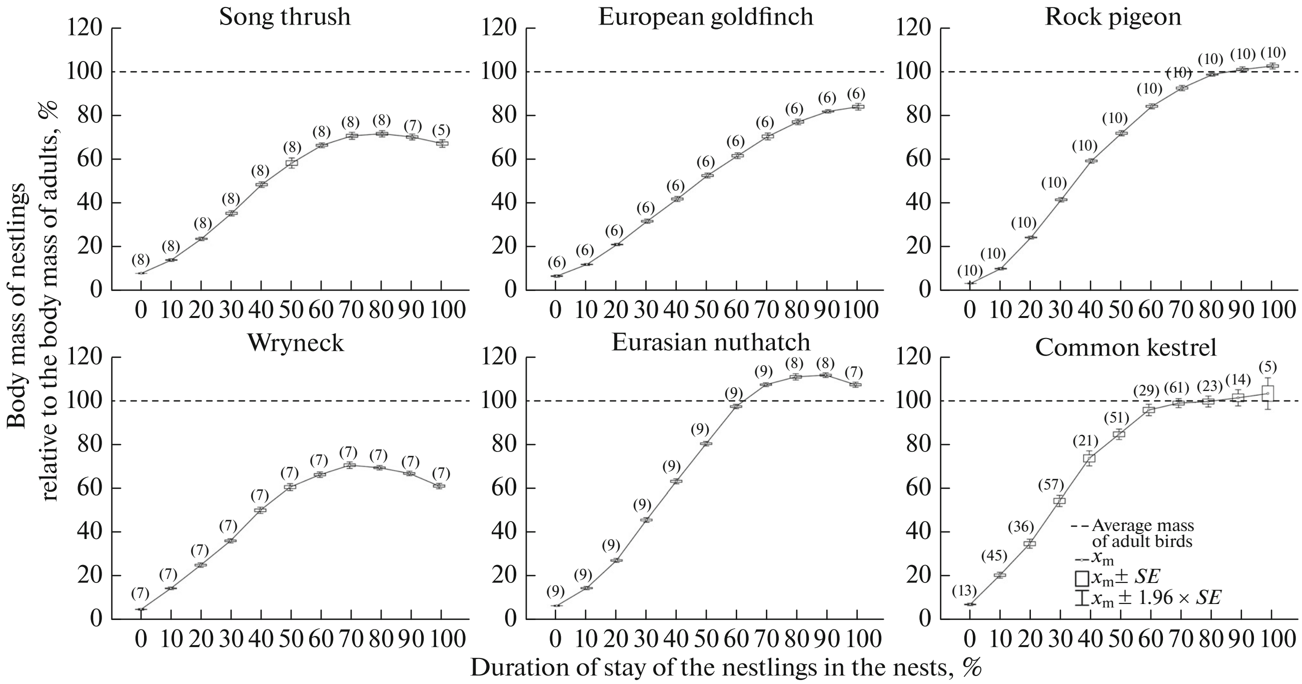

Fig. 2. Dynamics of the body mass growth of nestlings of the song thrush, goldfinch, rock pigeon, wryneck, nuthatch, and common kestrel. The sample size is given in parentheses.

140.8) and 88.3 ± 1.2% (n = 86, lim 63.1–115.2), respectively.

In large species, the relative body mass of nestlings on the day of hatching and before their departure from their nests does not depend on the type of nesting. In medium-sized species, this index depends on that factor only in nestlings before the departure from the nests ($F_{(1;23)} = 62.6$, $P < 0.0001$). This parameter is considerably higher in the nestlings of closed-nesting species compared to open-nesting ones: 90.6 ± 1.3% (n = 10, lim 83.4–98.2) and 73.0 ± 1.6% (n = 15, lim 63.1–84.3), respectively. In the hatchlings of small species, the relative mass depends on the type of nesting ($F_{(1;101)} = 12.2$, $P = 0.0007$). In the nestlings of open-nesting species, it is higher (8.5 ± 0.2%; n = 29, lim 6.3–11.5) than in closed-nesting ones (7.3 ± 0.2%; n = 74, lim 4.2–12.1).

The rate of growth of the mass of nestlings naturally decreases in the course of the nestling period. In the dynamics of the specific growth rate of nestlings, three periods are usually distinguished (Dinesman, 1940; Poznanin, 1979; Rodimtsev, 1984; etc.). The beginning of postembryogenesis is characterized by a sharp decline in the growth rates, and at the end of the breeding period, they stabilize. Reduction in the rate of growth of this parameter in nestlings is due to the expenditure of matter and energy on growth, development of the internal organs, and differentiation of feathers. The marked slowdown in body mass growth rates that occurs in the first week of life is due to the formation of feather stumps below the skin and their appearance on its surface. Subsequently, the formation of feathering and motor activity of the nestlings, which require large energy inputs, lead to slower growth in the body mass.

The specific growth rate of the mass of nestlings in different species closely and negatively correlated with the duration of the nestling period ($r = -0.76$, $P < 0.0001$) and moderately with the definitive sizes of the birds ($r = -0.51$, $P < 0.0001$). This parameter depends on the time spent by the nestlings in the nests ($F_{(2;185)} = 229.1$, $P < 0.0001$). The specific growth rate of mass is higher in the nestlings of those species that have a short nestling period, compared with the nestlings of the species with average and long nestling periods, and it amounts to 0.212 ± 0.006 (n = 38, lim 0.157–0.312), 0.143 ± 0.002 (n = 88, lim 0.099–0.191), and 0.107 ± 0.002 (n = 62, lim 0.076–0.137), respectively.

The specific growth rate of body mass also depends on the type of nesting and sizes of birds ($F_{(1;186)} = 18.5$, $P < 0.0001$). Thus, the highest average values of the specific growth rate over the nestling period among the studied species of birds were observed in the nestlings of open-nesting species: $C = 0.159 \pm 0.006$ (n = 86, lim 0.076–0.312); the lowest average values were registered in closed-nesting species: $C = 0.133 \pm 0.002$ (n = 102, lim 0.090–0.190). This parameter depends on the different size groups of species ($F_{(2;166)} = 171.2$, $P < 0.0001$). The nestlings of larger species grow less intensely compared with the medium- and small-sized ones: $C = 0.107 \pm 0.002$ (n = 62, lim 0.076–0.137), $C = 0.164 \pm 0.008$ (n = 25, lim 0.112–0.222), and $C =$

0.164 ± 0.004 ($n = 101$, lim 0.099–0.312), respectively. Among the open-nesting species, the minimum average value of this indicator was observed in the nestlings of the red-footed falcon and the maximum value was registered in the yellow wagtail; among the closed-nesting species, the lowest values of average specific growth rate are characteristic of the nestlings of the rock pigeon and the highest are characteristic of the tree sparrow.

The specific growth rate of the mass of nestlings of different size groups with the exception of large species with a long nesting season depends on this factor in medium ($F_{(1;23)} = 133.7$, $P < 0.0001$) and small ($F_{(1;99)} = 144.6$, $P < 0.0001$) species. It is higher in species with a short nestling period (size group: medium species: fieldfare and song thrush ($C = 0.193 \pm 0.005$; $n = 15$, lim 0.157–0.222); small species: chaffinch and white and yellow wagtails ($C = 0.224 \pm 0.009$; $n = 23$, lim 0.180–0.312)) compared with species with a medium nestling period (size group: medium-sized species: common starling ($C = 0.121 \pm 0.002$; $n = 10$, lim 0.112–0.128); small species: wryneck, tree sparrow, Eurasian nuthatch, great tit, European goldfinch, black-headed goldfinch, barn swallow, common redstart, pied flycatcher, and coal tit ($C = 0.146 \pm 0.002$; $n = 78$, lim 0.099–0.191). This indicates the existence of a direct correlation between the rate of growth of nestlings, the time spent in the nest of birds, and the definitive sizes of the birds.

The specific rate of growth of nestlings depends on the type of development ($F_{(1;50)} = 58.8$, $P < 0.0001$) and is higher in the representatives of altricial bird species (rook, magpie, and jackdaw) compared with the semialtricial ones (rock pigeon, common kestrel, and red-footed falcon): 0.115 ± 0.002 ($n = 30$, lim 0.097–0.137) and 0.093 ± 0.002 ($n = 22$, lim 0.076–0.102), respectively. The time spent by nestlings in the nest in altricial and semialtricial species averages 29.7 ± 0.4 ($n = 30$, lim 27.0–32.0) and 27.9 ± 1.4 ($n = 22$, lim 19.0–34.0), respectively. The differences were not statistically significant.

The maximum values of the specific growth rate, from 0.283 to 0.508, depending on the species, in most examined birds were registered in the first days of life of nestlings (table). These maximum values negatively and moderately correlate with the time spent by the nestlings in the nests and with the definitive sizes of the birds ($r = -0.50$, $P = 0.0179$ and $r = -0.57$, $P = 0.0052$, respectively).

The maximum specific growth rates of nestlings of the studied species with different types of nesting do not differ significantly. Among open-nesting species, magpie nestlings display the highest specific growth rates and the red-footed falcon nestlings have the lowest rates; in closed-nesting species, the highest maximum specific growth rate was observed in the nestlings of the tree sparrow and the lowest was in jackdaw nestlings. This parameter depends on the different size groups of birds ($F_{(2;19)} = 7.0$, $P = 0.0054$). Among the nestlings belonging to different size groups, it has the highest values in medium-sized species ($n = 3$) and the lowest values in large species ($n = 7$), averaging 0.475 ± 0.023 and 0.370 ± 0.029, respectively.

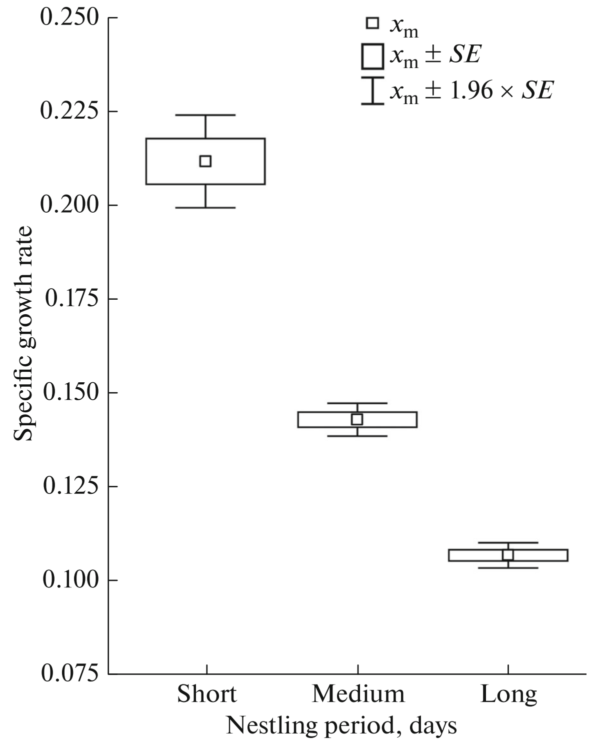

Fig. 3. Distribution of the specific body mass growth rates in the nestlings of species with different durations of the nestling period.

Different views exist on the dynamics of the specific growth rate of the mass of nestlings in early postembryogenesis. According to some authors (Bannikov, 1939; Poznanin, 1979; etc.), the maximum specific rate of mass growth in small and medium-sized altricial birds occurs on the 1st–2nd days of life. Other specialists (Denisova and Artamonova, 1971, 1977) identified two types of growth in passerine nestlings: the first one with a maximum specific rate of weight growth on the 1st day and the second type, on the 3rd–6th days. Our research revealed the existence of a definite correlation: in the small and medium-sized birds, the maximum specific growth rates of the nestlings were always established in the 1st or 1st–2nd days of life, whereas in large species, this is observed later: on the 2nd–4th days (Fig. 4). This might be a general rule for the growth of semialtricial and altricial birds. In some species with a long nestling period, the maximum specific growth rate of nestlings is observed on the 1st–2nd days.

The reasons for the slower growth of nestlings of closed-nesting species compared with the open-nesting ones in connection with the adaptive value of accelerated growth for the nestlings with a short nest-

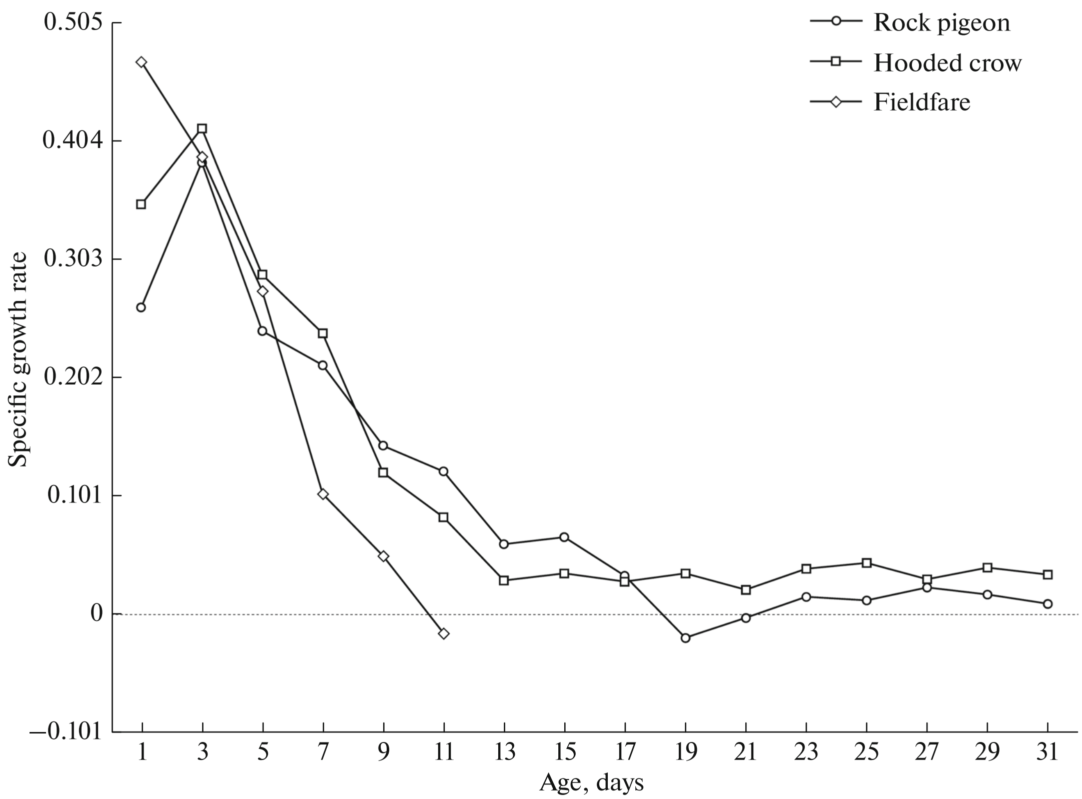

Fig. 4. Dynamics of the specific body mass growth rates in the rock pigeon, hooded crow, and fieldfare nestlings.

ling period have been repeatedly discussed in literature. The nestlings of closed-nesting species are relatively smaller at hatching than the nestlings of open-nesting species with similar sizes of their parents' bodies (Mal'chevskii, 1959). During the nestling period, the nestlings of closed-nesting species grow significantly larger than the nestlings of open-nesting species (Poznanin, 1948; Mukhtarov, 1977; etc.). This information was confirmed by our data.

Differences in the growth of nestlings of different ecological groups of birds are associated with the time spent by them in the nest. The nestlings of closed-nesting species stay longer in the nest than those of open-nesting species of similar size. With an increase in the nestling period, their average specific growth rate decreases. However, the nestlings of hollow-nesting birds reach a maximum mass well before the departure from the nest, which later decreases. Thus, the mass of nestlings of big tits is greater on the 12th day of life than on the 17th–19th days, when they leave their nests. The mass of the common starling nestlings is higher on the 14th day (departure on the 20th–22nd days) and that of pied flycatchers and common redstart, on the 10th day (departure on the 14th–16th days). However, the intensity of growth of nestlings of open and closed-nesting species of similar size in the postembryogenesis periods 0–6th and 6th–12th days do not differ significantly, nor does their relative body mass. The evolution of closed-nesting birds led to the fact that their young stay in their nests longer, their various systems of organs and feathering develop and form better, and by the time of leaving the nest, they are more adapted to independent life than the nestlings of open-nesting species.

After leaving the nests, nestlings come under the influence of many factors of the changing environment. As mentioned above, in some species, nestlings leave the nest with a greater mass than adult birds. This was found in the red-footed falcon, kestrel, rock pigeon, barn swallow, yellow wagtail, common nuthatch, and pied flycatcher. The literature suggests that this pattern is also characteristic of Blyth's reed warbler (*Acrocephalus dumetorum*) and the marsh warbler (*Acrocephalus palustris*) (Bannikov, 1939) and the common kingfisher (*Alcedo atthis*) and whinchat (*Saxicola rubetra*) (Poznanin, 1979). The nestlings of the wryneck, fieldfare, and song thrush had the lowest mass upon leaving the nest. After leaving the nests and dispersal of the broods, the mass of the young birds continues to decrease. This is probably due to their increased activity and energy losses in order to maintain a constant body temperature. The increase in weight is resumed after the fledglings transition to a fully independent life and the development of necessary behavioral stereotypes for active searching and foraging.

CONCLUSIONS

This study revealed that the body mass of nestlings on the day of hatching and before their departure from the nest and that of adult birds are associated with the duration of the nestling period. This parameter is higher in large open-nesting species compared with small and medium-sized closed-nesting ones. The relative body mass of nestlings on the day of hatching did not differ in birds with different types of nesting; however, before leaving the nests, it was higher in closed-nesting species. Over the period of staying in the nest, the nestlings of most studied species did not reach the mass of adult birds.

The average specific growth rate of nestlings over the nestling period depends on the nesting type, time spent in the nests, and definitive sizes of the species. The maximum specific growth rate in small and medium-sized birds is observed in the first days of life; in larger species, it is found from the second to the fourth days. This parameter does not depend on the type of nesting, but is inversely related to the time spent by the nestlings in the nests and the definitive sizes of the birds. In some species with a long nestling period, the maximum specific growth rate of nestlings is observed on the first and second days. The nestlings of larger species grow less intensely compared with the nestlings of medium and small species.

Thus, the growth characteristics of semialtricial and altricial birds during the nestling period depend on a number of factors: the type of development and nesting, the duration of stay of nestlings in the nest, the size groups of species, and the definitive sizes of birds. Equally important are the parental care for the nestlings, the competition for food among the nestlings, and specific features of the ecology of individual species.

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