ISSN 1995-4255, Contemporary Problems of Ecology, 2016, Vol. 9, No. 4, pp. 503–513. © Pleiades Publishing, Ltd., 2016.
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Comparison of Fatty Acid Compositions in Birds Feeding in Aquatic and Terrestrial Ecosystems

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Received October 5, 2015; in final form, November 2, 2015

Abstract—Fatty acid (FA) contents and compositions in the pectoral muscles of 18 bird species from Novosibirsk, Volgograd, and Yaroslavl oblasts were studied. Three groups of birds that had significantly different FA compositions were distinguished based on a multivariate statistical analysis: Passeriformes, Columbiformes, and a group of waterfowl and waterbird species (Charadriiformes, Anseriformes, Podicipediformes, and Ciconiiformes). The highest content of physiologically important docosahexaenoic acid (22:6n-3, DHA), which is considered a marker of aquatic food, was surprisingly found in the biomass of Passeriformes, which are terrestrial feeders, rather than in the biomass of waterfowls and waterbirds. It was suggested that Passeriformes species had the ability to synthesize large quantities of DHA from short-chain omega-3 FAs, which is rare among animals.

Keywords: polyunsaturated fatty acids, birds, aquatic ecosystems, terrestrial ecosystems

DOI: 10.1134/S1995425516040065

INTRODUCTION

As is known, one of the key problems of ecology is to study the fluxes of matter and energy in natural ecosystems. In recent years, along with the traditional study of these fluxes in food webs of individual ecosystems, there has been a significant growth in attention of ecologists to the processes of transport of organic carbon between ecosystems, including aquatic and terrestrial ecosystems (Baxter et al., 2005; Ballinger and Lake, 2006; Gratton and Vander Zanden, 2009). The amount of organic matter entering with biogenic fluxes from water to land can be very high. For example, the share of the biomass of freshwater organisms in the annual ration of forest aviafauna in Japan surpasses 25% (Nakan and Murakami, 2001). Moreover, the products of water ecosystems can give not only a large quantitative, but also an important qualitative contribution to the feeding of terrestrial consumers. In aquatic ecosystems, diatoms, dinophytes, and cryptophytes synthesize de novo a large amount of long-chain polyunsaturated fatty acids (FAs) of omega-3 family (PUFAs), namely eicosapentaenoic acid (20:5n-3, EPA) and docosahexaenoic acid (22:6n-3, DHA), which are essential food components in most animals, both aquatic and terrestrial ones, including humans (Arts et al., 2001). Since terrestrial organisms (some bacteria, fungi, and animals, but not higher plants!) are able to produce EPA and DHA only in very limited quantities, aquatic ecosystems serve as the main source of these physiologically important substances in the biosphere (Gladyshev et al., 2009, 2013, 2015). PUFAs synthesized by microalgae are transfered through the food chains to invertebrates and fish and are brought out to the land mainly through waterfowls and waterbirds and the emergence of amphibiotic insects. According to the available estimates, amphibiotic insects supply 240×10^6 kg year^{-1} EPA+DHA on a global scale, and birds bring out 432×10^6 kg year^{-1} (for comparison: humans take out 180×10^6 kg year^{-1} EPA + DHA from aquatic ecosystems at the expense of fishery) (Gladyshev et al., 2009).

Thus, waterfowls and waterbirds are a very important factor of organic-matter transport from aquatic to terrestrial ecosystems not only in the quantitative but also in the qualitative respect. Nevertheless, the data on the FA composition of the biomass of waterfowls and waterbirds are few and scattered in the literature. The FA composition of waterfowls and waterbirds has not yet been compared with that of terrestrial birds. Therefore, the goal of our work was to compare the FA composition in different waterfowl and waterbird species with birds that feed on the land. We checked the following hypothesis: the content of EPA and DHA in the biomass of waterfowls and waterbirds that directly consume the products of aquatic ecosystems is higher than in birds that are terrestrial feeders.

MATERIALS AND METHODS

Research Areas

Various bird species were caught in different years in the following areas. Chistoe Lake (Gorky Reservoir Basin, Yaroslavl oblast), June–August 2008: gray heron (*Ardea cinerea* Linnaeus; the number of individuals taken for analysis was $n = 9$); the Baraba forest steppe (Novosibirsk oblast), July–August 2009: yellow wagtail (*Motacilla flava* Linnaeus, $n = 1$), common tern (*Sterna hirundo* Linnaeus, $n = 1$), barn swallow (*Hirundo rustica* Linnaeus, $n = 1$), heron (*A. cinerea*, $n = 1$), white wagtail (*Motacilla alba* Linnaeus, $n = 1$), and oriental turtle dove (*Streptopelia orientalis* Latham, $n = 1$); the Lantsug and Chernavka Rivers (Elton Lake Basin, Volgograd oblast), August 2010 and 2014: common greenashank (*Tringa nebularia* Gunnerus, $n = 1$), red-necked phalarope (*Phalaropus lobatus* Linnaeus, $n = 1$), great crested grebe (*Podiceps cristatus* Linnaeus, $n = 1$), pied avocet (*Recurvirostra avosetta* Linnaeus, $n = 1$), common shelduck (*Tadorna tadorna* Linnaeus, $n = 1$), and Kentish plover (*Charadrius alexandrinus* Linnaeus, $n = 1$); the Kulunda steppe (the Novosibirsk oblast), July–September 2012: tree sparrow (*Passer montanus* Linnaeus, $n = 8$), reed bunting (*Emberiza schoeniclus* Linnaeus, $n = 3$), sedge warbler (*Acrocephalus schoenobaenus* Linnaeus, $n = 2$), common starling (*Sturnus vulgaris* Linnaeus, $n = 2$), rock dove (*Columba livia* Gmelin, $n = 2$), white wagtail (*M. alba*, $n = 1$), and black-headed gull (*Larus ridibundus* Linnaeus, $n = 1$).

Sampling

Samples were taken for subsequent analyses of FAs from pectoral muscles, i.e., the tissue that is the basis of the edible bird biomass. Muscle samples weighing 0.5–1 g were fixed immediately after being taken with the chloroform: methanol mixture (the volume ratio of 2 : 1) and then kept at –20°C up to further treatment for no more than a month. The biochemical analysis of FAs was made by the methods and under the conditions described earlier (Gladyshev et al., 2014).

Lipids were extracted from the samples with chloroform and methanol in the ratio of 2 : 1. Methanolysis of FAs of total lipids (i.e., the formation of methyl esters) was performed in a water bath at 85°C for 2 h. Methyl esters of FAs were analyzed by a gas chromatograph equipped with a mass spectrometer detector (model 6890/5975C, Agilent Technologies, United States). The conditions of the analysis were as follows: helium was used as a carrier gas; split entry was performed; a HP-FFAP capillary column with a length of 30 m and internal diameter of 0.25 mm was used; the temperature of entry and interface was 250 and 280°C, respectively; the ionization energy of the detector was 70 eV; and scanning was performed in the range of 45–450 atomic units. Chromatographic peaks of FAs were identified by mass spectra in comparison with those available in the NIST-2005 Database (Agilent Technologies), as well as by comparison of the retention times with those of the standards (Sigma, United States). The quantitative content of FAs in the biomass was determined according to the value of the internal standard nonadecanoic acid (19:0), a fixed amount of which was added to the samples before extracting lipids.

In the subsequent calculations, the total amount of n-3 FAs consisted of the following acids: 18:3n-3 + 18:4n-3 + 20:3n-3 + 20:5n-3 + 22:5n-3 + 22:6n-3. The total amount of n-6 FAs consisted of the following acids: 18:2n-6 + 18:3n-6 + 20:2n-6 + 20:3n-6 + 20:4n-6 + 22:4n-6 + 22:5n-6.

Statistical Analysis

The values of standard errors in mean were calculated conventionally. ANOVA accompanied by the post-hoc Fisher test calculation for the least significant differences (LSDs) was used to determine the significance of differences. The canonical correspondence analysis was also used to process data (the method of multivariate classification that permits multidimensional data (from the table) to be reduced to the least number of measurements (factors), under which the distances (variance) between individual cells (rows and columns) are shown in the "chi-square" values defined as an analogue of inertia (Legendre, P. and Legendre, L., 1998). The calculations were all performed using the standard Statistica software package (version 9, StatSoft, United States).

RESULTS

The totality of samples was detected to contain 79 FAs. The levels (the percentage of the total amount of acids) of quantitatively significant FAs are shown in Tables 1 and 2. The levels of short-chain FAs (12:0 and 14:0) varied insignificantly in the studied species. However, in Columbiformes, *S. orientalis*, and *C. livia*, 12:0 was not found, and 14:0 and 16:0 had the minumum level (Tables 1 and 2). FAs with a branched chain (iso-acids) and with an odd number of atoms

Table 1. Average content of quantitatively significant FAs (% of the total amount of FAs ± standard error) in the pectoral muscles of the bird species: sparrow *Passer montanus* (the number of tests $n = 8$), bunting *Emberiza schoeniclus* ($n = 3$), reed bunting *Acrocephalus schoenobaenus* ($n = 2$), starling *Sturnus vulgaris* ($n = 2$), white wagtail *Motacilla alba* ($n = 2$), heron *Ardea cinerea* ($n = 10$), and dove *Columba livia* ($n = 2$). The averages designated by the same latter (in rows) do not have significant differences according to the Fisher LSD test (post hoc for the ANOVA); if ANOVA is insignificant, the test was not made and there are no literal designations

	Sparrow	Bunting	Reed bunting	Starling	White wagtail	Heron	Dove
12:0	0.1 ± 0.0^{A}	0.1 ± 0.0^{AC}	0.7 ± 0.4^{B}	0.1 ± 0.0^{AC}	0.4 ± 0.3^{C}	0.1 ± 0.0^{A}	0.0 ± 0.0^{AC}
14:0	0.5 ± 0.1^{A}	1.4 ± 0.7^{A}	4.3 ± 0.9^{B}	1.2 ± 0.2^{A}	2.7 ± 2.4^{B}	1.4 ± 0.1^{A}	0.2 ± 0.0^{A}
i15:0	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.1 ± 0.1^{A}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.4 ± 0.0^{B}	0.0 ± 0.0^{A}
ai15:0	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.1 ± 0.1^{B}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.2 ± 0.0^{B}	0.0 ± 0.0^{A}
15:0	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.1 ± 0.0^{A}	0.1 ± 0.0^{A}	0.1 ± 0.0^{A}	0.4 ± 0.0^{B}	0.1 ± 0.0^{A}
16:0	20.6 ± 0.6^{A}	19.3 ± 0.6^{AB}	16.7 ± 0.7^{BD}	17.8 ± 0.1^{ABD}	17.0 ± 0.5^{BD}	15.7 ± 0.8^{D}	12.5 ± 0.2^{C}
16:1n-9	0.1 ± 0.0^{A}	0.1 ± 0.0^{A}	0.2 ± 0.0^{AB}	0.3 ± 0.0^{AB}	0.1 ± 0.0^{A}	0.5 ± 0.1^{B}	0.3 ± 0.1^{AB}
16:1n-7	1.1 ± 0.1^{A}	0.9 ± 0.1^{A}	3.6 ± 1.6^{B}	2.7 ± 0.0^{AB}	2.6 ± 1.6^{AB}	8.3 ± 0.5^{C}	1.9 ± 0.2^{AB}
i17:0	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.1 ± 0.0^{A}	0.0 ± 0.0^{A}	0.1 ± 0.0^{A}	0.6 ± 0.1^{A}	0.0 ± 0.0^{A}
ai17:0	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.1 ± 0.1^{A}	0.0 ± 0.0^{A}	0.1 ± 0.0^{A}	0.5 ± 0.1^{B}	0.0 ± 0.0^{A}
16:2n-4	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.2 ± 0.0^{B}	0.0 ± 0.0^{A}
17:0	0.1 ± 0.0^{A}	0.2 ± 0.1^{AB}	0.5 ± 0.0^{C}	0.3 ± 0.1^{B}	0.5 ± 0.1^{C}	0.6 ± 0.0^{C}	0.2 ± 0.0^{AB}
17:1	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.2 ± 0.1^{A}	0.1 ± 0.0^{A}	0.1 ± 0.1^{A}	0.6 ± 0.1^{B}	0.0 ± 0.0^{A}
18:0	19.3 ± 0.5^{A}	20.6 ± 0.9^{A}	18.5 ± 2.2^{A}	19.2 ± 1.2^{A}	20.5 ± 1.9^{A}	15.1 ± 0.9^{B}	21.9 ± 1.4^{A}
18:1n-9	10.1 ± 0.4^{A}	8.4 ± 0.9^{A}	9.5 ± 0.3^{A}	18.4 ± 0.1^{B}	11.1 ± 1.7^{AC}	16.5 ± 0.5^{BD}	14.1 ± 2.3^{CD}
18:1n-7	1.7 ± 0.1^{A}	2.2 ± 0.1^{AB}	3.2 ± 0.5^{C}	2.0 ± 0.1^{A}	2.9 ± 0.0^{BC}	4.8 ± 0.2^{D}	2.4 ± 0.0^{AC}
18:2n-6	15.2 ± 0.7^{A}	15.1 ± 0.7^{A}	8.9 ± 2.0^{BC}	10.6 ± 1.3^{B}	10.4 ± 1.7^{B}	7.0 ± 0.4^{C}	23.0 ± 1.5^{D}
18:3n-3	1.3 ± 0.1^{AB}	0.9 ± 0.3^{AC}	2.5 ± 0.2^{D}	2.0 ± 0.4^{BD}	3.0 ± 1.0^{D}	2.7 ± 0.1^{D}	0.4 ± 0.2^{C}
18:4n-3	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.3 ± 0.0^{B}	0.0 ± 0.0^{A}
20:0	0.5 ± 0.0^{AB}	0.5 ± 0.0^{AB}	0.4 ± 0.0^{AC}	0.4 ± 0.0^{CD}	0.6 ± 0.0^{B}	0.3 ± 0.0^{D}	0.6 ± 0.1^{B}
20:1n-9	0.3 ± 0.0^{A}	0.2 ± 0.0^{A}	0.1 ± 0.0^{A}	0.3 ± 0.1^{A}	0.2 ± 0.0^{A}	0.9 ± 0.1^{B}	0.2 ± 0.0^{A}
20:2n-6	0.3 ± 0.0^{AC}	0.3 ± 0.0^{AB}	0.2 ± 0.1^{AC}	0.2 ± 0.1^{AC}	0.1 ± 0.0^{A}	0.4 ± 0.0^{B}	0.3 ± 0.0^{BC}
20:3n-6	0.3 ± 0.1^{AB}	0.1 ± 0.0^{A}	0.1 ± 0.0^{A}	0.2 ± 0.0^{AB}	0.1 ± 0.0^{A}	0.4 ± 0.0^{B}	0.3 ± 0.0^{AB}
20:4n-6	6.7 ± 0.2^{AB}	4.7 ± 0.2^{A}	4.9 ± 0.7^{AB}	8.6 ± 0.0^{BD}	7.4 ± 1.2^{AB}	9.8 ± 0.8^{D}	14.8 ± 1.0^{C}
20:3n-3	0.0 ± 0.0^{A}	0.0 ± 0.0^{AC}	0.1 ± 0.0^{B}	0.0 ± 0.0^{AB}	0.1 ± 0.0^{BC}	0.2 ± 0.0^{D}	0.0 ± 0.0^{A}
20:5n-3	0.3 ± 0.1^{A}	0.5 ± 0.1^{AB}	1.1 ± 0.1^{ABC}	1.6 ± 0.1^{B}	1.8 ± 0.4^{C}	3.3 ± 0.3^{D}	0.4 ± 0.2^{AB}
22:0	0.2 ± 0.0^{A}	0.2 ± 0.0^{AB}	0.3 ± 0.0^{BC}	0.3 ± 0.0^{BC}	0.3 ± 0.0^{B}	0.2 ± 0.0^{A}	0.2 ± 0.0^{ABC}
22:4n-6	0.5 ± 0.1^{A}	0.6 ± 0.1^{AB}	0.2 ± 0.0^{A}	0.4 ± 0.1^{A}	0.3 ± 0.1^{A}	1.0 ± 0.1^{C}	1.0 ± 0.1^{BC}
22:5n-6	1.8 ± 0.2^{A}	2.5 ± 0.5^{B}	0.7 ± 0.2^{C}	0.3 ± 0.1^{C}	0.5 ± 0.2^{C}	0.6 ± 0.0^{C}	0.4 ± 0.0^{C}
22:5n-3	1.1 ± 0.1^{A}	2.7 ± 0.7^{B}	2.7 ± 0.2^{B}	2.7 ± 0.0^{B}	3.5 ± 0.1^{B}	1.1 ± 0.1^{A}	2.9 ± 0.8^{B}
24:0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
22:6n-3	17.3 ± 0.6^{A}	18.0 ± 0.6^{A}	19.0 ± 0.1^{A}	9.4 ± 0.0^{B}	12.5 ± 2.2^{D}	2.8 ± 0.3^{C}	1.5 ± 0.0^{C}

Table 2. Content of quantitatively significant FAs (% of the total amount of FAs) in the pectoral muscles of the bird species (single samples): yellow wagtail *Motacilla flava*, swallow *Hirundo rustica*, phalarope *Phalaropus lobatus,* avocet *Recurvirostra avosetta*, tern *Sterna hirundo*, greenashank *Tringa nebularia*, plover *Charadrius alexandrinus*, gull *Larus ridibundus*, great crested grebe *Podiceps cristatus*, common shelduck *Tadorna tadorna,* and oriental turtle dove *Streptopelia orientalis*

	Yellow wagtail	Swallow	Phalarope	Avocet	Tern	Greenashank	Plover	Tern	Great crested grebe	Common shelduck	Oriental turtle dove
12:0	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0
14:0	1.2	0.6	1.7	1.7	0.6	1.2	0.9	0.8	1.0	1.3	0.1
i15:0	0.0	0.0	0.1	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.0
ai15:0	0.0	0.0	0.1	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.0
15:0	0.1	0.1	0.5	0.5	0.5	0.3	0.1	0.4	0.3	0.3	0.0
16:0	16.3	14.5	17.9	15.9	15.2	14.1	17.4	11.2	12.5	15.5	10.1
16:1n-9	0.0	0.3	0.2	0.2	0.0	0.2	0.3	0.3	0.3	0.1	0.2
16:1n-7	1.2	4.5	6.7	7.9	4.2	3.1	3.7	4.3	3.5	6.2	0.8
i17:0	0.1	0.1	0.1	0.2	0.5	0.2	0.1	0.1	0.3	0.2	0.0
ai17:0	0.1	0.1	0.1	0.1	0.1	0.3	0.0	0.1	0.1	0.1	0.0
16:2n-4	0.0	0.0	0.6	1.0	0.1	0.1	0.2	0.1	0.2	0.9	0.0
17:0	0.5	0.4	0.9	0.7	0.9	0.9	0.3	0.7	1.0	0.9	0.1
17:1	0.2	0.2	0.3	0.7	0.6	0.3	0.2	0.6	0.4	0.3	0.0
18:0	21.0	16.2	18.1	14.8	20.9	21.2	14.8	20.6	21.4	17.9	20.3
18:1n-9	8.7	23.9	16.5	14.1	15.8	15.0	23.8	18.4	11.6	11.5	8.1
18:1n-7	3.5	2.7	3.2	4.4	3.5	3.4	3.0	3.3	5.8	5.7	1.9
18:2n-6	12.5	12.0	7.2	7.5	6.0	12.0	13.1	10.6	10.3	8.5	22.3
18:3n-3	2.8	2.9	2.9	1.8	2.8	2.5	4.5	2.1	3.7	1.4	14.8
18:4n-3	0.0	0.0	0.2	0.4	0.2	0.0	0.1	0.0	0.2	0.2	0.0
20:0	0.6	0.4	0.5	0.4	0.4	0.6	0.3	0.5	0.5	0.6	0.6
20:1n-9	0.2	0.2	0.1	0.6	0.5	0.0	0.3	0.6	0.5	0.4	0.3
20:2n-6	0.2	0.1	0.0	0.0	0.3	0.1	0.2	0.2	0.2	0.1	0.1
20:3n-6	0.1	0.1	0.0	0.4	0.3	0.2	0.2	0.3	0.5	0.6	0.4
20:4n-6	6.8	5.9	9.2	7.7	14.7	13.9	8.0	14.4	12.2	4.2	10.8
20:3n-3	0.1	0.0	0.0	0.0	0.3	0.0	0.4	0.1	0.0	0.0	0.2
20:5n-3	2.5	1.1	7.8	8.7	2.4	4.1	2.8	3.8	6.0	11.6	2.5
22:0	0.2	0.2	0.3	0.3	0.2	0.3	0.2	0.5	0.3	0.5	0.2
22:4n-6	0.4	0.3	0.5	1.0	1.0	0.6	0.5	0.9	1.3	0.6	0.2
22:5n-6	0.5	0.6	0.2	0.1	0.9	0.1	0.2	0.8	0.3	0.1	0.1
22:5n-3	5.2	2.4	1.5	3.5	1.0	2.4	1.3	0.9	2.5	5.5	2.4
24:0	0.2	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.2	0.4	0.2
22:6n-3	13.5	8.8	0.7	1.1	3.7	1.6	2.0	2.9	1.0	1.9	2.1

(i15:0, ai15:0, 15:0, i17:0, ai17:0, 17:0, and 17:1) had the maximum levels (in sum, from 1.9 to 4.8%) in *A. cinerea*, *P. cristatus*, *T. tadorna* and Charadriiformes (*P. lobatus*, *R. avosetta*, *S. hirundo*, *T. nebularia* and *L. ridibundus*) (Tables 1 and 2). Among unsaturated acids, we should note the absence of 16:2n-4 and 18:4n-3 in all representatives of the Passeriformes order (*P. montanus*, *E. schoeniclus*, *A. schoenobaenus*, *S. vulgaris*, *M. alba*, *M. flava* and *H. rustica*) and the Columbiformes order (*S. orientalis* and *C. livia*) (Tables 1 and 2). Essential alpha-linolenic acid (18:3n-3, ALA) also had the maximal level in *S. orientalis*, but its minimum level was noted for *C. livia* (Tables 1 and 2). The level of physiologically important docosahexaenoic acid was the highest among the representatives of the Passeriformes order: from 8.8% in *H. rustica* to 19.0% in *A. schoenobaenus*, whereas it was only from 0.7% (*P. lobatus*) to 3.7% (*S. hirundo*) in the representatives of other orders (Tables 1 and 2). The levels of other acids, including oleic acid (18:1n-9, OA), arachidonic acid (20:4n-6, ARA), and eicosapentaenoic acid, varied without any obvious regularities both within the studied orders and between them (Tables 1 and 2).

The multidimensional canonical correspondence analysis in the space of two canonical factors resulted in marking out the cluster including the species of Passeriformes order, the cluster formed by the species of the Columbiformes order, and the cluster including all other studied species (figure). The first canonical factor that shows 49.2% of the total variance (inertia) was caused primarily by the differences between the levels of 16:2n-4 and 18:4n-3, as well as iso- and odd FAs in waterfowls and waterbirds and the level of 22:6n-3 in Passeriformes and other species (figure). The second canonical factor that shows 17.5% of inertia was caused mainly by the differences in the levels of 18:3n-3 and 18:2n-6 and level of 12:0 in Columbiformes and other birds (figure).

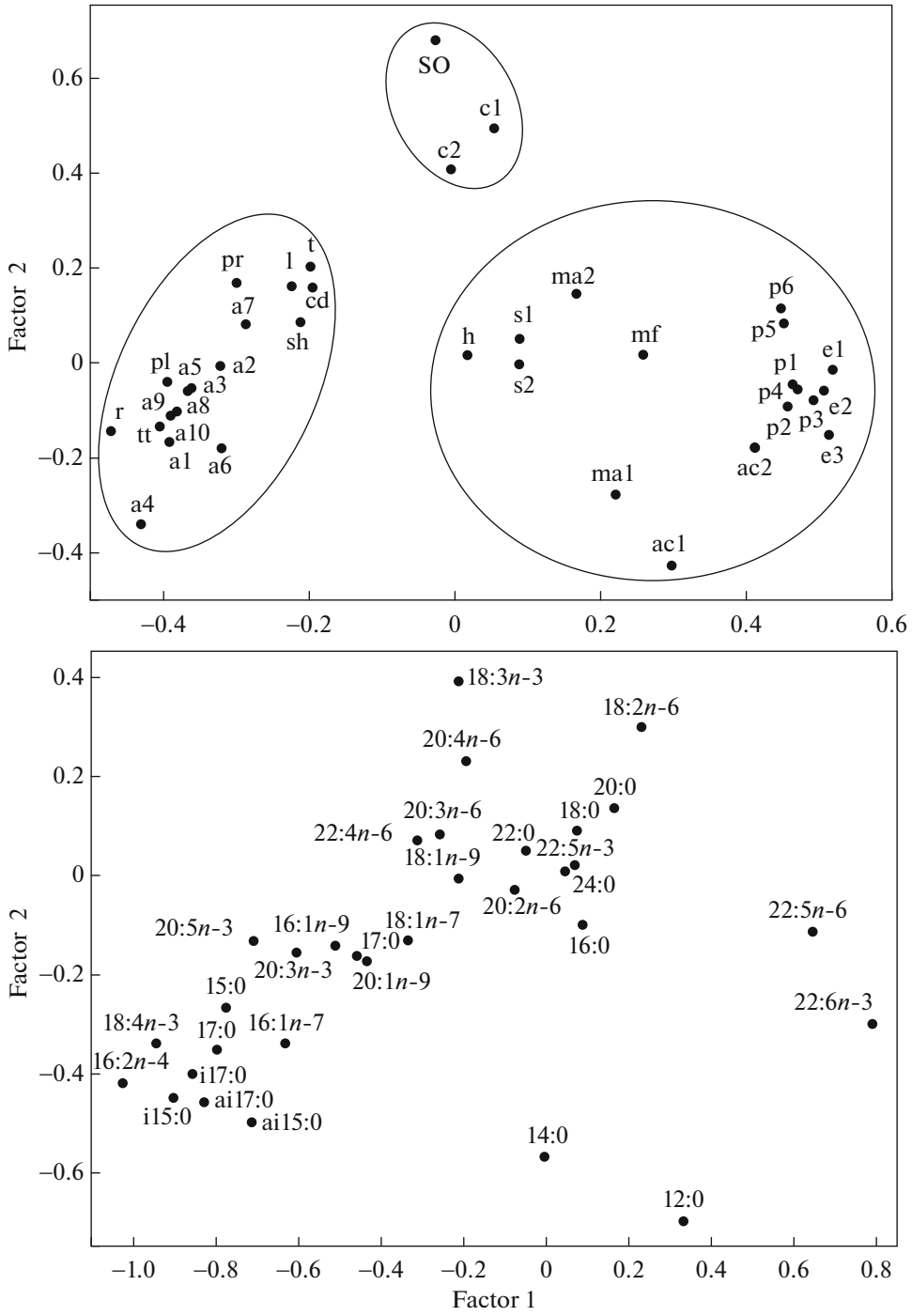
The content of two physiologically important polyunsaturated FAs EPA and DHA in the wet weight is presented in Table 3. The maximum values of the content of EPA were found in Charadriiformes. In addition, the high (>1 mg/g) values of the content of EPA were found in *T. tadorna* (Anseriformes) and *P. cristatus* (Podicipediformes) (Table 3). The maximum values of the content of DHA proved to be a distinctive feature of Passeriformes (Table 3). The studied species were all detected to have the low values of the ratio between the sums of FAs n-6/n-3, except for *C. livia* (Table 3).

DISCUSSION

The conducted research studied the FA content and composition in two major groups of birds, namely aquatic and terrestrial feeders. The first group included waterfowls and waterbirds, the major food of which is aquatic invertebrates, amphibians, and fish: phalarope *P. lobatus* (Rubega and Inouye, 1994), pied avocet *R. avosetta* (Goutner, 1985), tern *S. hirundo* (Bugoni and Vooren, 2004; Danhardt et al., 2011), greenashank *T. nebularia* (Kalejta, 1993), plover *C. alexandrinus* (Castro et al., 2009; Pedro and Ramos, 2009), gull *L. ridibundus* (Moreira, 1995; Kubetzki and Garthe, 2003), shelduck *T. tadorna* (Anders et al., 20090; Ferns and Reed, 2009), great crested grebe *P. cristatus* (Gwiazda, 1997; Gagliardi et al., 2007), and heron *A. cinerea* (Fasola and Cardarelli, 2015). The second group consisted of birds, the diet which contains terrestrial plant and animal foods in different ratios: warbler *A. schoenobaenus* (Bibby et al., 1976. Schaub and Jenni, 2001; Zając and Solarz, 2004; Surmacki, 2005), sparrow *P. montanus* (Sakurai, 2011), swallow *H. rustica* (Orłowski and Karg, 2013; Orłowski et al., 2014), yellow wagtail *M. flava* (Gilroy et al., 2009), bunting *E. schoeniclus* (Orłowski et al., 2013), starling *S. vulgaris* (Rhymer et al., 2012), oriental turtle dove *S. orientalis* (Nakamura and Matsuoka, 1987), and rock dove *C. livia* (Baldaccini et al., 2000). White wagtail *M. alba* is able to feed with both adult terrestrial insects, including flying insects, and aquatic insect larvae and pupae, getting them near the water edge (Davies, 1976), so this species should be regarded as an intermediate between the two discussed bird groups.

As a result of the multidimensional canonical correspondence analysis, the group of waterfowls and waterbirds was separated from the "terrestrial" group. However, contrary to the original hypothesis, the main factors of this separation of the species in the multidimensional space were not EPA and DHA, but the 16:2n-4 marker of diatom algae and bacterial acids with an odd number of carbon atoms and a branched carbon chain. Moreover, the group of birds with terrestrial feeding objects (Passeriformes) was separated from other species by the high level of DHA.

The high (>20%) level of DHA in Passeriformes had been noted earlier in some works (Klaiman et al., 2009; Rodríguez-Turienzo et al., 2010); however, no comparison with other bird groups had been made, and the quantitative content in biomass had not been determined. The quantitative content of DHA in the biomass of Passeriformes was measured by us for the first time, and the high values were a complete surprise. As was noted above, most of the studied species from this order are mainly insectivorous, and among them only white wagtail *M. alba* gets part of its food (larvae and pupae) from water (riparian sludge). The content of DHA in the biomass in the discussed species from the Passeriformes order was from 1.5 to 3.5 mg g^{-1} wet weight; i.e., it largely surpassed the one not only in the waterfowls and waterbirds from the Charadriiformes, Anseriformes, Podicipediformes, and Ciconiiformes orders, but also in many fish species (Gladyshev et al., 2013).



Canonical analysis of the correspondence between bird species and their fatty acid composition: ac, sedge warbler (*Acrocephalus schoenobaenus*); p, tree sparrow (*Passer montanus*); h, barn swallow (*Hirundo rustica*); mf, yellow wagtail (*Motacilla flava*); ma, white wagtail (*Motacilla alba*); e, reed bunting (*Emberiza schoeniclus*); s, common starling (*Sturnus vulgaris*); pl, Red-necked phalarope (*Phalaropus lobatus*); r, pied avocet (*Recurvirostra avosetta*); sh, common tern (*Sterna hirundo*); t, common greenshank (*Tringa nebularia*); cd, Kentish plover (*Charadrius alexandrinus*); l, black-headed gull (*Larus ridibundus*); pr, great crested grebe (*Podiceps cristatus*); tt, common shelduck (*Tadorna tadorna*); a, gray heron (*Ardea cinerea*); so, oriental turtle dove (*Streptopelia orientalis*); and c, rock dove (*Columba livia*). Ciphers designate the numbers of samples taken in several replications.

What is the source of DHA in the biomass of Passeriformes? As was noted above, the basis of their diet is insects. However, as is known, terrestrial insects contain neither DHA nor EPA (Ryan et al., 1982; Buckner and Hagen, 2003; Wang et al., 2006). Along with terrestrial insects, the studied Passeriformes species also consume imagoes of amphibiotic insects (Karpenko and Chernyshov, 1981; Prokof'eva, 2004;

Table 3. Content eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (mg g^{-1} wet weight) in the pectoral muscles of birds from natural habitats. Ranking was made based on the maximum value of the EPA + DHA sum in orders

Species	EPA	DHA	Sum	n-6/n-3
Passeriformes				
Sedge warbler (*Acrocephalus schoenobaenus*)	0.2	3.5	3.7	0.6
Tree sparrow (*Passer montanus*)	0.0	2.8	2.8	1.3
Barn swallow (*Hirundo rustica*)	0.3	2.4	2.7	1.3
Yellow wagtail (*Motacilla flava*)	0.4	2.3	2.7	0.9
White wagtail (*Motacilla alba*)	0.3	1.8	2.5	0.9
Reed bunting (*Emberiza schoeniclus*)	0.1	2.4	2.5	1.1
Common starling (*Sturnus vulgaris*)	0.3	1.5	1.8	1.3
Charadriiformes				
Red-necked phalarope (*Phalaropus lobatus*)	2.1	0.2	2.3	1.3
Pied avocet (*Recurvirostra avosetta*)	2.0	0.2	2.2	1.1
Common tern (*Sterna hirundo*)	0.4	0.7	1.1	2.2
Common greenashank (*Tringa nebularia*)	0.8	0.3	1.1	2.5
Kentish plover (*Charadrius alexandrinus*)	0.5	0.4	0.9	2.0
Blach-headed gull (*Larus ridibundus*)	0.5	0.4	0.9	2.8
Anseriformes				
Common shelduck (*Tadorna tadorna*)	1.6	0.3	1.9	0.7
Podicipediformes				
Great crested grebe (*Podiceps cristatus*)	1.3	0.2	1.5	1.9
Ciconiiformes				
Gray heron (*Ardea cinerea*)	0.6	0.6	1.2	1.9
Columbiformes				
Oriental Turtle Dove (*Streptopelia orientalis*)	0.3	0.2	0.5	1.5
Rock dove (*Columba livia*)	0.1	0.2	0.3	8.2

Chernyshov, 1981; Zając and Solarz, 2004; Gilroy et al., 2009), among which a special role is given to dragonflies. For example, Odonata (mainly, *Sympetrum* spp.) account for 64.2% of the total feed in the diet of yellow wagtail (Karpenko and Chenyshov, 1981; Chernyshov, 1981); in sum, the diet of Passeriformes was found to include representatives of nine genera, six families, and two suborders (Zygoptera and Anisoptera) of dragonflies (Prokofyeva, 2004). Nevertheless, amphibiotic insects contain a very small amount of DHA (Gladyshev et al., 2011; Sushchik et al., 2013). We can only assume that the species of the Passeriformes order have the ability to synthesize large amounts of DHA from essential alpha-linolenic acid (18:3n-3, ALA) and from EPA, which is quite rare among animals. ALA is contained in a large quantity in some terrestrial insects on which Passeriformes feed, for example, in butterflies (Wang et al. 2006; Sakurai, 2011). In turn, imagoes of amphibiotic insects (including dragonflies), which are also contained in the diet of Passeriformes, contain a lot of EPA (Gladyshev et al., 2011; Sushchik et al., 2013).

The physiological and biochemical significance of the high content of DHA in the pectoral muscles of Passeriformes is not quite clear. DHA is known to be the main component of phospholipids of the membranes of retinal cells and cells of the cerebral cortex; i.e., it plays the main role in the functioning of the organs of vision and nervous system (Lauritzen et al.,

2001; SanGiovanni and Chew, 2005; Bazan, 2009). Indeed, it was experimentally established that the ability of nestlings to learn to peck useful food and avoid harmful food decreased at a low content of n-3 PUFAs in the diet of the mother (Fronte et al., 2008). At the same time, there is a well-known hypothesis about the "membrane pacemaker of metabolism" that is based on the inverse allometric correlation between the content of DHA in different tissues, including muscles of vertebrates and body size (Hulbert, 2007; Pierce and McWilliams, 2014). Warm-blooded animals with a relatively small body weight, such as most Passeriformes, are characterized by high values of metabolic rate (i.e., the amount of oxygen consumed per unit time per unit body weight) (Londono et al., 2015). In turn, the high content of DHA in metabolically active membranes of small warm-blooded animals was shown to ensure the high rate of the work of "energy" enzymes—transmembrane ion pumps with the ATP synthase activity (Wu et al., 2004; Hulbert, 2007). Thus, the content of DHA in the pectoral tissues of Passeriformes may reflect a relatively high metabolic rate in these animals. It should be noted that the extremely high accumulation of DHA in the pectoral muscles of Passeriformes in comparison with other orders for the purpose of ensuring the necessary metabolic rate takes place at the expense of its own synthesis rather than at the expense of food sources.

Along with seven representatives of the Passeriformes order, our study involved another order with a relatively high number of species (six): Charadriiformes. In the representatives of the Charadriiformes order, which we studied, the levels of EPA and DHA varied within 2.4–8.7% and 0.9–2.4%, respectively. Meanwhile, according to the literature, the levels of EPA and DHA in the Artic sea birds from the Charadriiformes order varied from 3.6 to 14.2 and from 2.5 to 9.0%, respectively (Wold et al., 2011); i.e., they on average largely surpassed those in the Charadriiformes that live or feed in the migration period at freshwater and saline lakes and rivers. In the studied birds of the Charadriiformes order, the amounts of FAs of n-6 family, namely, essential linoleic acid and arachidonic acid, were 6.0–13.1% and 8.0–14.7%, respectively, whereas in the sea birds of the same order the amounts of LA and ARA varied within 3.3–4.8% and 4.3–10.1%, respectively (Wold et al., 2011). Therefore, lake and river Charadriiformes on average had higher levels of LA and ARA than sea Charadriiformes.

Based on the example of freshwater and marine semi-aquatic and aquatic mammals, it was shown that the level of n-6 acids in the biomass of freshwater species was higher due to a large contribution of terrestrial food sources (Koussoroplis et al., 2008). It was suggested that the contribution of terrestrial food sources should be determined using the DHA/LA ratio, which proved to be much higher in marine mammals than in freshwater ones (Koussoroplis et al., 2008). The results of our studies permit the abovementioned ideas to be extended to birds. Moreover, the DHA/LA ratio in the Charadriiformes we studied varied within 0.10–0.61, whereas this ratio in marine species was 0.69–2.57 (we made the calculation based on the data of Wold et al., 2011). However, it should also be noted that the higher level of ARA in birds may be due not only to the contribution of terrestrial food sources, but also to the larger share of animal foods in their diet (Ramirez et al., 2009). In addition, the level of ARA in bird muscles may also depend on the properties of thermoregulation processes (Ben-Hamo et al., 2014).

The arguments and comparisons presented above are based on the levels of some FAs in bird tissues, which were expressed as a percentage of their total amount. However, in analyzing the trophic interactions in ecosystems, it is important to know the quantitative content of FAs in biomass rather than their levels. Unfortunately, the quantitative data on the content of FAs per unit of biomass of wild birds, which require the use of the internal standard in chromatography, are very scarce in the literature. Therefore, we can only compare the quantitative values of the content of EPA and DHA, which we established, with the data of one work. The published content of EPA and DHA in pectoral muscles was 0.023 mg g^{-1} and 0.437 mg g^{-1} in pheasant *Phasianus colchicus* (the Galliformes order), 0.495 mg g^{-1} and 0.387 mg g^{-1} in bald-coot *Fulica atra* (the Gruiformes order), and 0.258 mg g^{-1} and 0.261 mg g^{-1} raw weight in mallard *Anas platyrhynchos* (the Anseriformes order), respectively (Nuernberg et al., 2011). On the whole, the values of the content of EPA and DHA obtained in our study proved to be comparable with the published data given above.

In recent years, when discussing the problem of the relationship between the influence of dietary and genetic factors on the FA composition of animals, researchers have been giving more and more evidence to support the leading role of the genotype (species identity) (Makhutova et al., 2011; Gladyshev et al., 2012; Lau et al., 2012). Our work has also showed that the FA composition of an individual taxon—the Passeriformes order—reliably differs from the one in birds of all other orders. Moreover, contrary to the initially proposed hypothesis, the highest biomass content of DHA was typical for the Passeriformes species that consume mostly terrestrial food, which is almost devoid of this FA. In contrast, waterfowls and waterbirds from other orders that consume aquatic biota, which is rich in DHA, contained a significantly smaller amount of DHA in their biomass than Passeriformes.

ACKNOWLEDGMENTS

This work was supported by the State Task of the Ministry of Education and Science of the Russian Federation to the Siberian Federal University to con-

duct research no. 6.1089.214/K; by the State Task within the Program of Fundamental Research of the Russian Federation, project nos. 51.1.1 and VI.51.1.9; and grants from the Russian Foundation for Basic Research, project nos. 13-04-00860 and 13-04-00740.

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Translated by L. Solovyova