

Composition of Pied Flycatcher (*Ficedula hypoleuca* Pall.) Nestling Diet in Industrially Polluted Area

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Abstract—The composition of pied flycatcher (*Ficedula hypoleuca* Pall.) nestling diet was studied in the zone of strong pollution with emissions from the Middle Ural Copper Smelter (Revda, Sverdlovsk oblast) and in the background area from 2005 to 2007. The results show that diversity of the diet decreases and prevalence in it of one insect taxon (Lepidoptera) increases near the source of emissions. The proportion of uncharacteristic food objects (orthopterans, herpetobiont invertebrates) and variation in the size of invertebrates brought by parents to their nestlings increase, which is explained by degradation of forest habitats in the polluted area. Pied flycatchers provide nestlings with sufficient quantities of food, but its quality in the polluted zone is lower than in the background area.

Key words: pied flycatcher, *Ficedula hypoleuca*, diet, industrial pollution.

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Food is one of the most important ecological factors determining the distribution, abundance, and role of particular animal species in the biogenic cycles of matter and energy. Research in this field is intensive, but only a few publications deal with changes in the bird diet under the influence of industrial pollution (Gilyazova, 1999; Eeva et al., 1997, 2005). Meanwhile, environmental pollution affects all components of ecosystems and can alter parameters of community structure and productivity, including the abundance and diversity of invertebrates (Kataev et al., 1983; Bogacheva, 1986; Vorobeichik et al., 1994; Eeva et al., 1997; Kozlov, 1997; Butovsky, 2001; Bel'skaya and Zinov'ev, 2007). This may lead to transformation of established trophic relationships, which are especially important to consumers of higher trophic levels. The observed impairment of bird reproductive parameters in polluted areas may be due both to poisoning and to deterioration of food quality (Eeva et al., 1997, 2005). However, this problem has not yet been studied sufficiently. In particular, there are no data on changes in the structure of bird diets and in the size of food objects they collect in industrially polluted areas of the Urals.

The purpose of this study was to characterize the taxonomic and size structure of invertebrates in the diet of pied flycatchers and to estimate the quantity of food consumed by their nestlings in southern taiga forest ecosystems of the Middle Urals polluted with heavy metals and sulfur dioxide.

MATERIAL AND METHODS

The study was carried out in the vicinity of the Middle Ural Copper Smelter (MUCS) located in the outskirts of Revda, Sverdlovsk oblast, from 2005 to 2007. The MUCS is one of the largest nonferrous metallurgical works in Russia. In 1989, emissions from it (containing sulfur and nitrogen oxides, fluorine compounds, and dust enriched with metals) amounted to 140 700 t/years (Vorobeichik et al., 1994). Since then, the emissions have been reduced fivefold, with their amount in 2005 being 27 500 t/years (*Gosudarstvennyi...*, 2006). However, pollutants accumulated in the environment continue to exert strong toxic pressure upon all ecosystem components. The MUCS have been in operation over 60 years, which accounts for the formation around it of a geochemical anomaly where the content of heavy metals (Pb, Cu, Zn, Cd), As, and other elements in the soil is 10 to 100 times higher than in the background zone.

Zones with different levels of heavy metal pollution and forest ecosystem degradation were delimited in the MUCS environs (Vorobeichik et al., 1994; Bel'skii et al., 2005): the impact zone (strong pollution, up to 3 km from the smelter); the buffer zone (moderate pollution, 3–15 km from the smelter); and the background zone (pollutant contents in natural accumulating substrates do not exceed the regional background level, over 15 km from the smelter).

Permanent plots with artificial nest boxes (two boxes per hectare) were established in forest areas within each zone. The material was collected in

aspen–birch forests on two plots in the impact zone (1 and 1.5 km from the smelter; 41 and 13 ha in area, respectively) and on one plot in the background zone (27 km west of the smelter, 25 ha). Samples of food were collected from pied flycatcher nestlings in 35 nests located in the impact zone (666 food objects) and 45 nests in the background zone (940 food objects). To this end, the neck of a nestling was ligated with fishing line for 30–50 min (Kuligin, 1981). Before removing the ligature, food boluses were taken out of the esophagus with forceps. Regurgitated food was collected from the nest bottom. If a bolus broke up into several pieces and was difficult to identify, the material was used for characterizing the structure of the diet but not for determining bolus weight. The age of the nestlings was 6–11 days (hatching was assumed to be on day 0). It was shown that the size of food portions brought by parent birds to their nestlings stabilizes beginning from day 6 of nestling's life (Slagsvold and Wiebe, 2007). Thus, our data characterize the diet of nestlings during most of their life in the nest (pied flycatcher nestlings usually fledge at about 15 days of age).

Food boluses were stored individually in Eppendorf tubes filled with 70% ethanol. In the laboratory, boluses were removed from the tubes and placed on filter paper in Petri dishes. Invertebrates were then carefully separated, straightened when necessary, and dried on filter paper until the fixative evaporated from the surface. Weight loss during evaporation was monitored with KERN 770 electronic scales. The weight indicated by the scales was recorded with an accuracy of 0.1 mg after it remained unchanged for 5–10 s. Bolus weight was calculated by summing up the weights of all objects it contained.

Invertebrates were identified to families, and their body length (straightened) was measured from the anterior head margin to the tip of elytra (in coleopterans and hemipterans) or to the tip of the abdomen in adult lepidopterans, dipterans, and other long-winged insects as well as in spiders and lepidopteran and Symphyta larvae. Measurements (0.1 mm accurate) were made under an MBS-10 binocular microscope with an ocular micrometer.

The frequency of nestling feeding was observed from a hide in the morning (from 7 to 11 a.m. local time; on average, 3 h per nest), in dry weather. The nestlings were 10–12 days of age. Only nests where both parents were feeding their nestlings were included in analysis. The total observation time was 28.4 h at 10 nests in the background zone and 31.2 h at 11 nests in the impact zone.

The composition of insects in the pied flycatcher diet was analyzed at the level of orders using the Berger–Parker index (proportion of the prevalent taxon in the sample), which characterizes the degree of dominance, and the polydominance index (the inverse value of the Simpson dominance index), which

characterizes the degree of taxonomic diversity (Pesenko, 1982).

To reveal changes in the role of particular taxa in the pied flycatcher diet under strong toxic stress in comparison with the background zone, we used the parameter (I) hereinafter termed “diet change index” and calculated as follows:

$$I = (P_{ni} - P_{nb}) / (P_{ni} + P_{nb}),$$

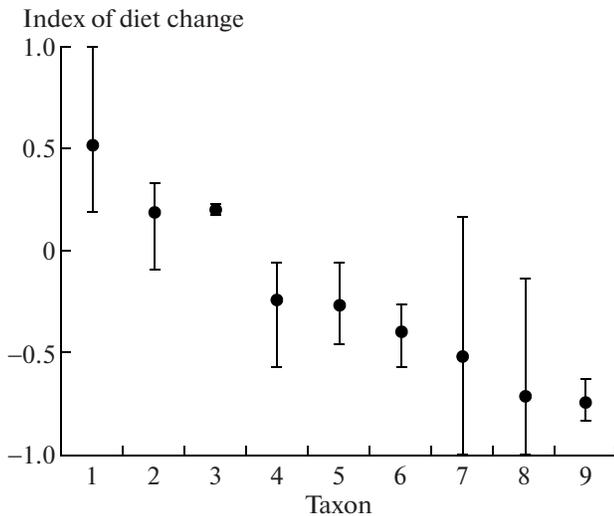
where P_{ni} and P_{nb} are the proportions (% biomass) of n th taxon in the diet of nestlings in the impact and background zones, respectively. This parameter varies from -1 (the taxon is present in the nestling diet in the background zone, but absent in the impact zone) to 1 (the taxon is present in the nestling diet in the impact zone but absent in the background zone). If the proportions of a particular taxon in both zones are equal, the index value is zero. Only taxa regularly occurring in the diet and also orthopterans and mollusks were included in analysis.

Arithmetic mean and confidence interval were used to characterize food boluses and objects in cases of normal distribution, geometric mean was used in cases of lognormal distribution, and median and interquartile range were used in cases of unknown distribution type.

To estimate the abundance of invertebrates in the tree canopy (where pied flycatchers often collect their food), we swept the lower branches of birch trees with an insect net on the same plots where food boluses were collected. Three samples of 50 net sweeps were taken on each plot in 2006 at the end of June, during the period of mass feeding. In addition, the relative abundance of phyllophagous insects was estimated indirectly, from damage to the leaves of white birch (*Betula alba* L.). On each plot, 30 trees located at intervals of at least 20 m were randomly chosen on each plot, and one branch 30–40 cm long (with 15–40 leaves) was cut from each tree on the southern side of the crown, 1.5–2 m above the ground. Each branch was placed in an individual polyethylene bag. Leaf damage was studied in the laboratory within the shortest possible time after sampling, taking into account leaf areas eaten completely (both mesophyll and veins) or skeletonized (with veins more or less intact). This kind of damage is typical for the larvae of Lepidoptera and Hymenoptera Symphyta and for Coleoptera larvae and adults.

RESULTS

At the first stage, we used the percentage of each taxon among food objects to characterize the structure of the pied flycatcher diet. Analysis of these data showed that the basis of the diet was constituted by several orders: Aranea (in unpolluted areas their proportion varied from year to year from 18.0 to 24.3% of the total number of food objects), Lepidoptera (12.9–20.8%), Diptera (8.1–24.3%), Coleoptera (9.4–17.6%), Hymenoptera



Index of diet change ($n = 3$ years): average values and variation range. Taxa: (1) Orthoptera, (2) Aranea, (3) Lepidoptera, (4) Diptera, (5) Coleoptera, (6) Hymenoptera, (7) Hemiptera, (8) Mollusca, and (9) Homoptera

(9.7–16.0%), Homoptera (8.3–14.6%). In the impact zone, compared to the background zone, the proportion of Aranea increased in one of the years to 33.7%; of Lepidoptera, to 25.8%; and of Homoptera, to 24.6%. The proportion of Hymenoptera in the nestling diet was invariably smaller in the impact zone than in the background zone.

The structure of the diet varied from year to year. Differences between the samples were significant both in the background zone (analysis by contingency tables: $\chi^2 = 84.7$, $df = 14$, $p < 0.001$) and in the impact zone ($\chi^2 = 129.9$, $df = 14$, $p < 0.001$); for this reason, the comparison of the zones was made separately for each year of study. Differences in diet structure between the plots were significant: in 2005, $\chi^2 = 28.7$, $df = 9$, $p < 0.001$; in 2006, $\chi^2 = 24.5$, $df = 7$, $p < 0.001$; in 2007, $\chi^2 = 26.8$, $df = 6$, $p < 0.001$ (orders represented by less than five individuals were pooled in this comparison).

It is noteworthy that the number of individuals representing certain prey, which is often used to characterize diet structure, may fail to reflect the role of particular objects in bird feeding. The amount of energy consumed with each particular food component depends on its weight. Even when the number of small insects is great, their role in energy supply remains minor. In 2006, for instance, Homoptera (mostly Aphidinea) were second most abundant by numbers but only seventh or eighth most abundant by weight in the diet of nestlings in the impact zone. We believe that the biomass of particular categories of food objects allows more adequate estimation of their role in the diet of birds.

During the entire study period, Lepidoptera formed the basis of the diet of pied flycatcher nestlings

(Table 1). The second most abundant order (by biomass) was, in different years, either Coleoptera or Diptera in the background zone and Aranea in the impact zone. The group of basic food objects included also Hymenoptera. Other taxa regularly recorded as food objects included Homoptera and Hemiptera together with mollusks in the background zone and Orthoptera in the impact zone. Other taxa (less than 1% each) did not appear in the diet in some years.

Analysis of the structure of the pied flycatcher nestling diet at the level of orders revealed its greater diversity, estimated by the polydominance index, in the background zone compared to the impact zone (Table 1). Dominance was more distinct in the impact zone, where the Berger–Parker index was greater than in the background zone in any year.

Comparisons of diet change indices between different taxa indicated three orders whose contribution to the nestling diet increased in the impact zone: Orthoptera, Aranea, and Lepidoptera (figure). The average proportions of other taxa in the impact zone over the three years of study were smaller than in the background zone, although in some seasons the proportions of Diptera, Coleoptera, and Hemiptera in the impact zone were close to those in the background zone.

The average food bolus weight was higher in the impact zone than in the background zone over the entire study period; however, significant differences were recorded only in 2006 (Mann–Whitney test, $p = 0.02$), whereas the average number of objects per bolus was greater in the background zone than in the impact zone. This difference was observed over the entire study period, but it was significant only in 2006 and 2007 (Table 2). Evidently, the greater weight of boluses and the smaller number of food objects per bolus in the impact zone were explained by greater individual size of prey.

Analysis of the size of invertebrates captured by the pied flycatcher showed that the weight of one food object in the impact zone was significantly greater than in the background zone only in 2007 (Table 2; Mann–Whitney test, $p < 0.01$). The median values in the plots compared were similar in all years, but the range of variation in the weight of a food object increased: maximum values in the impact zone were 1.7–3.3 times greater than in the background zone. The average proportion (\pm SE) of large objects (100 mg and more) near the smelter was $14.5 \pm 0.7\%$, being significantly greater ($t = 2.8$, $p < 0.05$) than in the background zone ($7.4 \pm 1.4\%$).

Analysis at the level of orders revealed the significant effect of the factor “pollution zone” on the weight of spiders and lepidopteran larvae collected by the pied flycatcher (Table 3). The factor “year” has a significant effect only on the weight of dipterans. The interaction of both factors was significant in most orders. The weight of adult lepidopterans showed no dependence on either the zone or the year. Flycatchers in the

Table 1. Structure of pied flycatcher nestling diet in two zones near the pollution source, proportion of taxa as percentages of wet food weight (2005–2007)

Taxon	Zone					
	background			impact		
	2005	2006	2007	2005	2006	2007
Lepidoptera	45.5	28.2	28.0	65.7	44.3	39.7
Coleoptera	14.4	14.3	8.1	5.4	8.0	7.2
Hymenoptera	13.0	9.1	18.8	6.4	2.5	10.8
Aranea	12.4	11.3	13.1	10.3	22.0	25.5
Diptera	8.1	23.6	27.4	7.2	19.0	7.5
Homoptera	2.8	4.5	1.9	0.6	0.6	0.2
Hemiptera	1.3	3.7	0.1	1.8	0.6	0
Mollusca, Pulmonata	1.1	2.6	2.2	0.8	0	0
Orthoptera	0.4	1.8	0	0.9	2.6	6.2
Raphidioptera	0.3	0	0	0	0	0.3
Blattoptera	0.3	0	0.2	0	0	0
Neuroptera	0.2	0	0	+	0.4	1.0
Opiliones	0.1	0.7	0	0	0	0
Psocoptera	0.1	0	0	0	0	0
Mecoptera	0	0.2	0	0.3	0	0
Trichoptera	0	0	0	0.6	0	1.2
Isopoda	0	0	0	0	0	0.4
Chilopoda	0	0	0.2	0	0	+
Total biomass, mg	15219.1	8409.4	9531.6	16081.9	8778.7	9412.8
Total number of individuals	374	278	288	291	203	172
Number of orders	14	11	10	12	9	12
Berger–Parker index	0.46	0.28	0.28	0.66	0.44	0.40
Polydominance index	3.74	5.51	4.69	2.20	3.46	4.02

Note: (+) less than 0.05%.

impact zone captured larger spiders and lepidopteran larvae (2005–2007), adult dipterans (2006–2007), adult coleopterans and hemipterans (2005). On the other hand, adult dipterans collected by the birds in 2005 were smaller in the impact zone than in the background zone. The weight of adult coleopterans and hymenopterans did not differ significantly between the two zones in 2006–2007.

The average length of a food object did not differ between the zones in 2005 and 2006 (Table 2), but in 2007 it was greater in the impact zone than in the background zone (one-way ANOVA, $F = 4.0$, $df = 1$, 449; $p < 0.05$). The body length distribution of food objects in the plots compared was similar in different years: the modal interval was 5.0–9.9 mm (38–43% of all objects); the interval 10.0–14.9 mm was second in relative frequency (18–32% of the objects); and then followed the interval 0–4.9 mm (17–20%, increasing to 31% only in the impact zone in 2006). The Kolmogorov–Smirnov test revealed no significant differences

in the length distribution of food objects between zones in 2005 and 2007, but the difference in 2006 was significant ($p < 0.05$). Although average values recorded in both zones were close to each other, the range of variation in food object size was greater in the impact zone. The minimum length of invertebrates was similar in both zones, whereas their maximum length was greater in the impact zone than in the background zone.

The cuticle of larger invertebrates as well as of adults in comparison with larvae is chitinized more strongly, making them less suitable for feeding the nestlings. Even within a group of generally soft food objects such as lepidopteran larvae, there were some caterpillars (from the family Nymphalidae) with a setous body and large, usually branching protuberances. The proportion of such poorly digestible objects was 4.8–9.5% of the total lepidopteran larvae biomass in the background zone and 30.3–48.0% in the impact zone in 2005 and 2006. The average contribution of

Table 2. Characteristics of food boluses and objects fed to pied flycatcher nestlings in two zones near the pollution source

Index	Zone					
	background			impact		
	2005	2006	2007	2005	2006	2007
Bolus weight, mg						
Geometric mean (<i>n</i>)	89.6 (133)	68.6 (78)	67.2 (80)	92.6 (111)	85.4* (76)	80.7 (86)*
Confidence interval	80.8–99.3	60.2–78.1	56.2–80.4	79.7–107.6	73.6–99.1	69.1–94.4
Min–max	17.5–371.8	10.7–206.0	3.3–234.9	13.3–500.0	18.6–680.4	14.5–499.0
Number of objects per bolus						
Median (<i>n</i>)	2 (133)	2 (78)	2 (80)	2 (112)	1 (76)*	1 (86)
Interquartile range	1–3	1–3	1–3	1–3	1–3	1–2
Min–max	1–9	1–10	1–11	1–8	1–18	1–15
Weight of one food object, mg						
Median (<i>n</i>)	25.6 (367)	23.3 (269)	24.7 (283)	24.1 (287)	20.5 (198)	35.0** (171)
Interquartile range	10.0–54.1	8.3–40.6	9.7–47.4	10.8–47.8	1.2–50.7	13.8–77.4
Min–max	0.7–287.7	0.4–206.0	0.2–168.0	0.7–500.0	0.7–680.4	0.4–499.0
Length of one food object, mm						
Arithmetic mean (<i>n</i>)	9.5 (362)	8.4 (267)	8.7 (280)	9.5 (285)	8.1 (198)	9.6*** (171)
Confidence interval	9.0–10.0	7.9–8.9	8.2–9.2	8.9–10.1	7.4–8.8	8.8–10.3
Min–max	2.3–29.0	1.8–22.5	1.8–23.0	1.7–33.7	2.4–30.3	2.1–27.2

Note: Differences between the impact and background zones in a particular year are significant at * $p < 0.05$ (Mann–Whitney test), ** $p < 0.01$ (Mann–Whitney test), or *** $p < 0.05$ (ANOVA *F*-test).

Table 3. Results of two-way ANOVA for differences in the weight of pied flycatcher food objects between years and zones (logarithmic data)

Factors and their interaction	Aranea (<i>df</i> = 343)		Lepidoptera				Diptera, adults (<i>df</i> = 221)		Coleoptera, adults (<i>df</i> = 128)	
	<i>F</i>	<i>p</i>	adults (<i>df</i> = 85)		larvae (<i>df</i> = 185)		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
			<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>				
Year	1.34	0.26	0.15	0.86	1.49	0.23	3.48	<0.05	2.40	0.09
Zone	30.02	<0.001	0.62	0.43	26.49	<0.001	3.09	0.08	1.49	0.22
Year × zone	8.03	<0.001	0.53	0.59	3.11	<0.05	8.04	<0.001	5.35	<0.01

Note: Significant differences are boldfaced.

adult ants (Formicidae) to the total biomass of all hymenopterans over three years was $22.3 \pm 13.0\%$ in the background zone and $39.8 \pm 8.1\%$ in the impact zone. Lycosidae spiders, which dwell on the surface of soil and forest litter, have large cephalothorax with hard exoskeleton. Their proportion among collected spiders increased from $8.9 \pm 3.7\%$ in the background zone to $40.5 \pm 10.4\%$ in the impact zone. On the other hand, the proportion of soft dipterans from the family Rhagionidae, which were readily consumed by pied flycatchers in the background zone ($46.9 \pm 12.9\%$ of the total dipteran biomass in the food of nestlings), abruptly decreased in the impact zone ($0.2 \pm 0.2\%$).

The average numbers of parent bird visits to the nest per nestling per hour in the background zone (6.29 ± 0.44 , $n = 10$ nests) and in the impact zone (5.23 ± 0.64 , $n = 11$) did not differ significantly (Student's test $t = 1.35$, $p > 0.05$). A slight decrease in the frequency of visits in the impact zone, compared to the background zone, was counterbalanced by a greater average weight of the food load brought by the adult bird. The quantity of food per nestling per hour, estimated as the product of the average bolus weight and the average frequency of nestling feeding over three years, was comparable in both zones: 472.3 mg in the background zone and 451.2 mg in the impact zone.

Table 4. Invertebrate abundance in birch (*Betula alba* L.) crowns in two zones near the pollution source (average number of individuals per 50 net sweeps \pm SE)

Taxon	Zone			
	background		impact	
	Adults	Larvae	Adults	Larvae
Lepidoptera	4.3 \pm 2.8	4.3 \pm 1.2	1.3 \pm 0.3	5.3 \pm 2.8
Coleoptera	15.7 \pm 3.5	1.0 \pm 0.6	7.0 \pm 1.7*	16.7 \pm 5.9*
Hymenoptera	24.3 \pm 9.9	0.3 \pm 0.3	53.7 \pm 11.3	0.3 \pm 0.3
Aranea	7.0 \pm 3.2	—	7.7 \pm 2.0	—
Diptera	48.3 \pm 8.4	0	36.7 \pm 14.3	0
Homoptera	5.0 \pm 0.6	20.3 \pm 4.3	26.0 \pm 5.0*	69.3 \pm 4.9*
Hemiptera	1.7 \pm 1.2	3.0 \pm 2.1	5.0 \pm 1.2	0.7 \pm 0.3
Mollusca, Pulmonata	0.3 \pm 0.3	—	0	—
Neuroptera	4.7 \pm 1.8	0	0.7 \pm 0.7	0
Opiliones	0.3 \pm 0.3	0	0	0
Psocoptera	4.3 \pm 0.3	0	3.0 \pm 0.0	0
Thysanoptera	2.3 \pm 0.9	0	2.3 \pm 0.9	0

* Differences between the impact and background zones are significant at $p < 0.05$ (Student's *t*-test).

Significant differences between the zones in the abundance of invertebrates in tree crowns were observed for only two orders (Table 4): in Coleoptera, the abundance of adults in the impact zone was higher and that of larvae was lower than in the background zone; in Homoptera, both adults and larvae were more abundant in the impact zone.

The abundance of phyllophagous insects estimated from damage to birch leaves was found to increase near the source of emissions, compared to the background area. The proportion of damaged leaves in 2005 and 2006 was greater in the background zone than in the impact zone: in 2005, $75.7 \pm 3.1\%$ ($n = 30$ trees in all cases) vs. $17.0 \pm 2.5\%$, respectively (comparison of proportions after the arcsin transformation: $F = 13.37$, $p < 0.01$); in 2006, $66.1 \pm 3.8\%$ vs. $30.5 \pm 3.5\%$ ($F = 7.96$, $p < 0.01$).

DISCUSSION

According to published data (Cramp and Perrins, 1993), the pied flycatcher is very flexible in the choice of food objects, with its foraging sites and diet depending on habitat and weather conditions. Nevertheless, this species prefers foraging in stands of deciduous trees and shrubs (Inozemtsev, 1978). To make the results comparable, we performed this study in areas of small-leaved forest, and the published data we refer to were also obtained in similar habitats. For instance, in

a small-leaved forest of Moscow oblast (Inozemtsev, 1978), the proportion of lepidopterans in the pied flycatcher diet was 21.9%; of hymenopterans, 19.9%; of coleopterans, 18.4%; of dipterans, 17.2%; and of spiders, 8.3% of the total number of food objects. In a birch forest of the Ilmen Nature Reserve, the Southern Urals (Zubtsovskii, 1978), the diet of this species was based on lepidopterans (35.6–50.6% of the total number of objects and 67–72.3% of the total biomass), spiders (20.1–34.2% and 11.4–16%), and coleopterans (6–14.3% and 8.1–6.4%, respectively).

Our data agree with those published by other authors. In the study area, lepidopterans, coleopterans, dipterans, spiders, and hymenopterans prevailed in the food of pied flycatcher nestlings (Table 1). Regularly, but in smaller numbers, the nestling diet included homopterans, hemipterans, and orthopterans. Mollusks were also regularly recorded in the background zone, although their contribution to the total food biomass was small. Members of several orders were consumed only occasionally. It would be incorrect to put mollusks in this category, because, although their proportion in the diet was relatively small, they are an important source of calcium necessary for the formation of skeleton in nestlings. Unusual findings include woodlice (Isopoda) and myriapods, dwellers of the forest litter and the upper soil horizons. To collect these invertebrates, flycatchers have to resort to the ways of foraging unusual for them. Remarkably,

small balls of dirt occur in food boluses along with invertebrates in the impact zone. Pied flycatchers probably use both woodlice and soil as additional sources of mineral food for nestlings when mollusks are in short supply.

The contribution of lepidopterans, spiders, and orthopterans to the nestling diet was found to increase in the impact zone (figure). This agrees with the results of studies carried out in the environs of the copper and nickel smelter in Harjavalta (Finland), where the proportion of Lepidoptera and Symphyta larvae in the diet of pied flycatchers also increased in the polluted zone (Eeva et al., 2005). However, these authors also found that the proportion of Coleoptera in the diet also increased while the proportions of adult Lepidoptera and Aranea decreased in the impact zone, unlike in our study area.

Structural rearrangements in the pied flycatcher diet are probably explained by changes in the abundance of different groups of invertebrates resulting from habitat transformation. Industrial pollution leads to suppression and thinning of tree stands, with consequent increase in the size of open areas and the illumination level (Vorobeichik et al., 1994). The herb-dwarf shrub layer is sparse and in some places missing; forest species inhabiting this layer are replaced with meadow and ruderal species. The invertebrate community is also restructured: relative and absolute abundance of sucking phytophages (Homoptera, Cicadinea; Hemiptera, Lygaeidae) increases; the proportion of gnawing phytophages (Lepidoptera larvae; Mollusca) and zoophages (Aranea; Hemiptera, Nabidae) decreases (Vorobeichik et al., 1994; Nesterkov and Vorobeichik, 2009). Our census of invertebrates in birch crowns also revealed an increased abundance of homopterans in the polluted zone (Table 4). Belskaya and Zolotarev (2004) observed that the abundance of herpetobiont invertebrates decreased, whereas the proportion of ground beetles (Carabidae) and Arachnida in the community increased in the area exposed to MUCS emissions. The increasing proportion of spiders in the diet of nestlings in the impact zone is explained by the improvement of their role in the community as well as by the fact that the birds can more easily detect them when the herbaceous layer is suppressed (see also Eeva et al., 1997). The contribution of Acrididae (Orthoptera, Caelifera) to the nestling diet increases in the polluted area because of their higher density (Nesterkov and Vorobeichik, 2009) and expansion of forest-free areas they inhabit. The proportion of mollusks in the diet decreases because they disappear from the soil macrofauna and chortobiont communities in the impact zone (Vorobeichik et al., 1994; Nesterkov and Vorobeichik, 2009). This effect is due to technogenic acidification of the environment and consequent ecosystem depletion of calcium, which is necessary for the building of mollusk shells, as well as to the changes in microclimate: air humidity in

the near-ground layer apparently decreases upon degradation of the herbaceous layer.

The structure of the diet of birds may provide information on where and how they collect their food. Near the copper and nickel smelter in Harjavalta, specialists observed a decreased abundance of dipterans (Heliövaara and Väisänen, 1989) as well as reduced frequency of food capture in the air by pied flycatchers (Eeva et al., 1997). Our data on the decreasing proportion of dipterans in the diet of nestlings in the area polluted with MUCS emissions agree with these results and also provide indirect evidence for the decreasing frequency of flycatcher foraging in the air. It was also shown that pied flycatchers feed on the soil surface more frequently in the polluted than in the background area (Eeva et al., 1997). This conclusion agrees with our data that the nestling diet near the MUCS contains increased proportions of spiders, especially from the family Lycosidae, as well as of Elateridae beetles and woodlice, which inhabit the surface and upper layers of the soil and forest litter. The increased frequency of foraging on the soil surface in polluted areas is explained by partial or complete degradation of the herbaceous layer, conspicuousness of herpetobiont invertebrates under such conditions, and decreased abundance of flying insects, compared to the background area. Such forced changes of foraging areas and habits were also recorded in other bird species and industrially polluted areas, e.g., in tits inhabiting the environs of a coal-powered thermal power plant in Spain (Brotons et al., 1998).

The ratio of invertebrates differing in size and degree of cuticle chitinization in the diet of birds allows estimation of its the nutrient value. Feeding on larger objects is more efficient in terms of energy supply, but the size of potential prey is limited by the ability of nestlings to ingest it. It was shown that the mortality of younger nestlings in asynchronous broods was caused exactly by their inability to swallow large food objects brought by the parents for senior nestlings prevailing in the brood (Slagsvold and Wiebe, 2007). The increasing proportion of larger objects in the polluted zone, compared to the background zone, in our study area agrees with observations made in southwestern Finland, where the average body weight of Lepidoptera and Symphyta larvae harvested by pied flycatchers was also somewhat greater near the smelter, compared to the background area (Eeva et al., 2005). The increased variation in the size of invertebrates captured by flycatchers and in the proportion of objects with hard cuticle (Nymphalidae caterpillars, adult ants, Lycosidae spiders) and the decreased proportion of soft objects suggest that pied flycatchers in the impact zone are less fastidious in their choice of prey.

To estimate the quantity of food consumed by nestlings, we measured the weight of boluses and the frequency of food delivery to nestlings by their parents. This frequency in our study area was similar to that in

Finland, where it also did not differ significantly between the background and polluted zones (5.4 vs. 5.7 visits per hour, respectively; Eeva et al., 2005); individual nestlings in the respective zones received 452 and 468 mg of food per hour, which is also close to our estimations. Adult pied flycatchers are probably capable of providing their nestlings with food even in degraded forest areas.

Comparing the abundance of invertebrates in the diet and in the ecosystem, it is possible to estimate the selectiveness of bird feeding. Analyzing damage to birch leaves, we revealed a decrease in the abundance of phytophages (represented largely by lepidopteran larvae) in the polluted zone, whereas samples taken from tree crowns with a sweep net did not differ between the zones. At the same time, the proportion of lepidopteran larvae in the diet of pied flycatchers increases in the polluted zone, which may be evidence that the birds selectively feed on them.

Thus, industrial pollution of the environment can lead to changes in the structure of pied flycatcher diet and in characteristics of food objects consumed by these birds. Its effects in this case are apparently not direct but mediated through changes in forest phyto-cenoses and consequent rearrangements in invertebrate communities.

The diversity of the diet decreases and the prevalence of a certain food object in it increases near the source of emissions. To some extent, the composition of prey reflects characteristics of habitats: in the polluted area, the proportion of atypical food objects (orthopterans, herpetobiont invertebrates) increases due to degradation of forest habitats. In the impact zone, increasing variation is observed in the size of invertebrates fed by birds to their nestlings. In general, pied flycatchers in the polluted area provide their nestlings with sufficient quantities of food, but its quality is apparently lower (e.g., because of the absence of mollusks and the increased proportion of invertebrates with a hard exoskeleton).

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