

Wing Length Variation in Pied Flycatchers *Ficedula hypoleuca* (PALL.) Breeding in the Vicinity of the Middle Ural Copper Smelter

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Abstract—The spatiotemporal variation in the wing length (WL) of pied flycatchers breeding near the Middle Ural copper smelter (MUCS) and in the background area was analyzed in 1996–2023, a period of significant reduction in industrial emissions. Females and males were on average smaller near MUCS than in the background area probably due to forcing the low-quality individuals into suboptimal (polluted) habitats. Yearlings had shorter wings than older birds. WL of males increased with increasing melanization of the upper body. Mean WL and proportion of old individuals among breeding birds increased over the study period. The body size of partners in breeding pairs did not correlate. The larger breeding birds, the earlier they started egg laying and the more eggs and fledglings produced.

Keywords: size structure, long-term dynamics, industrial pollution, reduction of industrial emissions, Middle Urals

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Analysis of morphological variation in natural bird populations provides information on environmental factors and process of adaptation to environmental conditions [1]. Chemical pollution is a strong anthropogenic factor that can change genetic and phenotypic structure of local populations [2, 3]. Body size is an important parameter determining competitive ability, survival and breeding success in birds. Researchers estimate body size of birds usually by wing or tarsus length [4–6]. Wing length correlates with tarsus length and body mass [7, 8].

Environmental pollution can affect body size in birds resulting in decreased body mass, wing length, increased fluctuating asymmetry (FA) of limbs and remiges, and delayed growth. Negative effects of pollution are more frequent in young birds than in adults [9]. At the same time, different researchers reported mixed results. In Tunisia, *Cercotrichas galactotes* nestlings showed delayed growth (shorter tarsi, remiges, and rectrices) and higher FA with increased intake of heavy metals (Pb and Zn) [10]. In China, *Passer montanus* nestlings exposed to heavy metal pollution had on average shorter wing, tarsus, lower body mass, and slower growth than chicks at the unpolluted area. Adult sparrows had on average shorter body and third digit (but not wing and tarsus), and lower body mass in polluted area than in the control [11, 12]. In Turkey, wing length and body mass in adult sparrows *Passer domesticus* correlated negatively with Cu and Zn concentrations in the body [13]. In Belgium (Antwerp),

the 15-day-old nestlings of great tits *Parus major* had lower body mass near a non-ferrous smelter than in the control area, although tarsus length did not differ among sites. In breeding adult great tits wing, tarsus length, and body mass did not differ among sites [14], although in the non-breeding season birds had on average shorter wings near the smelter than far away [15]. Wing length and body mass in blue tits *Parus caeruleus* in Antwerp did not differ among sites, at the same time tarsus was longest at the moderately polluted site [16]. In Finland (Harjavalta), pollution from the Cu-Ni smelter did not affect negatively the body size of birds. In this area, mean wing length in pied flycatcher *Ficedula hypoleuca* and great tit females did not differ among pollution zones [17]. Another study in Harjavalta did not reveal association of the length of tarsus and primaries in pied flycatcher and great tit nestlings with the distance to the smelter, at the same time FA of these parameters increased with pollution [7]. In an urban area in USA, the tarsus length of *Turdus migratorius* and *Dumetella carolinensis* did not depend on Pb concentration in the blood [18].

Many authors analyzed the dependence of bird body size only on the contaminant exposure and did not take into account other environmental factors. At the same time, environmental conditions can modify the effect of pollution on the body condition in free-ranging birds [17, 19]. Most studies analyzed data of a few years of observation. The long-term dynamics of the size structure of local bird populations under envi-

ronmental pollution remains understudied. Importance of long-term studies is obvious given the ongoing climate change and the reduction of industrial emissions that has occurred in recent decades in many industrial regions of the world [20].

Aim of this study was to analyze the spatiotemporal variation in the size structure of local populations of pied flycatchers breeding at sites differently polluted by emissions of a large copper smelter in the Middle Urals. We tried to identify factors affecting the size structure of local breeding populations of the species. We hypothesized that in the heavily polluted area birds are on average smaller than in the unpolluted area. We expected that differences in the size of individuals between polluted and unpolluted sites are greater in males than in females due to active competition among males for breeding territories. Given the reduction of industrial emissions from this smelter in recent decades, we expected an increase in the mean body size of flycatchers breeding near the smelter over the study period. We tested if the sizes of partners in breeding pairs correlate. We analyzed relationship between body size of birds and timing of breeding and clutch size. We expected that larger individuals start breeding earlier and lay more eggs than smaller birds.

MATERIALS AND METHODS

The study was performed in the vicinity of the Middle Urals copper smelter (MUCS) located near the town of Revda, Sverdlovsk region of Russia (56°51' N, 59°53' E) and has been operating since 1940. Its atmospheric emissions are dominated by sulfur oxides and dust containing heavy metals (Cu, Pb, Zn, Cd, Fe, Hg, etc.) and metalloids (As). In the 1980s, gross air emissions of MUCS reached 150–225 thousand tons of pollutants per year. Since the early 1990s, emissions have been gradually decreasing, and after radical reconstruction completed in 2009, they stabilized at the level of 3–4 thousand tons/year [21].

The observations were conducted in 1996–2023 at sites with nest boxes (NBs). The sites were established to the west of MUCS in zones of severe pollution (impact, 1–2 km to the smelter), moderate pollution (buffer, 4–8 km), and in unpolluted area (background, 16–27 km). In different years, 7–11 sites were monitored. Schematic map of the study area, description of sites and NBs were published earlier [22]. The pied flycatcher was the most common species occupying NBs [23].

The pied flycatcher is a small passerine bird (11–14 g), a long-distant migrant. It overwinters in sub-Saharan Africa, arrives to breeding sites in the Middle Urals in late April–early May, and has one clutch per season [24]. In the study area, pied flycatchers lay eggs in the second half of May–early June, and feed their chicks in the second half of June–early July.

NBs were checked at intervals of 3–7 days, starting from the nest construction stage until chicks fledged. The date of clutch initiation, number of eggs laid, chicks hatched and fledged were recorded in each nest. Females were captured on nests when incubating clutches or feeding chicks, males – usually when feeding chicks. Females were captured in 93% of nests with completed clutches and males in 77% of nests. Shutter traps, spring traps, and sometimes mist nets were used. Males captured on empty NBs before breeding started, as well as visitors who helped feed the chicks, were not included in the analysis. Birds were marked with aluminum rings and wing length (maximally flattened and straightened) was measured with the accuracy of 0.5 mm. Wing length (WL) was used as a measure of bird body size. Measurements were taken by both authors. The difference between persons by repeated measurements of the same birds did not exceed the measurement error.

The age of birds caught for the first time (1 year, i.e. born in the previous year vs 2 years and older) was determined by plumage characteristics [25]. In total, 2524 females and 2056 males were analyzed. Birds that could not be aged (4.3% females and 4.5% males) were excluded from the analysis in cases where predictors included age. In the case of repeated measurements of an individual within one season, mean value was used in the analysis. Birds with damaged tips of the primaries, in which the original WL could not be measured correctly, were excluded from the analysis.

Primary feathers are subjected to mechanical wear between two successive molts, especially in the breeding period due to high flying activity [26, 27]. Therefore, WL differences among birds can be associated both with their body size and the breeding stage when birds were measured. To calculate the abrasion (shortening) of the wing in pied flycatchers we analyzed our own repeated measurements of individuals during one breeding season made by the same observer (166 females and 98 males). Wing shortening between two measurements was observed in 34% of females and 17% of males. Since birds were measured only during reproduction, differences in the day of the breeding cycle among individuals usually did not exceed one month for females (from the start of incubation to the fledging) and two weeks for males (the period of feeding chicks). Samples in different zones were not biased relative to the day of the breeding cycle at the time of measurements. Females were measured at a median chick age of 9–11 days in different zones and males were measured at a median chick age of 12 days in all zones. Given the short measurement period in terms of phenology and the small proportion of individuals with the wing wear, we did not apply corrections to the measured WL values. The corrections would hardly have affected the results, since the rate of wear of primary feathers in passerines typically does not exceed 1% of the original length per month [27].

To compare distributions of WL among zones, the Kruskal–Wallis test and the median test were used. Differences in the bird WL among pollution zones and age groups were analyzed with a 2-way ANOVA, separately for females and males. For post hoc comparisons, Tukey's HSD test was used. The effect size of pollution zone was calculated with Cohen's d using online-calculator <https://www.campbell-collaboration.org/calculator/d-means-sds>. In subsequent analysis, general linear models (GLMs) were used. Females and males were analyzed separately. Categorical predictors included pollution zone (impact (1), buffer (2), and background (3)); age of a bird (1 year (1), 2 years and older (2)); period: before strong reduction of emissions, 1996–2009 (1), and after emissions reduction 2010–2023 (2); habitat: deciduous (1), coniferous (2)), as well as interactions of the variables. For males, the color score according to the seven-point Drost scale [28] was included. Continuous predictors included the site-specific breeding density in each year (\log_{10}) and mean air temperature in the first half of May (period of occupation of breeding territories). Breeding density (pairs/ha) was calculated as the ratio of the number of nests with a complete clutch (where incubation started) to the area of the site. The area of a rectangular site was calculated as the area of a rectangle with the addition of a 50 m peripheral strip. The area of sites with linear NB arrangement was calculated by the length of a line with a periphery of 50 m in all directions [29].

Weather data from the nearest weather station in Revda were provided by the Sverdlovsk Center for Hydrometeorology and Environmental Monitoring (1989–2019) and obtained from www.pogodaiklimat.ru (2020–2023).

During model optimization, non-significant terms were removed from the models one by one starting from the term with the highest p -value. The final models retained variables and interactions with $p < 0.1$, as well as variables included in significant interactions.

The long-term dynamics of the pied flycatcher body size was analyzed with GLMs using mean WL per year in a specific pollution zone as the dependent variable, and year, sex, zone, and their interactions as predictors. The proportion of old birds was not included in the analysis because of its correlation with the year.

The relationships between WL of females and males in breeding pairs, as well as between WL and the timing of clutch initiation, clutch size, and number of fledglings were assessed with Pearson linear correlation. Since timing of breeding differs among years, dates of the first egg in each nest were standardized for each year: $((x - SD)/\text{mean})$, where x is the number of the day of the first egg (1 May = 1), mean – yearly mean, and SD – yearly standard deviation. For bigamous males, only first nests were analyzed. Calculations were performed in the programs JMP.10.0.0. and Statistica 10.

RESULTS

Females had on average longer wings in the background zone than in the impact and buffer zones (Table 1). WL distributions differed among zones (Kruskal–Wallis test $H = 33.55$, $n = 2524$, $p < 0.001$). The proportion of large individuals (WL exceeding the median of the combined sample) in the background zone (45.8%) was greater than in the buffer zone (38.8%) and the impact zone (37.2%), median test $\chi^2 = 14.29$, $df = 2$, $p = 0.001$. Yearlings had shorter wings than older birds. WL of young females did not differ among zones and wings of older birds in the buffer zone were shorter than in the background zone.

Males had on average longer wings in the background and buffer zones than in the impact zone (Table 1). The body size of individuals of a known age (both yearlings and older) in the background zone was greater than in the impact zone. WL distributions differed among zones (Kruskal–Wallis test $H = 28.72$, $n = 2056$, $p < 0.001$). The proportion of large individuals in the background (45.1%) and buffer (40.6%) zones were greater than in the impact zone (34.9%), median test $\chi^2 = 13.58$, $df = 2$, $p = 0.0011$. The pollution zone effect in males was greater than in females. In males, the confidence interval for the effect size did not include zero in all age groups, while in females the effect was significant only in the combined group of individuals (Table 1).

The GLM analysis confirmed significant association of the pollution zone and age with WL of females (Table 2). Non-significant interaction between these predictors on WL indicates similar among-zone variation of the body size in both age groups. The association of the period and breeding density with WL was non-significant whereas their interaction was significant. In the first period, mean WL increased along with breeding density, while in the second period mean body size of females did not change with increased breeding density (Fig. 1a). The zone \times breeding density interaction on WL was significant. In the background and impact zones, breeding density increased due to larger individuals (mean body size increased), while in the buffer zone mean WL of females did not show association with breeding density (Fig. 1b). The body size of females showed no association with the habitat and air temperature in the first half of May (Table 2).

WL of males showed association with zone, age, and color score (Table 1). The lighter the dorsal coloration of a male (the greater Drost score), the shorter its wing was (Table 3). In the combined sample, males with the 7th Drost score had on average the shortest wing and males with the 2nd–5th scores had on average the longest wing. Within the latter group, differences in WL among phenotypes were non-significant. Males with the 6th score had an intermediate WL. In old males, there was clear association of WL with dorsal coloration, while in yearlings only difference

Table 1. Wing length (mm) of pied flycatchers breeding in different zones of pollution by emissions of MUCS

Age	Zone						Effect size (95% CI)
	impact		buffer		background		
	<i>n</i>	mean ± SE (min–max)	<i>n</i>	mean ± SE (min–max)	<i>n</i>	mean ± SE (min–max)	
Females							
All individuals*	522	79.81 ± 0.06 ^a (76.0–84.0)	356	79.85 ± 0.07 ^a (75.5–84.0)	1646	80.19 ± 0.04 ^b (75.0–85.0)	–0.26 (–0.36; –0.16)
1 year old	228	79.22 ± 0.08 ^c (76.0–83.0)	81	79.17 ± 0.16 ^c (75.5–83.0)	350	79.39 ± 0.07 ^c (76.0–83.5)	–0.13 (–0.30; 0.04)
≥2 years old	285	80.34 ± 0.08 ^{ab} (77.0–84.0)	246	80.11 ± 0.08 ^b (77.0–84.0)	1224	80.45 ± 0.04 ^a (75.5–85.0)	–0.08 (–0.21; 0.05)
Males							
All individuals*	398	81.67 ± 0.08 ^a (77.0–87.0)	288	82.02 ± 0.09 ^b (76.5–88.0)	1370	82.16 ± 0.04 ^b (76.0–86.5)	–0.32 (–0.43; –0.21)
1 year old	96	80.36 ± 0.15 ^e (77.0–83.5)	38	81.26 ± 0.28 ^{ed} (78.0–85.5)	177	80.98 ± 0.11 ^d (76.0–85.0)	–0.44 (–0.67; –0.18)
≥2 years old	299	82.09 ± 0.09 ^{bc} (78.0–87.0)	227	82.26 ± 0.09 ^{ab} (78.5–88.0)	1133	82.37 ± 0.04 ^a (77.0–86.5)	–0.20 (–0.32; –0.07)

*Including individuals with unknown age. Values with the same letter are not significantly different at $p < 0.05$ (1-way ANOVA for all individuals and 2-way ANOVA for birds of known age).

Table 2. General linear models for variation in the wing length of pied flycatchers breeding in the vicinity of MUCS

Source of variation	Females			Males		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Zone	2	3.97	0.019	2	5.78	0.003
Age	1	276.50	<0.001	1	152.73	<0.001
Period	1	0.04	0.835	1	0.71	0.401
Habitat	1		ns	1		ns
Dorsal coloration (Drost score)	5		NA	5	7.25	<0.001
Breeding density (log ₁₀)	1	1.24	0.266	1	1.02	0.313
Air temperature, May 1–15	1		ns	1		ns
Zone × age	2		ns	2		ns
Zone × breeding density	2	4.30	0.014	2		ns
Period × breeding density	1	7.95	0.005	1	4.81	0.028
Period × age	1		ns	1		ns
Residual	2400			1934		

Variables included in the final models are presented; ns—non-significant association; NA—variable was not included in the analysis.

between males with the 3rd score and males with 5th–7th scores was significant (Supplement, Table S1). WL had no association with the period and breeding density whereas their interaction on WL was significant. In the first period, mean WL increased along with breeding density, while in the second period mean body size of males did not change with increased breeding density (Supplement, Fig. S1). There was no

association between the body size of males, habitat, and air temperature in the first half of May (Table 2).

Analysis of the temporal WL variation in pied flycatchers showed significant effects of the year, pollution zone, and sex. The model with these three predictors explained 80.3% of the variance ($n = 165$, $F = 70.03$, $p < 0.001$). The body size of both females and males increased over the study period in all zones

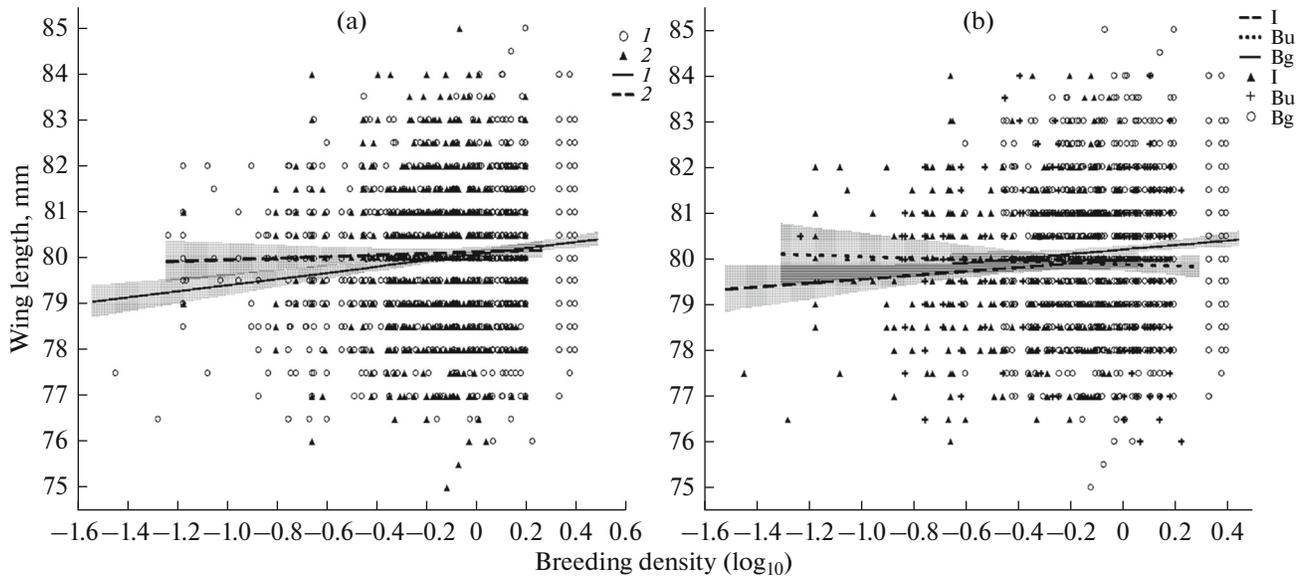


Fig. 1. Relationship between the wing length of pied flycatcher females and breeding density in different periods (a: (1)—1996–2009, (2)—2010–2023) and in different pollution zones (b: I—impact, Bu—buffer, Bg—background). Shaded areas denote 95% CI.

(Fig. 2). Interactions of predictors were non-significant (Table 4). In females and males breeding in the impact zone, the proportion of yearlings was greater than in the buffer and background zones (Supplement, Fig. S2). Analysis of temporal dynamics of the age composition of breeding birds showed increased proportion of older birds in females and males over the study period in all zones (Supplement, Fig. S3). Linear correlation of the proportion of older birds with the serial number of year equaled in females $r = 0.62 \pm 0.15$ (SE), $n = 28$ (zones combined), $p < 0.001$, and in males $r = 0.63 \pm 0.15$, $n = 28$, $p < 0.001$ (zones combined). A model of temporal WL variations with the predictor “proportion of older birds” instead of “year” also fits the data well, explaining 83.3% of the variance.

Association of the body size of partners in breeding pairs was not significant. Linear correlation of the female and male WLS equaled $r = 0.043 \pm 0.023$, $n = 1842$, $p = 0.064$. The larger breeding birds, the earlier they started egg laying (Fig. 3). Linear correlation of WL with standardized date of the 1st egg equaled in females $r = -0.101 \pm 0.020$, $n = 2476$, $p < 0.001$, and in males $r = -0.111 \pm 0.022$, $n = 1998$, $p < 0.001$. The larger females, the more eggs they laid (Supplement, Fig. S4). Linear correlation of the female WL with clutch size equaled $r = 0.143 \pm 0.020$, $n = 2484$, $p < 0.001$. The number of fledglings per nest increased with the body size of parents in all zones (Fig. 4).

DISCUSSION

The mean body size of pied flycatchers decreased towards the MUCS, especially in males. Changes in

the size structure of local populations in polluted areas can result from different reasons (toxic exposure during growth, habitat transformation, intraspecific competitive interactions etc.). In resident species, whose populations refill each year with birds of local origin, body size of adult birds depends on conditions during their growth. Intake of pollutants in the body can affect physiological processes, retard growth and development of chicks [30, 31]. In tree sparrow in China, nestlings and adult birds in the polluted area were smaller than in the unpolluted area [11]. Nevertheless, in most cases there is no clear relationship between morphological characteristics of nestlings and adults. In Finland, chicks of the great tit were smaller near a metallurgical factory than in the background area but breeding females did not differ between areas [30, 32, 33]. Lack of the one-to-one dependence between characteristics of nestlings and

Table 3. Wing length (mm) in pied flycatcher males with different dorsal coloration

Color Drost score	n	Mean ± SE (SD)	Min	Max
2	10	83.00 ± 0.34 (1.08) ^{ab}	81.0	84.5
3	278	82.37 ± 0.09 (1.42) ^a	78.5	86.5
4	362	82.39 ± 0.08 (1.43) ^a	79.0	86.5
5	724	82.17 ± 0.06 (1.56) ^a	76.0	88.0
6	518	81.70 ± 0.07 (1.51) ^b	77.0	86.0
7	131	80.96 ± 0.14 (1.55) ^c	76.0	84.5

Males with known and unknown age are combined. Values with the same letter are not significantly different at $p < 0.05$ (1-way ANOVA, Tukey’s HSD test).

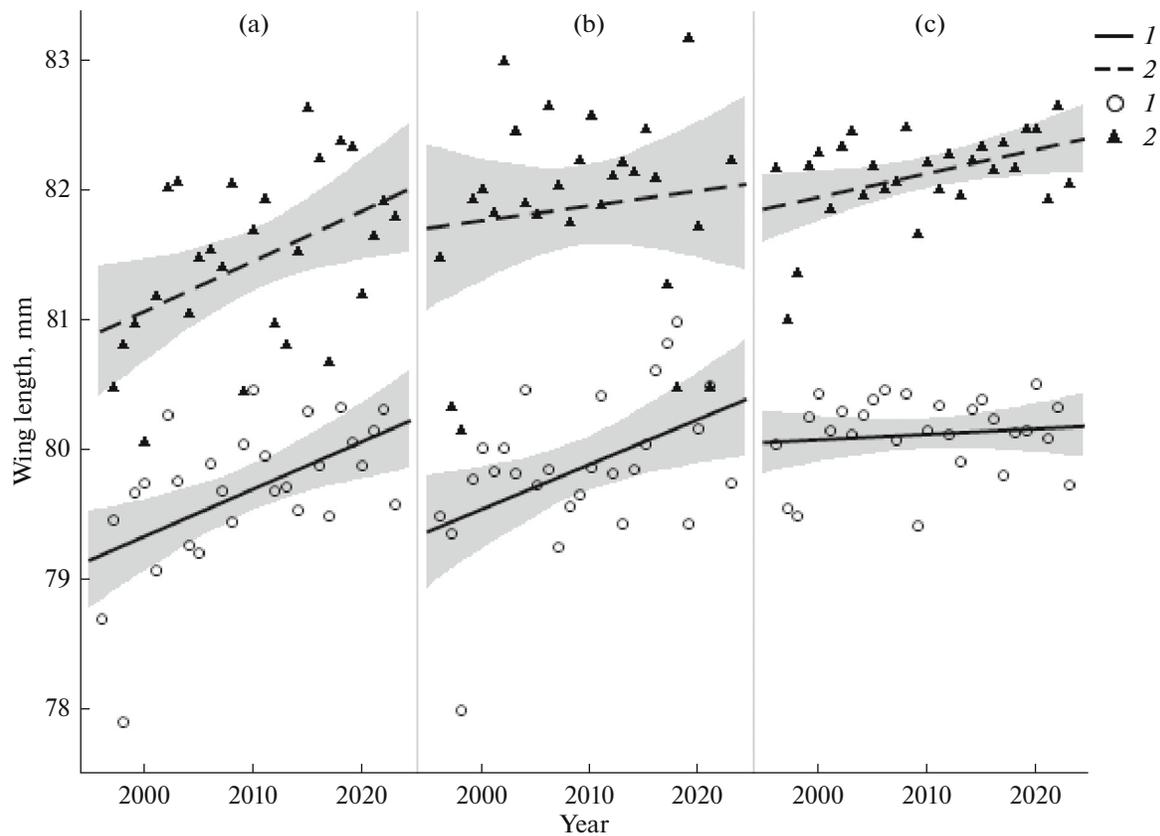


Fig. 2. Temporal wing length variation in pied flycatcher females (1) and males (2) breeding in the impact (a), buffer (b), and background (c) zones. Dots are yearly means in specific zones.

adults is likely due to high mortality of young birds at their first year of life. In small passerines, nearly one third of fledglings survive to reproductive age [34]. In addition, many young birds even in resident species

leave their area of birth at the first year of life [35]. Migrating species show considerable renewal of local breeding populations each year. In the pied flycatcher, typically no more than 10% of individuals return to their area of birth and no more than 50% of adults return to their former breeding area [29].

Table 4. General linear models for the temporal wing length variation in pied flycatchers breeding in the vicinity of MUCS

Source of variation	<i>df</i>	Slope \pm SE	<i>F</i>	<i>p</i>
Year	1	0.037 \pm 0.009	17.90	<0.0001
Zone	2		16.14	<0.0001
Zone [2–1]		0.316 \pm 0.100		
Zone [3–2]		0.245 \pm 0.099		
Sex [females]	1	–0.880 \pm 0.070	156.84	<0.0001
Sex \times Zone	2	ns	1.07	0.345
Year \times Sex	1	ns	0.03	0.867
Year \times Zone	2	ns	2.24	0.110
Residual	155			

Yearly means in specific zones were analyzed; ns—non-significant association.

One of the hypotheses put forward to explain the phenotypic differences among individuals in different habitats is the matching habitat choice hypothesis [36]. According to this hypothesis, individuals actively select the habitats that best suit their morphological, physiological and behavioral characteristics. Selection of habitats with the most suitable conditions allows maximizing individual fitness. For example, birds select habitats where size of their prey corresponds to the bill size of specific individuals [36], and invertebrates select microhabitats with a background that makes them less visible to predators [37]. From this point of view, difference in bird body size in different habitats can be explained. Large males of the pied flycatcher breed mainly in deciduous forests, while small males are more frequent in coniferous habitats [38, 39]. Bird body size corresponds to the size of their potential prey, insects, that are smaller in the coniferous forest than in the deciduous one [38].

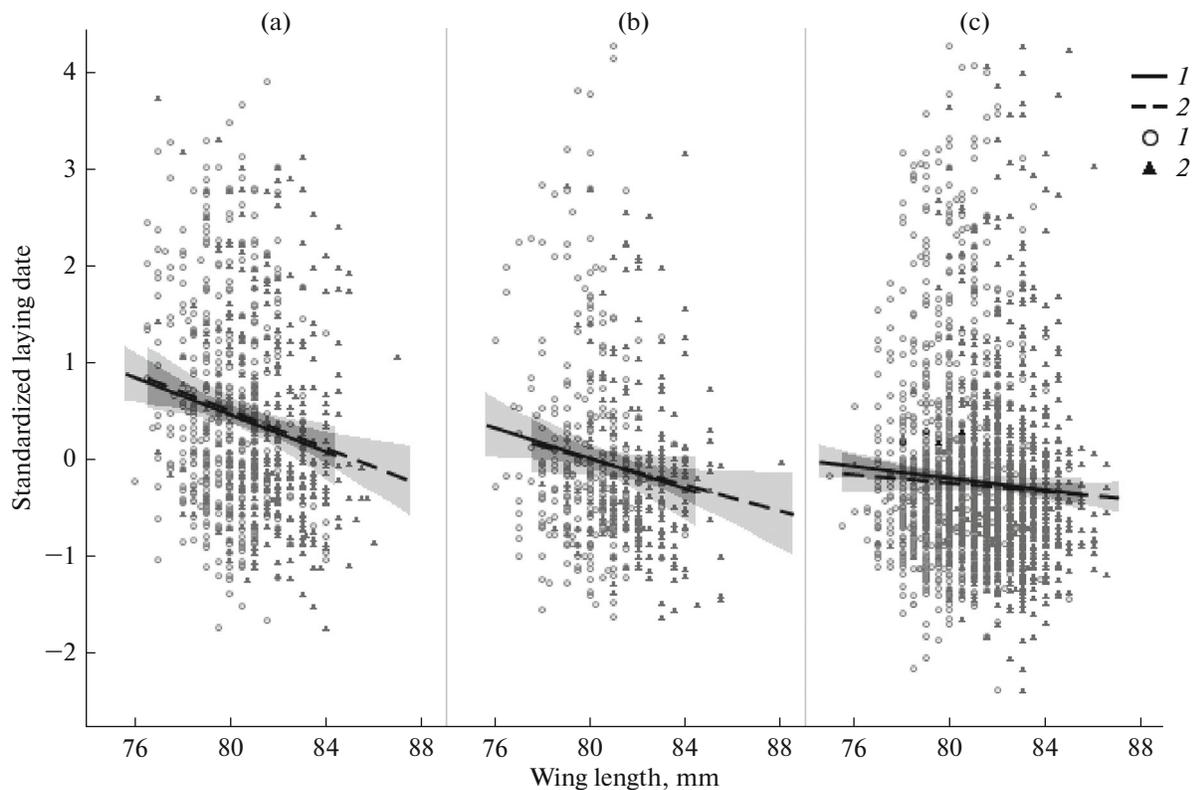


Fig. 3. Relationship of the date of the 1st egg with the body size of pied flycatcher females (1) and males (2) in the impact (a), buffer (b), and background (c) zones.

To test this hypothesis, it is necessary to assess the contribution of different phenotypes to reproduction of a local population, for example, recruitment success of their offspring [40]. Low return rate of locally born birds to our study area allows us to compare only numbers of fledglings in the nests of differently sized birds. If the hypothesis is true, then in the background zone (preferred by larger individuals) the number of fledglings in the nests of large-sized parents is expected to be greater than in the nests of smaller birds, whereas in the impact zone (preferred by smaller individuals) the opposite is expected. The data obtained don't support this hypothesis. In all pollution zones, the number of fledglings per nest increased with the body size of parents (Fig. 4). Therefore, fitness of birds assessed by the number of fledglings was higher in larger individuals regardless of the pollution zone.

Another hypothesis links differences between bird groups in different habitats with territorial behavior and social dominance [41, 42]. When competing for breeding sites, larger and more aggressive individuals that have an advantage in territorial conflicts [24], displace subdominant individuals into poorer quality habitats. Pied flycatchers prefer mature and middle-aged deciduous and mixed forests with hollow trees necessary for breeding, while coniferous forests are

less populated [24, 29]. Studies in Sweden [38, 43] have shown that pied flycatchers breeding in coniferous forests have on average shorter wings compared to those breeding in deciduous forests. This can be due to forcing smaller individuals into a suboptimal coniferous habitat with worse feeding conditions. Suboptimal habitats also include areas where pollution has led to the suppression of tree and field layers [21]. Low breeding density of this species near MUCS in the 1990s – early 2000s that is a period of high emissions, indicates low attractiveness of the impact zone for flycatchers [23].

Competition for breeding territories in males is stronger than in females. If the hypothesis of social dominance is true, then pollution-related change of the size structure of local populations in males is expected to be greater than in females. The data obtained are consistent with this hypothesis: the negative effect of pollution is stronger in males than in females. Competitive interactions can lead to changes in the population age structure due to forcing young birds into suboptimal habitats. Young birds are inferior to older individuals in competition for breeding sites due to their smaller size, later arrival at the breeding area [24], and lack of experience. In our study area, the proportion of yearlings both in males and females in the impact zone is higher than in the background

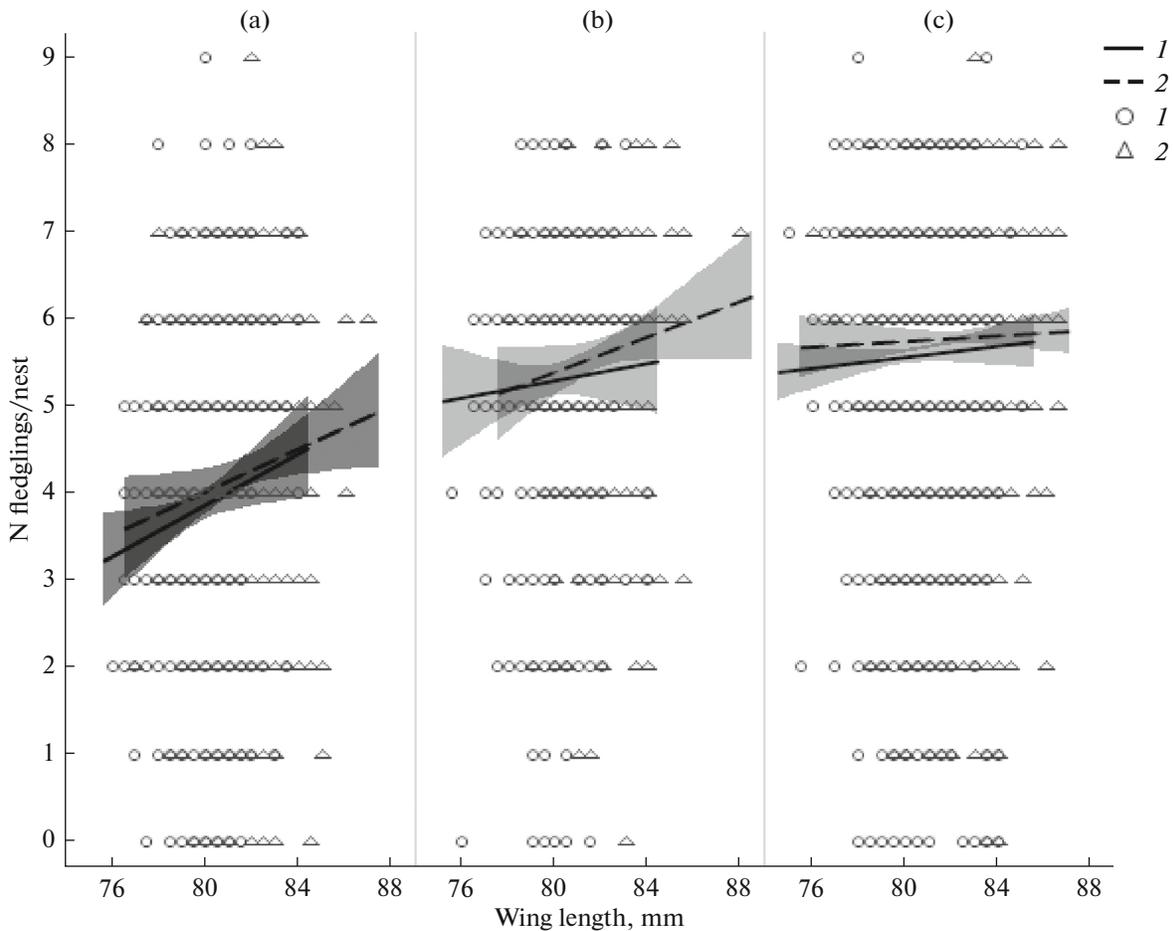


Fig. 4. Relationship of the number of fledglings per nest (including unsuccessful nests) with the body size of pied flycatcher females (1) and males (2) in the impact (a), buffer (b), and background (c) zones.

area (Supplement, Fig. S2). The social dominance hypothesis is supported by the delayed breeding of pied flycatchers in the impact zone compared to the background zone [44, 45]. The loss of time searching for free sites results in a delay of reproduction of individuals who have lost in territorial conflicts.

Analysis of the temporal WL variation showed increased mean body size of breeding birds in both sexes over the study period. Judging by the absence of significant interactions (Table 3), the long-term dynamics of the bird body size did not differ between sexes and pollution zones. Long-term variation of WL in pied flycatchers is clearly related to changes in the age structure of breeding birds. Proportion of birds at the age of 2 years old or older increased over the study period. Further, models of WL dynamics that use either year or proportion of older individuals as a predictor yield similar results. Change in the population age structure of pied flycatchers breeding near MUCS is likely due to ecosystem recovery that has started after radical reduction of industrial emissions. Over a 30-year period since the late 1980s, the acidity of the forest litter and soil copper concentrations decreased

near the MUCS [46], the projective cover of graminaceous plants increased [21], as did the species richness of anemochorous and myrmecochorous plants [47], as well as the abundance and diversity of soil invertebrates [48]. Increased breeding density of pied flycatchers in the impact zone [23] indicates improved conditions for these birds. Increased attractiveness of this habitat for flycatchers is reflected also in the growing proportion of older individuals in the local population and increasing mean body size of birds as a result.

Other our results are consistent with those of other researchers. It is known that WL of pied flycatcher males decreases as their coloration becomes lighter [8, 49, 50]. We observed this pattern in older birds whereas the data on yearlings are insufficient for a firm conclusion. In samples that combine birds regardless of age, the body size differences among phenotypes can result from various age compositions of the groups. Yearlings are smaller than older birds, but they predominate among males with the 7th score (56% in our sample). As the dorsal coloration became darker, the proportion of young birds decreased and the mean

body size increased. At the same time, analysis of more homogeneous groups (older males only) showed a significant association of WL with the color type. Males of different phenotypes are known to differ by physiology, behavior and reproductive strategies [51–53] but the relationship between coloration and WL remains to be explained.

We did not find association between the body sizes of partners in breeding pairs, although a positive correlation of WL in pairs of light males (5th–7th color scores) was previously reported [50]. Female mate choice depends on many factors, including the quality of a territory and nest site, and not only the body size and phenotype of a male [54–56]. Body size and weight did not matter in pairing in pied flycatchers in Spain [57]. Females took into account age, coloration of the male, and territory quality. Size-assortative pairing seems unlikely given the time constraints before the start of the breeding season.

The body size of birds affected their reproduction. Larger individuals started breeding earlier, laid more eggs, and raised more fledglings. The conclusion on the association of reproductive parameters with bird body size is consistent with the data of other researchers [58], although this relationship differs among populations [50]. The association of breeding success with bird body size likely reflects age characteristics of individuals. Old birds are larger than yearlings and are more productive due to greater experience and better condition [29, 59].

CONCLUSIONS

This study identified main factors affecting the size structure of local populations of the pied flycatcher in areas with different level of industrial pollution. The pollution-related decrease in the mean body size of individuals that was stronger in males than in females supports the social dominance hypothesis. This study showed that the size structure of local populations of birds could change under industrial pollution. In migrating species, this change reflects likely an indirect effect of pollution as a result of habitat transformation rather than direct toxic effect of pollutants. The study confirmed the hypothesis that the mean body size of birds increased under reduction of industrial emissions and the beginning of the ecosystem recovery. Absence of correlation of body sizes of partners in breeding pairs shows that male body size is not a main factor in the female mate choice. The hypothesis about the association of the timing of breeding and reproductive parameters with the body size of birds was confirmed. The data obtained emphasize the need to take into account a complex of environmental factors, the age-sex and phenotypic structure of local populations, breeding density, as well as migration status when analyzing morphological variation in birds.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1134/S1067413625600284>.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All our procedures were intravital for birds. After capture, measurements and ringing all birds were immediately released in the vicinity of their nests. The species under study is not included in the International Union for Conservation of Nature and Natural Resources (IUCN) List of Threatened Bird Species and Red Data Book of the Russian Federation. Conducting the research does not require special permission in accordance with Federal Law no. 52-FZ of 24.04.1995, Article 44.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interest.

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