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Improved breeding parameters in the pied flycatcher with reduced pollutant emissions from a copper smelter[☆]

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ABSTRACT

In recent decades, industrial emissions have been reduced in many countries, which provides an opportunity for the recovery of polluted ecosystems. However, our knowledge of the rate and factors facilitating the recovery of local bird populations after pollution abatement is incomplete. Long-term (1989–2021) annual observations on nest-box populations of a passerine bird, *Ficedula hypoleuca*, were used to analyze temporal dynamics of breeding parameters following a 50-fold reduction of industrial emissions from the Middle Ural copper smelter (MUCS) according to pollution zone, habitat, air temperature, and breeding density. In the heavily polluted (impact) zone (1–2 km of MUCS), egg and fledgling production were strongly impaired compared to the moderately polluted (buffer zone, 4–8 km of MUCS) and unpolluted control zone (16–27 km of MUCS). During the study period, the laying date advanced along with increasing spring air temperatures. The clutch size increased in the impact zone by 26%, in the buffer zone by 10%, and in control by 5%. The number of fledglings increased in the impact zone by 102% and the buffer zone by 17%. In the most recent year (2021), mean laying date, clutch size, fledgling production, and the frequency of nests with unhatched eggs in the impact zone did not reach the control level, whereas the frequency of nests with perished chicks did not differ among zones. Breeding parameters of birds in the impact zone improved slowly, likely due to the slow recovery of habitats. We conclude that bird reproduction may require many decades to recover fully in the heavily polluted zone.

1. Introduction

Industrial pollution poses both direct and indirect effects on ecosystems, including changes in habitat structure and productivity, food webs, and performance of populations and individuals (Newman and Schreiber, 1984; Hoffman et al., 1995; Clements and Newman, 2002). The emissions of non-ferrous smelters are especially harmful to natural ecosystems due to a combination of sulfur dioxide and polymetallic dust (Bennett and Knapp, 1989; Kozlov and Zvereva, 2007). Sulfur dioxide causes necroses in plants, acidification of soil, and nutrient leaching (Knabe, 1976). Heavy metals persist in soil for centuries (Maskall et al., 1995) and cause physiological disorders, impaired reproduction, and low survival in plants and animals (Scheuhammer, 1987; Nagajyoti et al., 2010; Jaishankar et al., 2014). In recent decades, the improvement of technologies has led to reducing industrial emissions (Pacyna et al., 2007; Kozlov et al., 2009) and the recovery of disturbed ecosystems (Vorobeichik et al., 2014, 2019; Mikhailova, 2020). However, our knowledge of the rate and factors facilitating the recovery of natural

systems after pollution abatement is incomplete. The need to predict and manage the recovery of populations, communities, and ecosystems in post-industrial areas emphasizes the importance of such studies (Depledge, 1998).

Previous studies on the recovery of bird populations after the reduction of industrial emissions have explored metal concentrations in the food and the body of birds (Eeva and Lehikoinen, 2000; Berglund et al., 2009, 2010, 2012, 2015; Berglund and Nyholm, 2011), eggshell thickness, body mass and age composition in breeding females (Eeva and Lehikoinen, 2015; Rainio et al., 2017), physiology (Berglund et al., 2010; Berglund and Nyholm, 2011), reproduction (Eeva and Lehikoinen, 2000, 2013, 2015; Berglund et al., 2010, Berglund and Nyholm, 2011), and the effect of weather on breeding success (Eeva et al., 2020). The recovery rate estimates of the same parameters differ among studies cited above. Some authors reported a rapid reduction of the contaminant exposure and an improvement of breeding and physiological parameters in birds (Eeva and Lehikoinen, 2000; Berglund et al., 2012). Other authors showed stable high toxic exposure and the slow recovery of the

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reproduction and physiology in birds due to the persistence of heavy metals in soils and sediments of water bodies (Blus et al., 1999; Berglund et al., 2009; Berglund and Nyholm, 2011). In addition, temporal trends of breeding parameters differ between species. For example, the breeding parameters in the pied flycatcher *Ficedula hypoleuca* improved as the emissions from the Cu–Ni smelter in Harjavalta (Finland) reduced (Eeva and Lehikoinen, 2015). In contrast, in the great tit *Parus major*, the clutch size decreased with time because the increased density affected reproduction stronger than the reduced industrial emissions (Eeva and Lehikoinen, 2013).

Many factors are modifying the effects of industrial pollution on bird reproduction in natural ecosystems. For example, cold weather can strengthen the negative effect of pollution on fledging success in the pied flycatcher, which is more weather-sensitive than the great tit (Eeva et al., 2020). Habitat characteristics can affect breeding performance in birds as well. For example, clutch and brood size in the pied flycatcher are smaller in coniferous than in deciduous habitats (Cramp and Perrins, 1993; Sanz, 1997). However, near Harjavalta, the clutch size in the pied flycatcher was smaller in territories where broad-leaved trees were abundant (Eeva and Lehikoinen, 2015). Therefore, population density, weather, and habitat are important confounding variables affecting temporal pollution-related changes in birds (Sanz, 1997; Eeva and Lehikoinen, 2013; Eeva et al., 2020). This is in line with the findings that pollution effects on biota depend on various environmental factors, including biome and climate (Laskowski et al., 2010; Kozlov and Zvereva, 2011). Most studies on the recovery of bird populations after industrial pollution abatement were performed in northern Europe (Eeva and Lehikoinen, 2000, 2013, 2015; Berglund et al., 2010; Berglund and Nyholm, 2011) but not sufficiently in other regions resulting in a geographic bias. Further studies in various regions are required to find a general pattern of the recovery of bird populations after the cessation of industrial pollution.

In this long-term study, we analyzed the temporal dynamics of breeding parameters in a passerine bird, the pied flycatcher, in vicinities of the Middle Ural copper smelter (MUCS), according to pollution zone, habitat, air temperature, and breeding density. Given the substantial reduction of industrial emissions over the last decades, we hypothesized that the reproduction of pied flycatchers has recovered in the polluted area. We expected that breeding parameters have changed significantly in the contaminated area and remained stable in the unpolluted area. In addition to clutch size and the number of fledglings, we studied laying date since clutch size depends on the timing of breeding (Lundberg and Alatalo, 1992). We also studied the frequencies of nests with egg and chick failures, affecting reproductive output.

2. Materials and methods

2.1. Study area

The study was performed in 1989–2021 near the MUCS (Revda, Sverdlovsk region of Russia, 56°51'N, 59°53'E). The MUCS, in operation since 1940, is one of the largest Cu smelters in Russia, with annual Cu production ca. 150,000 tons (UMMC-Holding, 2019). Significant pollutants in the area include sulfur and nitrogen oxides and polymetallic dust containing Cu, Pb, Cd, Zn, Fe, and As. After a radical modernization project completed in 2009 (Supplement 1, Fig. S1), total air emissions reduced approximately 50-fold, from 157,000 tons in 1989 (Kozlov et al., 2009) to 3000–4000 tons per year in 2010–2013 (Vorobeichik et al., 2014) and later on (State reports on the state and protection of the environment of the Sverdlovsk region, 1995–2021; Supplement 1, Fig. S2). The emissions of Cu equaled 2610 tons/year in 1989 and 0.8 tons/year in 2012, Zn 1753 and 118 tons/year, As 640 and 0.6 tons/year, and Pb 564 and 66 tons/year, respectively (Vorobeichik and Kaigorodova, 2017). Nevertheless, metal concentrations in the soil near the MUCS remain high (Vorobeichik and Kaigorodova, 2017) and cause heavy contaminant exposure and ongoing severe suppression of

vegetation (Trubina et al., 2014; Vorobeichik et al., 2014).

2.2. Observations on birds

Sites with nest boxes were established west of the MUCS, in an up-wind direction: at distances of 1–2 km in the heavily polluted (impact) zone (4 sites), 4–8 km in the moderately polluted (buffer) zone (6 sites), and 16–27 km in the control unpolluted (background) zone (3 sites) (Fig. 1). The zones were distinguished by the soil metal concentrations and by the degree of deterioration of forest ecosystems. In 1989, the forest litter concentrations (extraction with 5% HNO₃) equaled in the background, buffer, and impact zones: Cu 98.5 µg/g dw, 1362.8–1617.5 µg/g and 3312.2–4156.1 µg/g, respectively; Pb 86.6 µg/g, 491.5–541.8 µg/g and 885.7–1058.7 µg/g, respectively; Cd 4.0 µg/g, 6.3–11.3 µg/g and 6.1–7.8 µg/g, respectively; Zn 296.1 µg/g, 349.4–610.4 µg/g and 430.6–502.0 µg/g, respectively (Vorobeichik and Kaigorodova, 2017). Near the MUCS, chronic pollution resulted in the suppression of the tree and field layers; the latter was replaced with the resistant moss species *Pohlia nutans* over a large area. In recent years, large areas occupied with moss turfs are being overgrown with the grass *Agrostis capillaris* (Vorobeichik et al., 2014).

The number of study sites with nest boxes differed between years (7–11). We located sites in two forest habitats typical of the study region: spruce/fir forest (*Picea obovata* and *Abies sibirica*) and aspen/birch forest (*Populus tremula*, *Betula pubescens*, and *B. pendula*) with some admixture of pine (*Pinus sylvestris*). Nest boxes were arranged in the same way at most sites, in regular grids with the distance between parallel lines of 100 m and the distance between nest boxes in a line of 50 m. Fifteen to 80 nest boxes per site were mounted on trees at the height of 2.5–3.5 m with the average density of two nest boxes per 1 ha. At one site, we had hung nest boxes in a line with 50 m between nest boxes. Nest boxes made of wooden boards had a bottom area of 10 cm*10 cm and an entrance diameter of 30–35 mm. We checked nest boxes every 3–7 days, from the nest-building until fledging. After fledging, we examined nest material for unhatched eggs and dead nestlings.

The pied flycatcher is the most abundant species occupying nest boxes in our study area (Belskii and Lyakhov, 2021). This is a small (11–14 g), insectivorous, long-distance migrant. In our study area, flycatchers arrive at the end of April – the first half of May, lay eggs in the second half of May – beginning of June, and feed chicks in the second half of June – beginning of July. Nestlings fledge at the age of 15–16 days (Lundberg and Alatalo, 1992). Flycatchers raise one brood per season.

2.3. Data processing

We recorded laying and hatching dates, the number of eggs, and hatched and fledged nestlings in each nest. The laying date is the date of the first egg (May 1st = 1). If the exact date of clutch initiation was not known, it was back-calculated from the hatching date, assuming that incubation lasts for 14 days and one egg per day is laid. Clutch size is the number of eggs in the complete clutches. In the analysis, we used the number of fledglings per incubated clutch, including nests with no chicks hatched (hereafter referred to as “number of fledglings per nest”). To assess the egg and chick failures, we calculated the frequency of nests with at least one unhatched egg and the frequency of nests with at least one nestling perished before fledging. The abandoned incomplete clutches, nests disturbed by men, and depredated nests were excluded from the analysis. At the same time, nests depredated after chicks hatched were used to calculate egg failures during incubation. Approximately 3000 nests were monitored.

The temporal trends in breeding parameters (laying date, clutch size, and the number of fledged nestlings) were analyzed with linear mixed models (LMM) by using statistical software JMP 11.0.0 (SAS Institute Inc., 2013). Predictors were categorical variables zone (background,

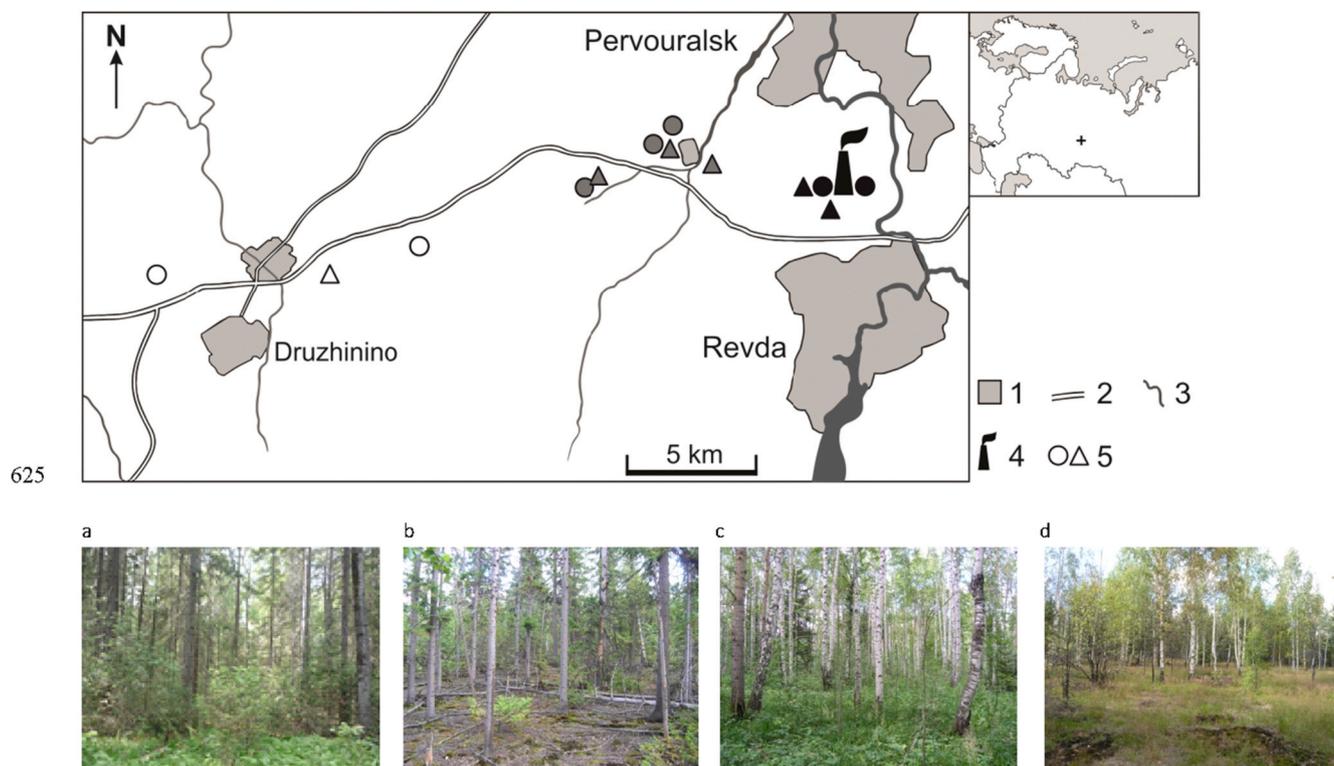


Fig. 1. Location of study sites near MUCS. Symbols: 1 – settlement; 2 – highway; 3 – river; 4 – Cu smelter; 5 – study sites (circles – deciduous forest, triangles – coniferous forest; open, grey, and black marks are background, buffer, and impact zones, respectively). Habitats: a – coniferous, background zone, b – coniferous, impact zone, c – deciduous, background zone, d – deciduous, impact zone.

buffer, and impact) and habitat (deciduous vs. coniferous). Continuous variables were year, year \times year, \log_{10} -transformed breeding density, and weather characteristics (see below). For clutch size, we added laying date as a predictor. The variable “year” strongly correlated with emissions from MUCS in 1989–2020 (Pearson correlation $r = -0.933$, $t = -14.18$, $n = 32$, $p < 0.0001$, Supplement 1, Fig. S2) and can be used as a proxy for the level of emissions. The second-order term year \times year was included because preliminary data inspection showed nonlinear temporal trends of some breeding parameters. The interactions year \times zone and year \times year \times zone were included to test if temporal trends differ among zones. Breeding density (pairs/km²) was calculated as the number of nests at a site divided by its area. The area of a rectangularly shaped site was determined as the area of a rectangle adding a periphery of 50 m. The area of a site with a linear arrangement of nest boxes was calculated as the length of a line with a periphery of 50 m in all directions (Artemyev, 2008). Such width of the periphery comes from observations by Alatalo and Lundberg (1984) that nest boxes at the distance of <50 m from an active nest in a deciduous forest are less likely to be occupied by other flycatchers than nest boxes further away. For laying date and clutch size, we included mean temperatures of April and May as spring weather and vegetation phenology characteristics. Temperature of April did not correlate with May and year: Pearson correlation $r = 0.23$ ($n = 33$, $t = 1.33$, $p = 0.19$) and $r = 0.14$ ($t = 0.79$, $p = 0.44$), respectively. Temperature of May correlated with year, but the correlation was weak: $r = 0.37$ ($t = 2.19$, $p = 0.036$). For the number of fledglings per nest, we included clutch size, hatching date, mean temperature and precipitation in June as weather characteristics instead of April and May. Although the clutch size and timing of breeding correlate, the variables show different things. Clutch size reflects the potential number of fledglings while hatching date determines the degree of match of maximal food demand and availability (Van Noordwijk et al., 1995; Visser et al., 2004). Study site nested within the zone was used as a random factor to control for possible non-independence of individual

nests within each site. Non-significant terms ($p > 0.05$) were dropped from the model one-by-one starting from the term with the highest p -value. The statistics for non-significant terms in the tables are values before dropping the variable from the model. Years with fewer than three nests per habitat and zone were excluded (1989 and 1990, impact zone and 1989, buffer zone). We used AICc to compare models. The reduced models had the lowest AICc values in most cases. For contrasts, JMP used the deviation coding, i.e., the mean of a dependent variable for a given zone was compared to the overall mean of the dependent variable.

Variations in the frequency of nests with unhatched eggs (0 = all eggs in a clutch hatched vs. 1 = at least one egg did not hatch) and in the frequency of nests with perished chicks (0 = all chicks in a brood survived until fledging vs. 1 = at least one nestling died before fledging) were analyzed using generalized linear models (GLM) with a binomial distribution and a logit link function. The predictors were the same as in the analyses of laying date, clutch size, and fledgling number. Individual nests were used as replications. Non-significant terms were dropped from the model one-by-one starting from the term with the highest p -value.

To visualize temporal trends in breeding parameters, we have plotted regressions of the parameters on the year in each zone. We used second-order polynomial or linear regressions according to LMM and GLM analyses. To explore if the observed breeding parameters in the impact and buffer zones reached the background level at the end of this study, we performed the 1-way ANOVA for the laying date, clutch size, and fledgling number and GLM for the frequency of nests with egg and chick failures with “zone” as a predictor using the data of 2021. For post hoc comparisons, Tukey’s HSD test was used in ANOVA and ChiSquare (χ^2) test for contrasts in GLM. Annual sample sizes and mean values for all the breeding parameters are presented in Supplement 2.

The temporal trends in mean temperatures of April and May were analyzed with linear regression. Data on temperatures at the nearest

weather station in Revda were provided by the Ural Department of Hydrometeorology and Environmental Monitoring (1989–2019) and the site www.pogodaiklimat.ru (2020 and 2021). Means in the text are given with their standard errors (\pm SE).

3. Results

The laying date depended on the zone. Birds started egg-laying in the background zone on average 0.9 days earlier than in the buffer zone and 7.5 days earlier than in the impact zone (Least Squares Means from the Linear Mixed Models, Table 1). Temperatures in spring affected laying date. The warmer the April and May, the earlier flycatchers started breeding. At the same time, temporal trend (1989–2021) of the mean temperature only in May was significant: the slope in April $b = 0.037 \pm 0.047$ (SE) °C/year ($df = 31, t = 0.787, p = 0.437$) and in May $b = 0.077 \pm 0.035$ °C/year ($t = 2.190, p = 0.036$) (Supplement 1, Fig. S3). The temporal trend in the laying date was nonlinear, as shown by the significant interaction year \times year \times zone and differed among zones. The laying date advanced faster in the impact zone compared to the background zone (Table 1, Fig. 2a). The predicted laying date advanced from 1991 to 2021 in the background, buffer, and impact zones by 8.8, 9.2, and 9.8 days, respectively. In the most recent year of observations (2021), the observed laying date in the impact zone 23.1 ± 0.9 ($n = 23$) did not reach the background level 19.7 ± 0.6 ($n = 56$; Tukey’s HSD test, $p < 0.05$) whereas in the buffer zone 21.8 ± 1.3 ($n = 11$) it did not differ from the background zone.

On average, clutches in the impact zone were smaller than in the background and buffer zones (Table 1). Clutch size decreased with increasing laying date and mean May temperature (Table 1). The temporal trend in the clutch size was nonlinear, as shown by the significant second-order term year \times year. Furthermore, the nonlinearity of trend lines differed among zones as indicated by the significant interaction year \times year \times zone (Table 1). In the buffer zone, the mean clutch size reached the background value in 2000 and remained near this level after that. In the impact zone, the mean clutch size was small until 2011 and increased thereafter (Fig. 2b). The predicted clutch size increased over the study period in the background zone by 0.30 eggs (+5% from the

first year of the observation), in the buffer zone by 0.58 eggs (+10%), and in the impact zone by 1.21 eggs (+26%). In 2021, the observed clutch size in the impact zone 5.35 ± 0.26 ($n = 23$) did not reach that in the background zone 6.69 ± 0.17 ($n = 55, p < 0.05$) and in the buffer zone 6.64 ± 0.38 ($n = 11, p < 0.05$), whereas in the buffer zone it did not differ from the background zone.

The number of fledglings per nest in the background and buffer zones were similar and exceeded that in the impact zone (Table 1). The earlier chicks hatched and the warmer the June, the higher fledgling production. Temporal trends in the number of fledglings were linear and differed among zones. In the impact zone, this parameter changed over the years faster than in other zones, as indicated by the significant interaction year \times zone (Table 1, Fig. 2c). The predicted fledgling production increased over the study period in the buffer zone by 0.81 (+17%) and in the impact zone by 1.88 (+102%), whereas it did not change in the background zone. Nevertheless, in 2021, the observed number of fledglings in the impact zone 4.27 ± 0.27 ($n = 22$) did not reach that in the background zone 6.23 ± 0.17 ($n = 53, p < 0.05$) and in the buffer zone 6.18 ± 0.38 ($n = 11, p < 0.05$), whereas in the buffer zone it did not differ from the background one.

The frequency of nests with unhatched eggs in the impact zone was higher than in other zones (Table 2). This parameter decreased with increasing May temperature and breeding density. The frequency of nests with unhatched eggs decreased linearly over the study period, nearly at a similar rate in all zones (Fig. 3a). The predicted frequency of egg failures decreased over the study period in the background zone by 0.06 (–17%), in the buffer zone by 0.24 (–47%), and in the impact zone by 0.15 (–20%). In 2021, the frequency of nests with unhatched eggs in the impact zone 0.55 exceeded the background level 0.22 ($\chi^2 = 7.47, p = 0.006$), whereas in the buffer zone it was 0.27 and did not differ from the background one ($\chi^2 = 0.16, p = 0.687$).

The frequency of nests with perished chicks was highest in the impact zone and did not differ between buffer and background zones (Table 2). This parameter increased with increasing breeding density, hatching date, and brood size. The interaction year \times zone was significant, indicating different temporal trends in different zones. The frequency of nests with perished chicks rose over the study period in the

Table 1

Linear mixed models for the variations in laying date (May 1st = 1), clutch size, and fledgling number in the pied flycatcher according to year, year \times year, pollution zone (impact [zone 1] vs. buffer [zone 2] and background [zone 3]), interactions year \times zone and year \times year \times zone, habitat (deciduous [habitat 1] vs. coniferous [habitat 2]), laying date (May 1st = 1), pied flycatcher breeding density (\log_{10} -transformed), and weather variables. Site was used as a categorical random variable. Terms left in the reduced models are shown in bold. LSMeans and 95% confidence intervals in parentheses are presented, n – number of nests. LSMeans with different letters differ significantly (Tukey’s HSD test, $p < 0.05$). Estimates for zones were calculated using the deviation coding by comparing each level to the grand mean.

	Laying date (n = 3130)			Clutch size (n = 2995)			Fledgling number (n = 2633)		
	Estimate±SE	DFDen	t	Estimate±SE	DFDen	t	Estimate±SE	DFDen	t
Impact zone	33.43 ^a (32.30–34.55)			4.92 ^a (4.66–5.18)			4.39 ^a (4.24–4.55)		
Buffer zone	26.81 ^b (25.84–27.78)			6.43 ^b (6.22–6.64)			5.34 ^b (5.20–5.49)		
Background zone	25.94 ^b (25.21–26.67)			6.41 ^b (6.18–6.63)			5.21 ^b (4.94–5.49)		
Source of variation	Estimate±SE	DFDen	t	Estimate±SE	DFDen	t	Estimate±SE	DFDen	t
Intercept	393.591 ± 47.999	1217	8.20***	–21.398 ± 6.559	1168	–3.26**	10.252 ± 9.408	1182	1.09
Zone[1]	4.702 ± 0.419	43.24	11.22***	–0.995 ± 0.093	13.19	–10.67***	–0.590 ± 0.061	45.52	–9.67***
Zone[2]	–1.916 ± 0.386	44	–4.96***	0.507 ± 0.083	13.02	6.08***	0.359 ± 0.057	50.24	6.31***
Habitat[1]	0.042 ± 0.236	11.78	0.18	–0.090 ± 0.042	7.463	–2.13	0.035 ± 0.021	–	–1.69
Year	–0.173 ± 0.024	1217	–7.21***	0.015 ± 0.003	1153	4.55***	–0.004 ± 0.005	1139	–0.91
Year \times Zone[1]	–0.125 ± 0.032	1680	–3.86***	0.027 ± 0.004	1625	6.26***	0.014 ± 0.007	1608	2.05**
Year \times Zone[2]	0.119 ± 0.037	721.2	3.19**	–0.012 ± 0.005	630.3	–2.24*	0.001 ± 0.007	881.4	0.17
Year \times Year	–0.0008 ± 0.0027	2529	–0.32	0.0013 ± 0.0004	1830	3.72***	–0.0007 ± 0.0005	1066	–1.54
Year \times Year \times Zone[1]	–0.016 ± 0.004	2960	–4.05***	0.0025 ± 0.0005	2666	4.81***	–0.0004 ± 0.0009	2487	–0.49
Year \times Year \times Zone[2]	0.018 ± 0.004	2110	4.43***	–0.0016 ± 0.0005	1113	–2.97**	–0.00004 ± 0.0009	2101	–0.05
Density(\log_{10})	–0.876 ± 0.769	40.95	–1.14	–0.056 ± 0.104	–	–0.54	–0.016 ± 0.156	17.82	–0.11
Laying (hatching) date ^a	NA	–	–	–0.069 ± 0.002	2979	–30.12***	–0.044 ± 0.004	2587	–10.39***
Clutch size	NA	–	–	NA	–	–	0.741 ± 0.029	2563	25.31***
Temperature in April	–0.497 ± 0.060	3118	–8.29***	0.011 ± 0.008	–	1.46	NA	–	–
Temperature in May	–1.345 ± 0.072	3119	–18.74***	–0.067 ± 0.010	2982	–6.98***	NA	–	–
Temperature in June	NA	–	–	NA	–	–	0.038 ± 0.016	2071	2.39*
Precipitations in June	NA	–	–	NA	–	–	0.0002 ± 0.0011	2620	–0.23

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NA – variable was not analyzed.

^a Laying date for clutch size, hatching date for fledgling number.

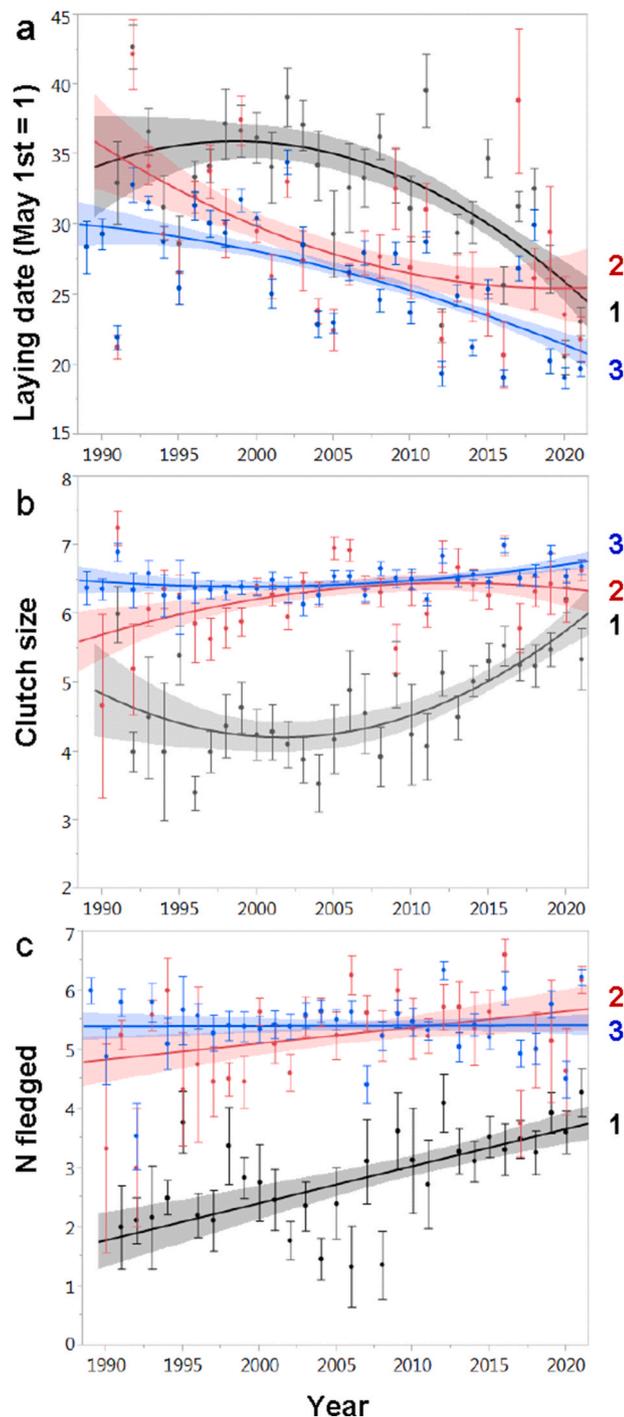


Fig. 2. The temporal trends in the laying date (a), clutch size (b), number of fledglings per nest (c) in the pied flycatcher in different zones of pollution from the MUCS (1 – impact, black dots and line; 2 – buffer, red dots and line; 3 – background, blue dots and line). Points are yearly means per zone, error bars – standard errors. Lines are regression lines fitted to the data. Shaded areas denote 95% Confidence Intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

background and buffer zones by 0.11 (+67%) and 0.21 (+162%), respectively, and remained the same in the impact zone (Fig. 3b). In 2021, the frequency of nests with perished chicks did not differ among zones (GLZ: $\chi^2 = 0.54$, $df = 2$, $p = 0.763$). Reproductive losses were higher during incubation of clutches than during the feeding of nestlings (Table 2, no overlap in confidence intervals).

4. Discussion

We observed the recovery of egg and fledgling production in the impact zone over the study period, during which the emissions from the Cu smelter decreased steadily. The rate of temporal changes was higher in the impact zone than in the buffer zone, whereas in the background zone, egg and fledgling production was relatively stable over the study period. Clutch size showed a non-linear temporal trend, especially in the impact zone. It increased markedly in the 2010s, which coincided with the sharp reduction of industrial emissions. Although emissions stabilized last decade, clutch size continued to grow in the impact zone, whereas it remained relatively stable in the background zone. Potential explanations might be the onset of ecosystem recovery (i.e., enhancing habitat quality) near the MUCS and advance in laying date, which occurred faster in the impact zone than in the background zone.

Although breeding parameters increased in the impact zone, they did not reach the background level over three decades. This suggests that the full recovery of bird reproduction in the heavily polluted area is a long process. This is consistent with Eeva and Lehtikoinen's (2000, 2015) findings near the Harjavalta smelter. Although the clutch size and fledgling number in the pied flycatcher increased rapidly in the 1990s, they leveled off in the 2000s and did not reach the background level during the 23-year study period. Apparently, multiple factors influence the spatial and temporal dynamics of bird reproduction in natural ecosystems exposed to industrial pollution.

Trace elements emitted by industries enter food webs, accumulate in the body of birds (Lebedeva, 1999; Dauwe et al., 2005; Sánchez-Virosta et al., 2015), and cause physiological disorders in adult birds and their offspring (Scheuhammer, 1987; Snoeijs et al., 2004; Koivula and Eeva, 2010) thus negatively affecting bird reproduction. Reducing contaminant exposure due to pollution abatement contributes to improving breeding parameters. For example, near the Harjavalta smelter, the metal concentrations in food items and the body of birds (pied flycatcher and great tit) decreased in the period 1991–2009 because of the 99% reduction of emissions (Berglund et al., 2012, 2015). At the same time, heavy metals (the most harmful components of industrial emissions) have a long retention time in soils, from where they enter the food webs. The 50-fold reduction in the MUCS' emissions in 1989–2010 did not cause the same decrease in the contaminant exposure. At the distance of 1–2 km from the MUCS, soil Cu concentrations reduced 1.5–3-fold in the period 1989–2012, whereas Pb, Cd, and Zn concentrations did not decrease or even increased (Vorobeichik and Kaigorodova, 2017). In the same area, Cu, Zn, and Pb concentrations in food (plants and mushrooms) of the bank vole (*Myodes glareolus*) did not decrease in the period 1990–2015, whereas Cd concentrations increased 2-fold (Mukhacheva, 2017). At the same time, Cu, Cd, and Zn concentrations in birch leaves (*Betula pubescens* and *B. pendula*) in the impact zone decreased 1.6–3-fold in the period 2008–2014, whereas Pb concentrations reduced 40-fold (Belskaya, 2018). These data show that contaminant exposure is species-specific and that exposure remains high near the MUCS for a long time after emissions have reduced.

Egg production in the pied flycatcher largely depends on the timing of breeding due to a negative relationship between the date of clutch initiation and clutch size (Lundberg and Alatalo, 1992). In the polluted area, birds started egg laying on average later than in the unpolluted area. Although laying date advanced during our study (likely due to spring warming), especially near the MUCS, differences among zones remained significant. Delayed breeding in the pied flycatcher seems to be a common phenomenon in polluted areas (Eeva et al., 1997a; Berglund and Nyholm, 2011; Eeva and Lehtikoinen, 2015).

There are some potential reasons for delayed breeding in polluted areas: habitat deterioration, competition for nesting sites in optimal habitats, age and condition of breeding birds (Lundberg et al., 1981; Lundberg and Alatalo, 1992; Sternberg et al., 2002; Artemyev, 2008). Pollution-induced habitat deterioration in forest areas is indicated by suppression of the tree stand: it becomes sparse due to the death of old

Table 2

Generalized linear models for the variations in the frequency of nests with egg and chick failures (0 = all eggs in a clutch hatched vs. 1 = at least one egg did not hatch; 0 = all chicks in a brood survived vs. 1 = at least one nestling died) in the pied flycatcher according to year, year × year, pollution zone (impact [zone 1] vs. buffer [zone2] and background [zone 3]), interactions year × zone and year × year × zone, habitat (deciduous [habitat 1] vs. coniferous [habitat 2]), laying date (May 1st = 1), pied flycatcher breeding density (log₁₀-transformed), and weather variables. Means and 95% confidence intervals in parentheses are presented. Values with different letters differ significantly (χ^2 test for contrasts in GLZ, $p < 0.05$; contrasts with the deviation coding). Terms left in the reduced models are shown in bold.

	Frequency of nests with unhatched eggs (n = 2840)			Frequency of nests with perished chicks (n = 2587)		
Impact zone	0.651 ^a (0.609–0.693)			0.298 ^a (0.256–0.340)		
Buffer zone	0.389 ^b (0.345–0.434)			0.235 ^b (0.194–0.276)		
Background zone	0.328 ^b (0.307–0.350)			0.233 ^b (0.213–0.252)		
Source of variation	Estimate±SE	χ^2	p	Estimate±SE	χ^2	p
Intercept	19.848 ± 11.118	3.19	0.074	−65.570 ± 15.914	17.17	<0.001
Zone[1]	0.737 ± 0.091	67.35	<0.001	0.491 ± 0.124	15.73	<0.001
Zone[2]	−0.269 ± 0.077	12.38	<0.001	−0.219 ± 0.098	5.04	0.025
Habitat[1]	0.119 ± 0.055	4.73	0.030	−0.089 ± 0.067	1.79	0.181
Year	−0.010 ± 0.006	2.93	0.087	0.030 ± 0.008	14.70	<0.001
Year × Zone[1]	−0.0003 ± 0.0105	0.001	0.975	−0.035 ± 0.011	9.10	0.003
Year × Zone[2]	−0.008 ± 0.010	0.59	0.441	0.027 ± 0.012	4.87	0.027
Year × Year	−0.0001 ± 0.0008	0.02	0.887	0.0012 ± 0.0008	2.54	0.111
Year × Year × Zone[1]	0.0006 ± 0.0013	0.26	0.609	−0.0007 ± 0.0014	0.24	0.626
Year × Year × Zone[2]	−0.0009 ± 0.0013	0.45	0.505	−0.0005 ± 0.0016	0.08	0.778
Density(log ₁₀)	−0.421 ± 0.206	4.24	0.040	0.441 ± 0.222	4.00	0.045
Laying (hatching) date ^a	0.006 ± 0.005	1.12	0.291	0.061 ± 0.007	87.63	<0.001
Brood size ^b	−0.005 ± 0.043	0.01	0.911	0.232 ± 0.039	36.77	<0.001
Temperature in May	−0.087 ± 0.021	16.75	<0.001	NA	–	–
Temperature in June	NA	–	–	0.026 ± 0.029	0.79	0.375
Precipitations in June	NA	–	–	0.002 ± 0.002	1.37	0.241

^a Laying date for the frequency of nests with unhatched eggs, hatching date for the frequency of nests with perished chicks.

^b Clutch size for the frequency of nests with unhatched eggs, number of hatched nestlings for the frequency of nests with perished chicks.

trees; young and low trees prevail (Kozlov et al., 2009; Vorobeichik et al., 2014). Such habitats are unfavorable for the pied flycatcher, judging by the low breeding density of this species near MUCS, in areas without nest boxes (Belskii and Lyakhov, 2003; Belskii and Mikryukov, 2018). The reduction of industrial emissions facilitated the gradual recovery of the diversity and abundance or productivity of a few groups of plants and animals near the MUCS: epiphytic lichens (Mikhailova, 2020), some herbaceous plants (Trubina, 2020), soil macrofauna (Vorobeichik et al., 2019), and leaf-eating invertebrates in birch crowns (Belskaya, 2018). At the same time, the recovery of the tree stand and the field layer in the study area is slow (Trubina et al., 2014; Vorobeichik et al., 2014; Trubina, 2020). There are some potential explanations for why flycatchers avoid polluted areas. Pollution-induced death of old trees reduces potential nesting sites for this hole-nesting species. Another reason can be a repellent action of pollutant discharges. Sulfur dioxide (SO₂) is the primary pollutant among those emitted by MUCS and comprises >90% of the total discharge (Vorobeichik and Kaigorodova, 2017). Sulfur dioxide causes necroses in plants and irritation and damage to epithelium and capillaries in animals' eyes and respiratory system (Goriz et al., 1994; Sanderfoot and Holloway, 2017). In the period of heavy emissions, high air SO₂ concentrations may have had repellent and toxic effects on birds preventing them from occupying the area close to the smelter.

Birds occupy optimal habitats first, whereas, in inferior habitats, breeding starts later (Lundberg et al., 1981; Artemyev, 2008). Young birds, which arrive at nesting sites later than older birds, are forced into inferior habitats or skip breeding due to competition with old birds (Lundberg and Alatalo, 1992; Sternberg et al., 2002; Both et al., 2017). Therefore, the age composition of local populations can indicate the quality of habitats from the birds' viewpoint. The proportion of young birds breeding in the impact zone of the MUCS exceeded that in the background zone (Eeva et al., 2009) and could partly explain the delayed breeding near the MUCS. Our data are consistent with observations near the Harjavalta smelter, where breeding started later, and the breeding density of the pied flycatcher was lower than in the control area (Eeva et al., 1997b).

Another reason for the delayed breeding is calcium (Ca) deficiency in females. Ca is necessary for eggshell formation. Small passerines obtain

Ca from food immediately before egg-laying (Krements and Ankney, 1995; Graveland and Berends, 1997; Bureš and Weidinger, 2003). Low Ca content in poor soils and soils acidified with industrial emissions is a reason for the disappearance of Ca-rich food items (snails, woodlice, and millipedes). This results in Ca-shortage in pied flycatchers near the MUCS (Belskii and Grebennikov, 2014) and near the Harjavalta smelter (Eeva and Lehikoinen, 2004; Eeva et al., 2010). In these areas, birds brought fewer snail shells to nestlings at the heavily polluted sites than at unpolluted sites, resulting in reduced Ca intake as shown by the lower Ca concentrations in nestling feces (Eeva and Lehikoinen, 1995). An increased proportion of clutches with thin and porous eggshells in the heavily polluted areas (20–50% near the MUCS) indicates that many females suffer from Ca deficiency. Females with a Ca-deficient diet spend extra time searching for Ca-rich prey (Graveland and Berends, 1997), resulting in delayed breeding. In addition, Ca deficiency increases the toxicity of heavy metals (Scheuhammer, 1996). Near the Harjavalta smelter, the negative effect of high Cu concentrations on fledgling production in pied flycatchers was especially strong in areas where Ca-rich food items were lacking (Eeva and Lehikoinen, 2004).

The delayed start of breeding negatively affects the outcome of all stages of bird reproduction. Delayed breeding results in smaller clutches and reduces the potential number of fledglings. In addition, delayed breeding indicates a lower physiological condition or lack of experience (in young birds), limiting breeding success. The relatively high frequency of nests with unhatched eggs in the impact zone near the MUCS indicates some physiological problems in breeding birds or/and an embryotoxic effect of pollutants. Another adverse effect of the breeding delay in polluted areas is the risk of desynchronization of the phenology of birds and their prey. The mismatch of periods of maximal food demand in birds (chick feeding) and availability of optimal prey (butterfly and sawfly larvae) results in increased nestling mortality from malnutrition, which was observed near the MUCS (Belskii and Belskaya, 2021) and near the Harjavalta smelter (Eeva et al., 1997a).

The frequency of nests with unhatched eggs was 1.5–2 times as high as that of nests with perished chicks suggesting that the incubation stage was the primary source of reproductive losses in our area. Berglund and Nyholm (2011) found that improved breeding success in the pied flycatcher close to a sulfide ore smelter in northern Sweden was related

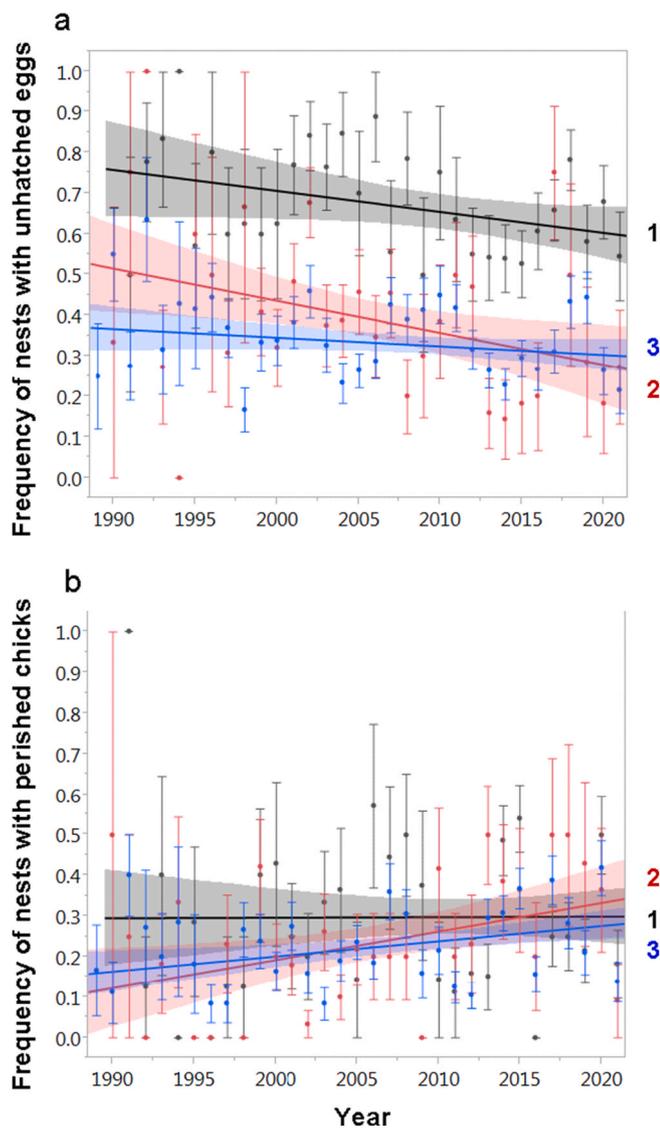


Fig. 3. The temporal trends in the frequency of nests with unhatched eggs (a) and frequency of nests with perished chicks (b) in the pied flycatcher in different zones of pollution from the MUCS (1 – impact, black dots and line; 2 – buffer, red dots and line; 3 – background, blue dots and line). Points are yearly means per zone, error bars – standard errors. Lines are regression lines fitted to the data. Shaded areas denote 95% Confidence Intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

to the increased hatching success between the 1980s and 2000s. In contrast, the nestling stage was critical for pied flycatchers near a lead mine at Laisvall in Sweden (Berglund et al., 2010) and at Harjavalta smelter (Eeva et al., 2020). In our study, egg failures decreased over the study period along with increasing air temperature in May. This is in line with the fact that temperature during incubation positively affects hatching success in the pied flycatcher, especially in the polluted area (Eeva et al., 2020). The negative association between the frequency of egg failures and breeding density hardly is a causal relationship but rather reflects concurrent temporal changes in these parameters in the impact zone. Although the breeding density of pied flycatchers increased in the impact zone over the years (Belskaya, 2018; Vorobeichik et al., 2019; Trubina, 2020), it was relatively low (≤ 1 pair/ha) and did not reach a level at which density-dependent effects occur. The frequencies of nests with eggs and chicks failures showed opposite

trends over the years. Reduction of egg failures over the years resulted in enlargement of broods, which might be a reason for higher chick mortality (Eeva et al., 2020). Opposite temporal trends in egg and chick failures seem to compensate each other in the buffer and background zones, resulting in a relatively stable chick production over the years. In the impact zone, egg failures decreased over the years, whereas chick failures did not change, resulting in gradually improving reproduction output. Given that hatching success depends on the condition and behavior of breeding females, reproductive recovery in flycatchers in the impact zone indicates mitigation of pollution pressure on females in recent years.

5. Conclusion

Our long-term study documented breeding parameters in the pied flycatcher before and during the substantial reduction of industrial emissions. In the heavily polluted zone, breeding parameters were strongly impaired compared to the unpolluted reference area. Further, bird reproduction improved in the heavily polluted area over 30 years, along with the 50-fold reduction of emissions. At the same time, breeding parameters in birds have not reached the control level in recent years. Thus, the recovery of bird reproduction is a slow process depending on the habitat recovery, circulation of pollutants in food webs, and other factors. An understanding of the complex suite of factors acting on birds and the recovery of their populations following pollution abatement requires long-term studies that incorporate the chronic impacts of contaminants, the recovery of habitats, and the dynamics of a changing climate.

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Author contribution

Eugen Belskii: Conceptualization, Investigation, Formal analysis, Writing – original draft, editing. Andrey Lyakhov: Investigation, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envpol.2022.119089>.

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