Weather effects on breeding parameters of two insectivorous passerines in a polluted area

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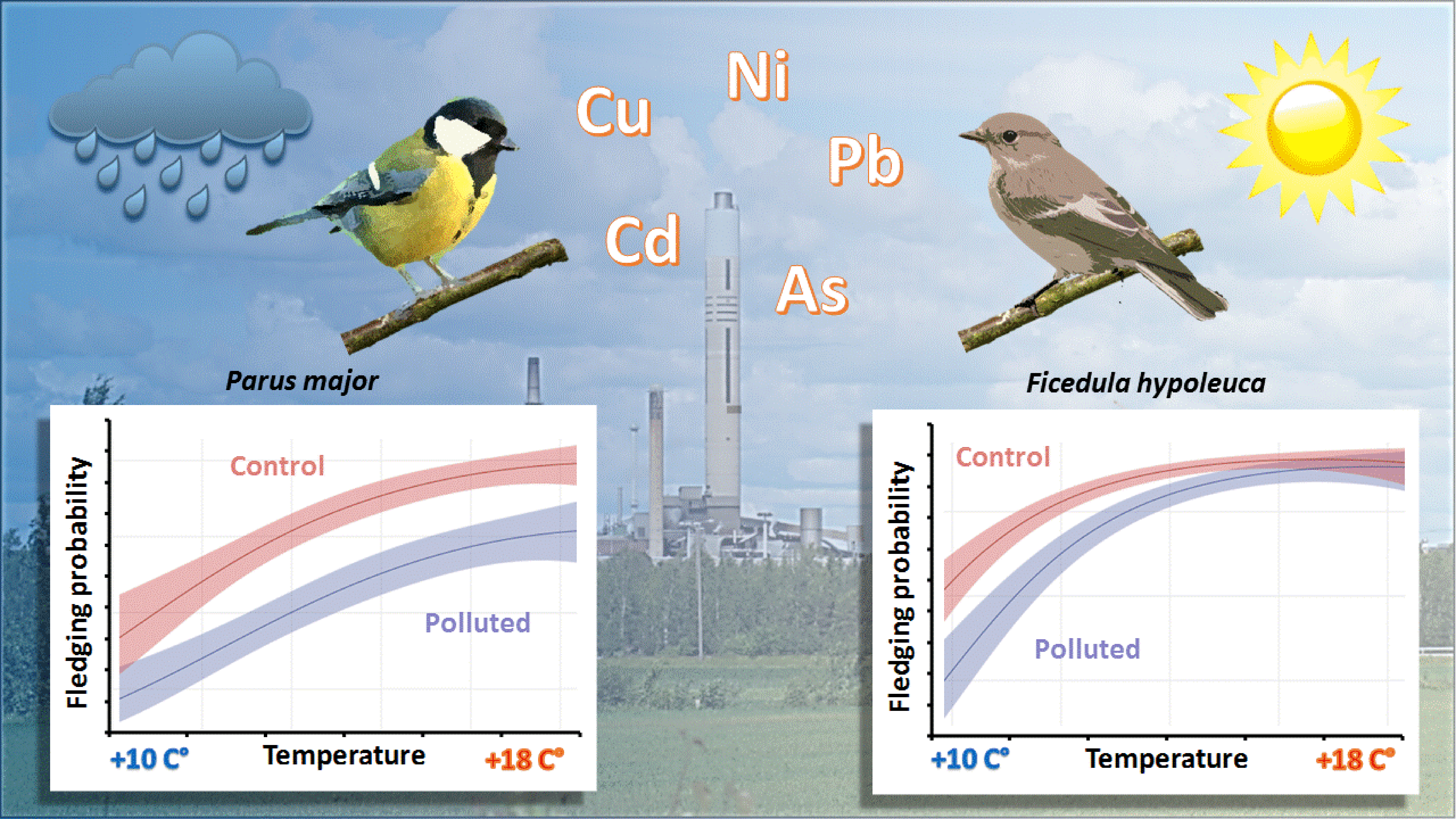
Ni
Cu
Pb
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Parus major
Ficedula hypoleuca
Control
Polluted
Fledging probability
+10 C°
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Control
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Fledging probability
+10 C°
Temperature
+18 C°

Abstract

Direct and indirect effects of environmental pollution affect negatively to birds' breeding performance in both urban and industrial environments, but much less is known on how pollution and natural stress factors work together. In our long-term study (1991−2018) we explored whether industrial pollution and associated habitat changes increase the sensitivity of breeding parameters (hatching and fledging success, nestling growth) to temperature and precipitation in two insectivorous bird species, the great tit (*Parus major*) and the pied flycatcher (*Ficedula hypoleuca*). We found that both species are rather weather sensitive in terms of their fledging success, but especially in the *F. hypoleuca*, the negative effect was strengthened in a polluted environment. For both study species, all the breeding parameters, except growth of *F. hypoleuca* nestlings, were inferior in the polluted area and negatively affected by cold weather. Independent of pollution, the duration of rainy spells during the nestling period had an overall negative effect on fledging success of *F. hypoleuca*, and this effect became stronger at cold temperatures. The length of rainy spells was, however, positively associated with nestling wing length in both species, possibly because of better availability of some important food resources for wing growth in more humid conditions. The weather-pollution interactions in our study populations were not overwhelmingly strong, but those found in *F. hypoleuca* show that such interactions exist, they are species-specific and in our study system most likely associated to pollution-related resource (e.g. food) limitation. Higher sensitivity of *F. hypoleuca* to low temperatures is likely related to its less well-insulated nests and higher dependence on aerial prey, the availability of which is especially reduced during cold and rainy spells. Our study indicates that anthropogenic stress, such as pollution, has synergistic effects with natural stress factors affecting passerine birds' breeding performance.

Key words: air pollution, breeding success, insectivorous passerines, nestling growth, weather sensitivity.

1. Introduction

Reproductive success of many insectivorous passerines is relatively sensitive to harsh weather because the mobility and detectability of their food items (insects and other small invertebrates) decrease during cold and rainy periods (e.g. Wiggins et al. 1994; Siikamäki 1996; Veistola et al. 1997; Newton 2003; Ward and Bryant 2006; Whitehouse et al. 2013). Bad weather during the breeding season can markedly decrease annual breeding success with consequences to population numbers (Cox et al. 2019, 2020). Anthropogenic pollution is an additional factor to many natural sources of stress in wild bird populations, such as bad weather, poor food availability, competition by conspecifics or parasites and diseases. Direct and indirect effects of pollution are well known to affect negatively birds' physiology and breeding performance in polluted environments (Eeva et al. 1997; Junker and Schmidt 2000; Janssens et al. 2003; Belskii et al. 2005; Berglund and Nyholm 2011; Sanchez-Virosta et al. 2015; Espín et al. 2016; Bauerova et al. 2017; Sanderfoot and Holloway 2017), but much less is known on how pollution and natural stress factors work together (Kozlov and Zvereva 2011). However, synergistic effects of pollution are possible and even likely with any other factors that have a negative effect on breeding (Coors and De Meester 2009).

The strength of natural stress factors typically varies in time and, when working in concert with pollution, may cause temporal and condition-dependent variation in sensitivity of a population to environmental pollution. For example, a free-living tree swallow (*Tachycineta bicolor*) population exposed to dietary Hg was found to show more severe Hg-related impairment of reproductive output when they experienced unusually high ambient temperatures (Hallinger and Cristol 2011). Therefore, the additional stress caused by direct (i.e. toxic) or indirect (e.g. resource limitation) effects of pollution could manifest in lower reproductive output, especially during the spells of extreme weather conditions. On the other hand, anthropogenic activities may depress invertebrate populations, lowering the available resources for breeding birds, as has been found around some point sources of pollution (Eeva et al. 1997; Eeva et al. 2005; Belskii and Belskaya 2013; Belskii and Grebennikov 2014), urban environments (Chamberlain et al. 2009;

Sepp et al. 2018; Seress et al. 2018) and acidified locations (Ormerod et al. 1986; Trevelline et al. 2018). Habitat degradation (i.e. any processes by which the quality of animal's environment is reduced) and lower resource availability may also make breeding populations less resilient to any other sources of stress (Sanz 1995). In line with this, pollution-related food limitation caused interruptions in a laying sequence of an insectivorous passerine, the great tit (*Parus major*, L.), in a weather-dependent manner: laying gaps caused by cold spells were more frequent in a polluted environment (Eeva and Lehikoinen 2010). There are, however, still very few studies on synergistic effects of weather and pollution. Interactions between natural and anthropogenic stresses would be important to reveal because detrimental effects of pollution may be underestimated if impact studies are done only in mild ambient conditions.

We studied whether long-term environmental pollution increases the sensitivity of breeding success to cold and rainy weather in two insectivorous bird species. Reproductive success of the pied flycatcher (*Ficedula hypoleuca* Pallas) and the great tit have been followed around a point source of toxic metals, a Finnish Cu-Ni smelter, for the last 28 years. Breeding success has been lower in the polluted area for both bird species, but also improved in time along with reduced metal emissions (Eeva and Lehikoinen 2000; Eeva and Lehikoinen 2015). A long-term time series gives a good opportunity to analyze weather-pollution interactions over an exceptionally large range of ambient conditions. With "pollution effect" we mean here not just possible toxic effects but also indirect effects e.g. due to resource limitation, which has had a marked role in our study area with moderate pollution levels (Eeva et al. 1997; Eeva et al. 2000; Eeva et al. 2005). We ask here the following questions: 1. Do cold and/or rainy spells have stronger effects on hatching success, nestling growth or fledging success of any of the two bird species in the polluted environment? 2. Do the bird species differ in their sensitivity to pollution-weather interactions? Since *F. hypoleuca* relies more on the use of aerial prey in nestling feeding than tits (Veistola et al. 1997; Eeva et al. 2005), availability of which is especially affected by cold and rainy weather, we expect *F. hypoleuca* to be more weather sensitive. 3. How do the two weather parameters (temperature and rain) interact in their effects on breeding success?

2. Methods

2.1. Study area

The data were collected in 1991–2018 (2001 missing) around a Cu-Ni smelter (61°20’ N, 22°10’ E) in Harjavalta town, southwestern Finland. Sulphur oxides (SO_x) and metallic elements (especially As, Cd, Cu, Ni, Pb and Zn) are common pollutants in this area (Kiikkilä 2003; Kozlov et al. 2009). Elevated metal concentrations occur in soil, vegetation, and fauna of the polluted area due to current and historical deposition (since 1945), and metal contents decrease exponentially with increasing distance to the smelter (Koricheva and Haukioja 1995; Eeva and Lehikoinen 1996; Eeva et al. 1997; Eeva et al. 2010; Berglund et al. 2012). More details on emissions and metal levels are given in Eeva et al. (2018) and Berglund et al. (2012; 2015). After the first years of the data series, when the emissions were still relatively high, the fecal metal levels of nestlings (= a proxy for dietary levels) have not shown a similar decrease than the emissions, likely because metals deposited in soil still enter in the food chain (Berglund et al. 2015). However, based on some physiological biomarkers, the levels in birds do not any more exceed a toxic load (Espín et al. 2016). Twenty-four study sites, each with 20 – 80 nest boxes (see Lambrechts et al. 2010), were established in the pollution gradient in three main directions (southwest, southeast and northwest; i.e. to get wide spatial coverage and replicate sites at different distances), in a range of 0.4 – 73 km from the smelter. Study sites were selected to represent similar Scots pine (*Pinus sylvestris* L.) dominated forests, with mixed Norway spruce (*Picea abies* [L.] Karst.) and birches (*Betula* spp.). The number of study sites varied in different years.

2.2. Data on breeding and weather

Nest boxes were checked weekly to record final clutch size, number of hatchlings and number of fledglings, and to ring nestlings. Handling of birds was based on the Finnish policy of ringing license issued by Finnish Museum of Natural History (1991-2007: 5976/434/87, 24/4342/92, 11/57/22/97, 17/57/13/2002) and Centers for Economic Development, Transport and the

Table 1. Generalized linear mixed models[1] for testing the effects of pollution and weather variables (temperature and rain) on hatching and fledging success of *Ficedula hypoleuca* and *Parus major*. Final reduced models are shown in bold. N = number of clutches/broods.

		F. hypoleuca				*P. major*			
Source of variation		Hatching success n = 5720		Fledging success n = 5002		Hatching success n = 2489		Fledging success n = 2151	
		Est.	F_{df}	Est.	F_{df}	Est.	F_{df}	Est.	F_{df}
Year		−0.0050	$1.30_{1,1147}$	0.0047	$1.32_{1,1632}$	−0.015	$\mathbf{7.61_{1,1180}}^{**}$	−0.019	$\mathbf{22.5_{1,1756}}^{***}$
Zone	Polluted	−0.59	$\mathbf{36.9_{1,12.9}}^{***}$	−1.57	$\mathbf{10.7_{1,1797}}^{**}$	−0.23	$\mathbf{4.37_{1,24.0}}^{*}$	−0.87	$\mathbf{34.1_{1,19.5}}^{***}$
	Control	0		0		0		0	
Zone × Year	Polluted	0.0031	$0.12_{1,1064}$	−0.0052	$0.35_{1,1457}$	−0.0062	$0.30_{1,952.3}$	−0.0094	$1.32_{1,1379}$
	Control	0		0		0		0	
Hatching date		−0.15	$\mathbf{22.6_{1,5709}}^{***}$	−0.41	$\mathbf{156_{1,4993}}^{***}$	−0.34	$\mathbf{58.6_{1,2168}}^{***}$	−0.10	$\mathbf{10.8_{1,2136}}^{***}$
Brood size[2]		0.098	$\mathbf{9.05_{1,5030}}^{**}$	−0.17	$\mathbf{34.3_{1,4951}}^{***}$	0.17	$\mathbf{38.7_{1,2455}}^{***}$	−0.081	$\mathbf{22.0_{1,2136}}^{***}$
Temperature[3]		0.087	$\mathbf{9.93_{1,5640}}^{**}$	0.86	$\mathbf{18.8_{1,4988}}^{***}$	0.35	$\mathbf{8.29_{1,2468}}^{**}$	0.70	$\mathbf{11.4_{1,2130}}^{***}$
Rainy days (MaxRD)[4]		0.18	$\mathbf{3.40_{1,5463}}$	−0.61	$\mathbf{9.17_{1,4993}}^{**}$	0.00062	$0.00_{1,2474}$	0.32	$\mathbf{8.96_{1,2130}}^{**}$
Temperature × Temperature		0.0038	$0.39_{1,5679}$	−0.027	$\mathbf{18.1_{1,4992}}^{***}$	−0.0098	$\mathbf{4.03_{1,2465}}^{*}$	−0.016	$\mathbf{5.17_{1,2125}}^{*}$
Zone × Temperature	Polluted	−0.045	$3.16_{1,5711}$	0.070	$\mathbf{4.75_{1,4974}}^{*}$	−0.0083	$0.06_{1,2451}$	−0.042	$1.99_{1,2142}$
	Control	0		0		0		0	
Zone × MaxRD	Polluted	−0.029	$0.60_{1,5507}$	0.012	$0.15_{1,4985}$	0.026	$0.37_{1,2450}$	0.0090	$0.050_{1,2138}$
	Control	0		0		0		0	
Temperature × MaxRD		−0.017	$\mathbf{5.67_{1,5477}}^{*}$	0.041	$\mathbf{8.64_{1,4993}}^{**}$	−0.010	$1.07_{1,2480}$	−0.022	$\mathbf{8.18_{1,2130}}^{**}$

[1] GLMM with binary error distribution and logit link function. Study site nested within zone and model residuals used as random factors. * = p < 0.05, ** = p < 0.01, *** = p < 0.001.

[2] Clutch size for hatching success, hatchling number for fledging success.

[3] Mean daily temperature (°C) during incubation (for hatching success) or nestling (for fledging success) periods.

[4] Maximum number of consecutive rainy days (MaxRD) during incubation (for hatching success) or nestling (for fledging success) period.

Table 2. Linear mixed models[1] for testing the effects of pollution and weather variables (temperature and rain) on wing length of *Ficedula hypoleuca* and *Parus major* nestlings. Final reduced models are shown in bold. N = number of broods.

Source of variation		*F. hypoleuca* n = 2609		*P. major* n = 1477	
		Est.	F_{df}	Est.	F_{df}
Year		0.014	$0.26_{1,864}$	−0.31	**$42.4_{1,925}^{***}$**
Zone	Polluted	−7.30	**$3.88_{1,2024}^{*}$**	−5.10	**$17.0_{1,18.5}^{***}$**
	Control	0		0	
Zone × Year	Polluted	−0.094	$2.36_{1,634}$	−0.20	$3.64_{1,801}$
	Control	0		0	
Hatching date		−1.21	**$24.1_{1,2592}^{***}$**	0.57	$1.93_{1,1386}$
Brood size		0.19	$0.87_{1,2519}$	−0.68	**$10.7_{1,1471}^{**}$**
Temperature[2]		5.83	**$20.4_{1,2602}^{***}$**	1.91	**$116.8_{1,1469}^{***}$**
Rainy days (MaxRD)[3]		0.78	**$23.2_{1,2596}^{***}$**	1.43	**$23.5_{1,1465}^{***}$**
Temperature × Temperature		−0.17	**$13.1_{1,2602}^{***}$**	0.079	$1.76_{1,1466}$
Zone × Temperature	Polluted	0.57	**$4.89_{1,2600}^{*}$**	0.62	$3.67_{1,1468}$
	Control	0		0	
Zone × MaxRD	Polluted	−0.15	$0.20_{1,2597}$	−0.11	$0.03_{1,1458}$
	Control	0		0	
Temperature × MaxRD		−0.0034	$0.00_{1,2595}$	0.19	$2.78_{1,1461}$

[1] LMM with normal error distribution. Dependent factor: proportion (%) of wing length residual (WLR) from a predicted value in a linear regression between wing length and age. Study site nested within zone and model residuals used as random factors. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

[2] Mean daily temperatures for nestling ages of 0−12 days for *F. hypoleuca* and 0−13 days for *P. major*.

[3] Maximum number of consecutive rainy days (MaxRD) for nestling ages of 0−12 days for *F. hypoleuca* and 0−13 days for *P. major*.

Environment (2008-2020: LOS-2007-L-1001–254, VARELY/959/07.01/2012, VARELY/3622/2017). Field protocols and bird handling followed all national and international guidelines. The number of hatchlings was determined from the numbers of recently hatched nestlings and unhatched eggs. The number of fledglings was determined from the numbers of nestlings prior to fledging and taking account dead chicks found in the nest after fledging. Nestling wing length was measured with a ruler to the nearest 1 mm by using the maximum method (i.e. from straightened and flattened wing). Hatching date (i.e. the day when eggs hatch) was estimated from the wing length of small (≤7 days) nestlings by comparing it with growth curves of nestlings with known age (**Appendix A**). Wing length was also normally measured again when nestlings were ringed (normally at the age of 6 − 13 days). All the other information was also used to time the hatching date as precisely as possible (e.g. visits to the nest right before hatching often increase the precision of timing). Nests where the estimated uncertainty in timing was more than ±1 days were omitted from the analyses. To compare the breeding parameters in different parts of the pollution gradient, we split the data in two parts: (i) the polluted area less than 2.2 km from the pollution source (median distance 1.3 km) is hereafter called ‘polluted zone’, and (ii) the rural area beyond 2.7 km from the source (median distance 10.4 km) is called ‘control zone’. Emission levels approach the background values beyond the distance of 2.7 km (Berglund et al. 2012). Second and replacement nests were discarded from all analyses.

The data on daily mean temperature and daily rainfall were downloaded from the open database provided by the Finnish Meteorological Institute (weather stations: Kokemäki, Rausenkulma [WMO 02762] 61.26°N 22.23°E, years 1991 − 2009; Kokemäki, Tulkkila [WMO 02937], 61.25°N 22.35°E, years 2010 − 2018). Both stations lie within 15 km from the smelter and within our study area. In summer 2018 we also measured weekly rainfall at 10 of our study sites with rain gauges. The average Pearson correlation coefficient between the study area and weather station for weekly rainfall values was high ($\overline{x}$ = 0.91, SD = 0.074, n = 13 weeks), indicating that the data from the weather station describes well the rainfall at the actual study sites.

Two weather parameters were chosen as explanatory factors for the analyses: mean daily temperature and maximum number of consecutive rainy days (days with rainfall >0 mm; hereafter MaxRD). These were calculated individually for each nest, separately for incubation period (set to 14 days for both species, excluding the hatching day) and nestling period (set to 14 days for *F. hypoleuca* and 18 days for *P. major*, including the hatching day) by using hatching day as a fixed point. Rainfall as such was not considered as a good explanatory factor because intense showers may produce high rainfall value but be short in duration, having little effects on birds. Instead, MaxRD was considered a better index, and also better than e.g. the total number of rainy days because our impression in the field was that especially the longer continuous rainy periods, typical for longer lasting depressions, cause more severe nestling mortality than occasional individual rainy days. Total number of rainy days was also considered as an additional independent factor but we did not finally include it because it correlated strongly with the MaxRD.

2.3. Statistical analyses

We studied three reproductive parameters: hatching success (probability of an egg to hatch), fledging success (probability of a hatchling to fledge) and nestling wing length. These were analyzed with generalized linear mixed models (GLMM) or linear mixed models (LMM) by using Glimmix procedure in the statistical software SAS 9.4 (SAS Institute Inc. 2013; Stroup 2013). The values of breeding parameters affected by predation, human disturbance or manipulations were not included in the analyses. Explanatory factors in the models for hatching and fledging success (see Table 1) were year, pollution zone (polluted vs. control), yearly-standardized hatching date, clutch size (for hatching success) or hatchling number (for fledging success), mean daily temperature and MaxRD during incubation/nestling periods. Because pollution levels decreased and some of the breeding parameters changed during this long-term study, we included year as a continuous variable in the models to take account of temporal trends in breeding parameters. These trends will not, however, be dealt with in detail here because more detailed analyses on them are recently given by Eeva and Lehikoinen (2013; 2015). The following interactions were further included in the models: zone × year, zone × temperature, zone × MaxRD, and temperature × MaxRD. The second order term for temperature (temperature × temperature) was also included because the visual inspection of the data indicated that temperature effects may not always be linear. For hatching and fledging probabilities, we modelled binomial proportions (events/trials syntax of the Glimmix procedure) with binary error distribution and logit link function. In all models, study site nested within zone was used as a random factor to control for possible non-independence of the observations within sites. Model residuals were further used as a random factor to control for overdispersion in the models. Year was not included as a categorical random factor because a great deal (81%) of temperature variation in the data was due to among-year variation. Variance inflation factors were <1.6 in all cases, indicating no serious multicollinearity among the explanatory factors. Non-significant terms were dropped from the models, starting from interactions. Effect size estimates given in the text are marginal means from the final model. Spatial autocorrelation was further tested for the residuals of all models with Moran's I coefficient, but in no case was the correlation significant and non-spatial covariance structure was used in all models. Annual sample sizes for both zones, and mean values for all the breeding parameters are given in the **Appendix A**.

Similar linear models as above were fitted to the data on nestling wing length (Table 2), though now based on normal error distribution and identity link function. In the analyses, we used wing lengths measured at the ages of 6 − 12 days for *F. hypoleuca* and 7 − 13 days for *P. major*, during which periods wing grows relatively linearly. Linearity was checked with a regression model (n = 2912 brood measurements of *F. hypoleuca*, n = 1576 brood measurements of *P. major*) containing both 1st and 2nd order terms of age: the 1st order term explained 84% (partial R^2) of variation in *F. hypoleuca* and 76% in *P. major* while the 2nd order term explained only 0.1% of variation in both species. Proportional wing length residuals (% of residual of the predicted value; hereafter WLR) from linear regression of wing length against age were used as a measure of relative size of nestlings. Brood means were used in the following analyses to avoid pseudoreplication. If the same brood was measured more than once, we used their mean in the analyses (n = 2609 broods of *F. hypoleuca*, n = 1477 broods of *P. major*). Normality of the data was visually checked from model residuals. We only included those broods where all nestlings were measured.

3. Results

3.1. Hatching success

In general, hatching probability was relatively high and higher in the control zone than in the polluted one (for polluted and control zone, respectively: *F. hypoleuca* 88% vs. 93%; *P. major* 87% vs. 90%; Table 1). In both species, hatching success decreased along the hatching date and was higher in large clutches (Table 1). In *P. major*, it also decreased slightly (2.7%) over the study years 1991 – 2018 (Table 1). In general, hatching success increased in both species along with increasing ambient temperatures during the incubation period, and in *P. major* this relationship was further non-linear, hatching probability increasing fast with temperature at cold weather but levelling off at warm weather (2^{nd} order term of temperature; Table 1; Figure 1). In *F. hypoleuca*, there was a temperature-dependent effect of rain: the negative effect of rainy spells got stronger at higher ambient temperatures (Table 1; Figure 2). However, there were no significant interaction effects on hatching success between weather and pollution in either species (Table 1). Note that the temperature range differs for the two species because *P. major* breeds ca. 2.4 weeks earlier than *F. hypoleuca*.

3.2. Fledging success

Fledging success decreased with the hatching date and increasing brood size (hatchling number) in both species (Table 1). Mean fledging probabilities for polluted and control zones were 81% and 88% for *F. hypoleuca* and 43% and 64% for *P. major*, respectively, being significantly lower in the polluted zone for both species (Table 1). Fledging success was non-linearly related to nestling time temperature in both species, increasing fast with increasing temperature at cold but levelling off at warm weather (2^{nd} order term of temperature; Table 1). In *F. hypoleuca*, the strength of temperature effect further depended on pollution level: cold days during the nestling period decreased fledging probability more in the polluted zone (Table 1, Figure 3a). Such an interaction was not found in the *P. major* (Table 1, Figure 3b). Ambient temperature and rain showed significant interactions in both species (Table 1). In *F. hypoleuca*, rainy days had strong negative effect on fledging probability at cold weather while the rain effect was positive at warm weather (Figure 4a). Instead, the opposite pattern was found for *P. major* (Figure 4b). In *P. major*, fledging probability decreased 17.9% over the years 1991 – 2018 (Table 1). To check if this temporal decrease was due to increasing population density over the study period, which has been reported in this area (Eeva and Lehikoinen 2013), we ran as a *post hoc* test the same model with nest box occupation rate (% nest-boxes occupied by *P. major* at each study plot) as an extra explanatory factor. The population density affected negatively on fledging probability (GLMM: $F_{1,1717} = 20.4$, $p < 0.0001$, Est = −0.018), and the estimate for the temporal change got smaller (Est = −0.011; c.f. Table 1) but was still significant (GLMM: $F_{1,1717} = 3.89$, $p = 0.013$), suggesting that other factors besides the population density explain the temporal change.

Since *F. hypoleuca* showed a pollution-related temperature response while *P. major* did not, we ran one further model for the combined data to test directly if these two species indeed show significantly different weather − pollution relationships. Here, we truncated the data to include only the observations over an overlapping temperature range (9 – 18°C) for both species. The model included species, zone, hatching date and hatchling number nested within species, temperature and its 2nd order term and a three-way interaction between species × zone × temperature, including all the lower level interaction terms. A significant three-way interaction (GLMM: $F_{1,7048} = 3.89$, $p = 0.049$) suggested that polluted environment enhanced the negative effect of temperature on fledging success more strongly in *F. hypoleuca* (cf. Figure 3a and 3b).

3.3. Nestling growth

Nestlings of *P. major* had shorter wings in the polluted than in the control zone and their wing length significantly decreased over the study years 1991 – 2018 (change in WLR: 8.4% units;

Table 2). WLR of *P. major* further decreased along with increasing brood size (Table 2). WLRs of *F. hypoleuca* did not show temporal trend nor were dependent on brood size, but they decreased along the hatching date (Table 2). WLR of both species increased with ambient temperature, but in *F. hypoleuca* this effect was nonlinear (2^{nd} order term of temperature; Table 2) and stronger in the polluted zone (interaction between zone and temperature; Figure 5). Unexpectedly, the length of rainy spells was positively associated with nestling wing length in both species (*F. hypoleuca*: change 6.6% units in a range of 0 – 8 rainy days; *P. major* 12.8% units in a range of 0 – 9 rainy days; Table 2). The average WLRs for polluted and control zones were 0.22% and −0.45% for *F. hypoleuca* and −4.1% and 2.3% for *P. major*, respectively.

4. Discussion

4.1. Effects of weather and pollution on breeding success

For both study species, all the breeding parameters, except wing growth of *F. hypoleuca* nestlings, showed lower levels in the polluted zone and were negatively affected by cold weather. However, significant temperature-pollution interactions were found only for nestling growth and fledging success of *F. hypoleuca*. In this species, decreasing temperature had stronger negative effect on growth and fledging success in the polluted environment, the latter being even 20% percentage point lower as compared to the control zone. In warm weather, however, fledging success of *F. hypoleuca* was not lower in the polluted zone and nestlings even grew faster there. Independent on pollution, the duration of rainy spells had an overall negative effect on hatching and fledging success of *F. hypoleuca*, but not of *P. major*. Expectedly, the negative effect of rainy spells on fledging success of *F. hypoleuca* was strongest at cold weather (see also Eeva et al. 2002). However, the negative effect of rain on hatching success of *F. hypoleuca* was stronger at higher ambient temperatures. The reason to this is unknown, but one possibility is that trans-eggshell microbial infections take place more commonly in warm and moist conditions, reducing hatchability (Cook et al. 2005; but see Horrocks et al. 2014). Alternatively, some weather-related changes in incubation behavior could have taken place (see Coe et al. 2015). Individual fitness shows seasonal decline in many bird species and hatching and fledging success decreased in the course of the breeding season also in our data. We cannot disentangle among different hypotheses presented for explaining such seasonal patterns but based on literature we consider an association between breeding time and parental quality one likely explanation (Wiggins et al. 1994; Verhulst et al. 1995).

In all, our results suggest that even though both of these insectivorous species are rather weather sensitive in terms of their breeding success, *F. hypoleuca* seems to be more sensitive to cold spells, and especially in a polluted environment. Although studies on weather-pollution interactions are still rare, corresponding interactions between weather and environmental quality have been observed elsewhere. For example, increasing rainfall was found to decrease the prey capture rates and body condition of pygmy owls (*Glaucidium passerinum*) especially in a suboptimal habitat (Terraube et al. 2017). Likewise, nesting success of the blackbird (*Turdus merula*) was more strongly influenced by rain in urban as opposed to rural habitat, likely due to associated food limitation (Miller et al. 2017). We also consider resource limitation the most likely explanation to the stronger effect of weather on breeding in the polluted part of our study area, because earlier studies indicate that some important food items for insectivorous birds are less abundant there (Eeva et al. 1997, Eeva et al. 2005). Both study species also have more laying-gaps (i.e. interruptions of laying) in the polluted environment and in a cold weather, which suggests difficulties in acquiring enough food for producing eggs (Eeva and Lehikoinen 2010). Clutches with laying gaps tend to show lowered hatchability (Eeva and Lehikoinen 2010).

4.2. Weather-related resource limitations

Negative effects of cold and rainy weather are generally thought to result from increased energy consumption by parent birds and their nestlings, and simultaneous decrease of available food resources and growth rates (see e.g. Keller and van Noordwijk 1993). With decreasing ambient temperatures, parent birds use more time for brooding of small nestlings, which again need more energy for their growth (Mertens 1977a). On the other hand, low temperatures and heavy rainfall depress flight and retard reproduction of poikilothermic invertebrates, and reduce their availability to birds (Kendeigh 1934; Dennis and Sparks 2007; Cox et al. 2019). Cold periods are known to decrease the number of flying insects, body condition during incubation, and feeding frequency of *F. hypoleuca* parents (Taylor 1963; Veistola et al. 1997; Eeva et al. 2002; Rainio et al. 2017). Polluted environments also tend to have changed food webs and they may become resource limited for some species. For example, insectivorous birds may be in shortage of some important food items, such as moths and caterpillars. This has been observed in our study area (Eeva et al. 1997; Eeva et al. 2005) and more widely in industrial and urban environments (Belskii and Belskaya 2009; Chamberlain et al. 2009; Seress et al. 2018). In our study area, folivorous caterpillars and ground-living arthropods were found to be less abundant in the polluted area and birds' diet was of lower quality (Eeva et al. 1997, 2005, 2008). In both study species, breeding success is positively associated to caterpillar numbers (Eeva et al. 1997). These results indicate decreased resource availability for birds, although this may vary among years (Eeva et al. 2012). Still, during the incubation period, *F. hypoleuca* females actually showed slightly higher body masses in the polluted zone, which could indicate better food availability during the early breeding phase, or active adjustment of body mass to lower resource availability (Rainio et al. 2017). In all, our findings support the hypothesis that cold spells decreased the availability of invertebrates and even more so for *F. hypoleuca,* which shows partly aerial feeding and relies more on mobile and flying insects than *P. major*.

4.3. Effects of weather and pollution on nestling growth

Food availability is a major determinant of postnatal growth in birds, and slower growth tends to have fitness costs (Perrins 1965, Alatalo and Lundberg 1986, Martin 1987, Tinbergen and Boerlijst 1990, Gebhard-Heinrich and Richner 1998). In the current study, *P. major* nestlings showed slower wing growth in the polluted zone and earlier studies have shown that the same applies to their body mass, most likely due to inferior quality of food (Eeva et al. 2009a; Eeva et al. 2009b; Sillanpää et al. 2009). By contrast, *F. hypoleuca* nestlings have not shown slower growth in the polluted zone (Eeva et al. 1994; Eeva et Lehikoinen 1996; Espín et al. 2016). In the current study, their wing growth was even better in the polluted zone, though it also decreased there more strongly at low temperatures. If partial mortality in a brood eliminates the smallest nestlings, the largest nestlings would become measured relatively more often. This could bias the values of the polluted area upwards. Our data, however, does not support this because in both study species proportional within-brood mortality and wing growth correlate negatively (result not shown). Alternatively, the better availability of some important food items (e.g. calcium rich small snails) in the polluted zone could speed up wing growth (Eeva et al. 2010; Espín et al. 2016). This could also explain the counterintuitive result of why nestlings of both species showed faster wing growth when they experienced longer rainy periods (see Table 2): rainy periods may increase abundance or mobility of some critical food items for wing growth, while dry and hot periods diminish their availability to birds. Although the effect of rainy periods on nestlings was primarily negative, hot and dry periods may reduce invertebrate prey availability, e.g. via suppressing plant growth (Bolger et al. 2005; Dennis and Sparks 2007).

4.4. Interspecific differences in nest insulation

Besides different food ecology, the two study species differ in their nest construction. Nests of *P. major,* especially in early spring, are constructed on moss and thick lining layer of animal fur, while the nests of *F. hypoleuca* contain bark, leaves and grass but practically no fur (Cramp and Perrins 1993). We are not aware of direct comparison of insulation properties of *P. major* and *F. hypoleuca* nests, but among Parids, insulation properties are found to be better the thicker the layer of lining material of the nest is (Glądalski et al. 2016). Furthermore, Skowron and Kern (1980) compared conductivity coefficients among lining materials of 11 bird species, and found that nests with animal fur lining had relatively low thermal conductivity. Therefore, eggs and nestlings of *P. major* might be better protected against cool ambient temperatures than in the *F. hypoleuca*, which lacks the fur lining. Moss nests of tits are also better to absorb the water that may get inside the nest cavity during heavy rain, keeping the nest cup drier and improving insulation (Mertens 1977b;

Deeming and Campion 2018). Furthermore, large broods of tits are more resistant against hypothermia due to their higher heat production than smaller broods of *F. hypoleuca* (Mertens 1969). Well-insulated and absorbent nests and larger broods may therefore help *P. major* to better tolerate the combination of cold weather and rainy days.

4.5. Trends in reproductive parameters over time

Nestling growth, and hatching and fledging success of *P. major* decreased over the long-term study period. Metal-rich dust emissions in our study area have decreased ca. 99% during 1991 − 2013 and changes in emissions are not likely to explain decreasing trends in reproductive parameters. Instead, temporal decrease in breeding parameters is more likely related to negative density-effect due to increasing population number, and/or temporal changes of food resources. Breeding densities of *P. major* increased threefold during 1991 − 2011 in our study area (Eeva and Lehikoinen 2013) and associated resource limitation partly explains the temporal changes in breeding parameters in the current study, although there seem to be other factors involved. Such could be e.g. temporal changes in food availability or population structure. Furthermore, although the breeding phenology of *P. major* has advanced over the years (Eeva and Lehikoinen 2013), it may still lack behind the ambient phenology, and a stronger temporal mismatch between birds and their food items is possible (see Visser et al. 1998; Radchuk et al. 2019), and should be studied in more detail.

5. Conclusions

Although the weather-pollution interactions in our study populations were not overwhelmingly strong, those found in *F. hypoleuca* show that such interactions exist, they are species-specific and, in our study system, most likely linked to pollution-related habitat deterioration and associated resource limitation. Currently, worst combinations of cold spells and rain are relatively rare in our study area. For example, in *F. hypoleuca*, only 6.4% of broods are exposed to rainy periods longer than one week and most rainy conditions typically take place at average temperatures rather than at very cold or very warm periods. Extreme weather events may, however, become more common along with climate change, and also the role of weather-habitat interactions may get more important in the future (Bolger et al. 2005; Kozlov and Zvereva 2011; Bailey and van de Pol 2016). Finally, we want to emphasize the paramount importance of unique long-term data series for studying joint effects of multiple stress factors in the wild, since their net effects are very difficult to study otherwise.

CRediT authorship contribution statement

TE, MR, SE and PSV planned the study and collected the data. TE analyzed the data and wrote the manuscript. TE, MR, SE and PSV revised the manuscript. All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing interests.

Acknowledgements

We thank Jorma Nurmi and all the other persons involved in the fieldwork over the past 28 years. Six anonymous referees are acknowledged for their help in improving the presentation. This study was financed by the Academy of Finland (T.E., project 265859), University of Turku Graduate School - UTUGS (P.S.-V.), *Fundación Séneca-Agencia de Ciencia y Tecnología de la Región de Murcia* (Saavedra-Fajardo Project 20031/SF/16 to S.E.) and *Ministerio de Ciencia, Innovación y Universidades* (Juan de la Cierva-Incorporación contract, IJCI-2017-34653 to S.E.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at…

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Figure captions:

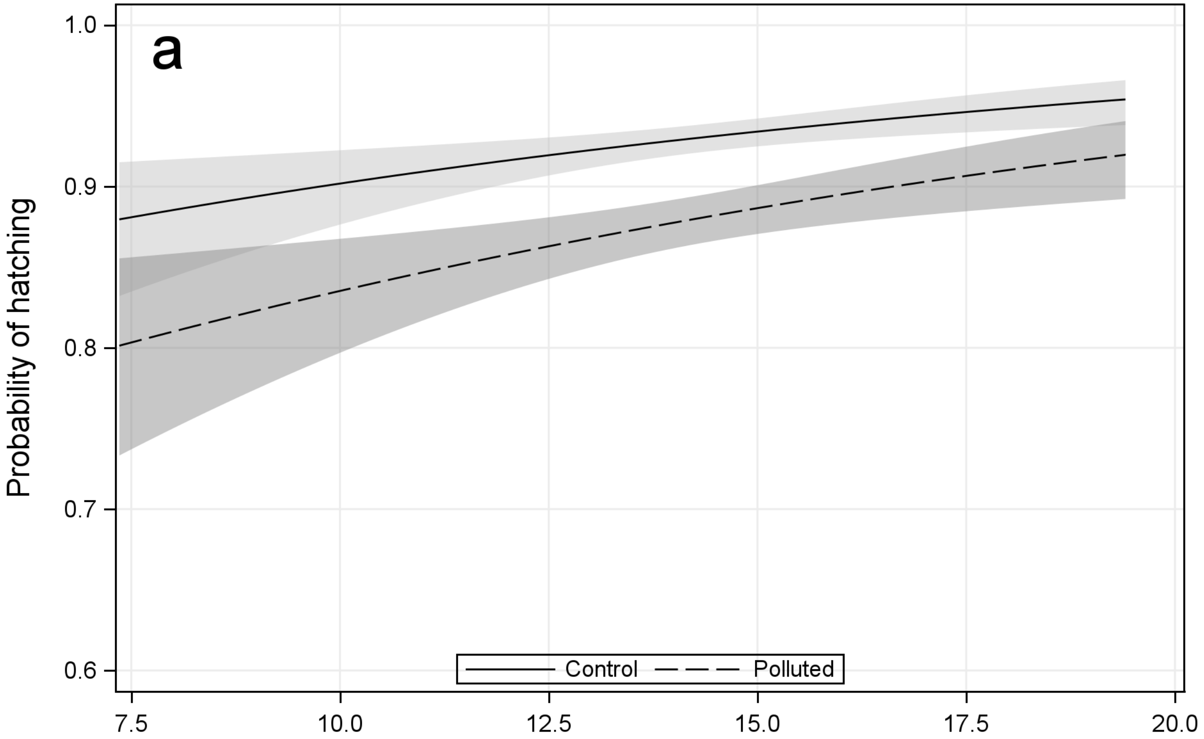
Figure 1. The effect of ambient temperature (°C) during the incubation period on hatching probability of (**a**) *F. hypoleuca* (n = 5720 clutches) and (**b**) *P. major* (n = 2489 clutches). Predicted values (±95% CLs) come from the GLMMs shown in Table 1.

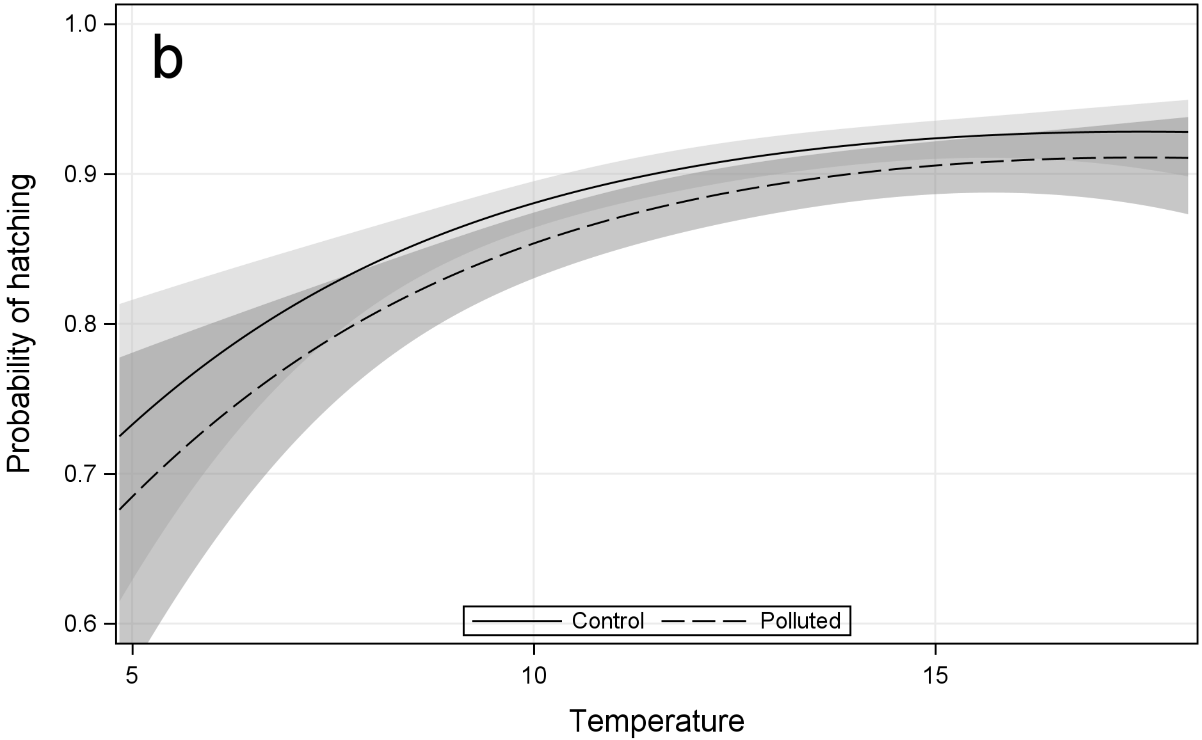
Figure 2. The effect of rainy spells (maximum number of successive rainy days during the incubation period) on probability of *F. hypoleuca* (n = 5720 clutches) eggs to hatch at different ambient temperatures (°C) during the incubation period. Predicted values (±95% CLs) come from GLMMs shown in Table 1. Selected temperatures correspond to approximately 10th, 50th and 90th percentiles of the distribution.

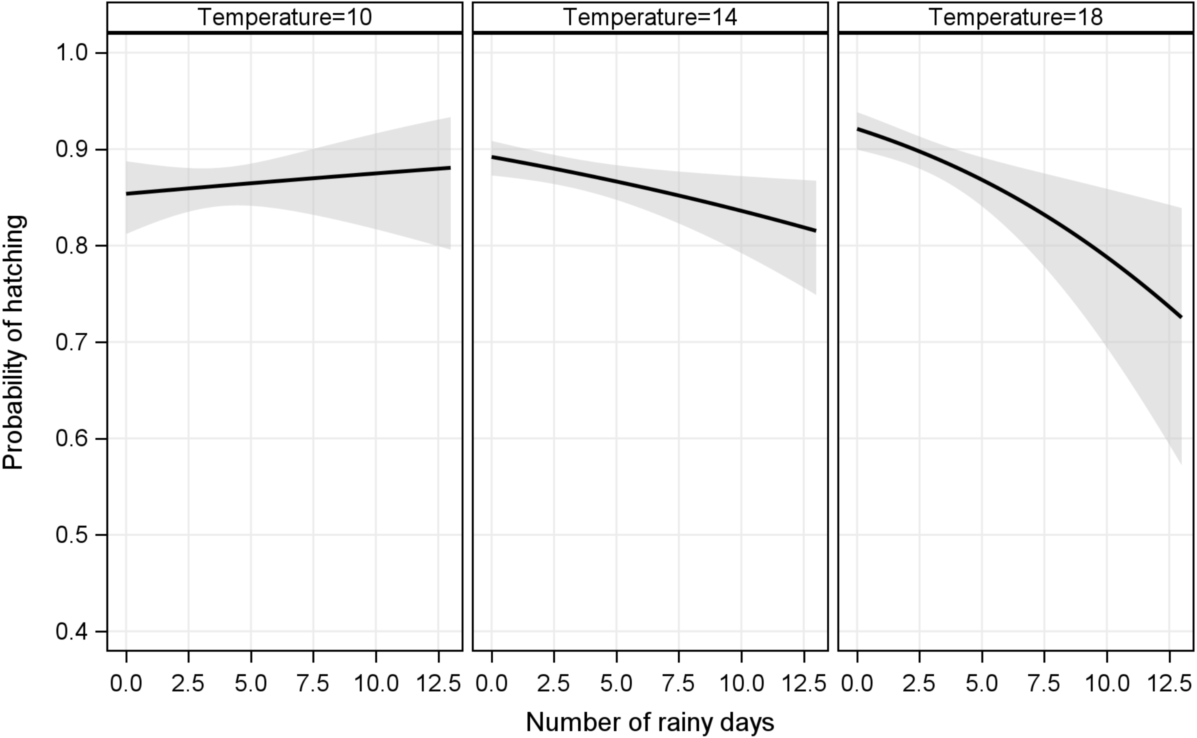
Figure 3. The effect of ambient temperature during the nestling period on the probability of (**a**) *F. hypoleuca* (n = 5002 broods) and (**b**) *P. major* (n = 2151 broods) hatchlings to fledge. Predicted values (±95% CLs) come from the GLMMs shown in Table 1.

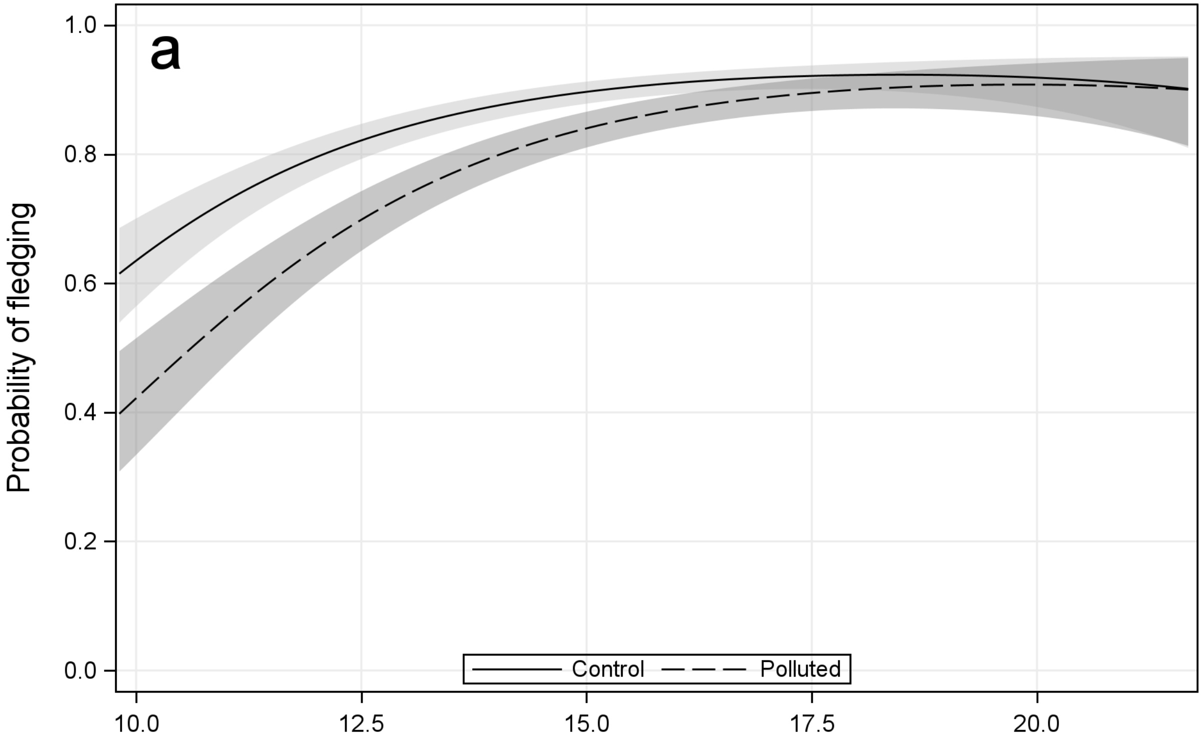
Figure 4. The effect of rainy spells (maximum number of successive rainy days during the nestling period) on probability of (**a**) *F. hypoleuca* (n = 5002 broods) and (**b**) *P. major* (n = 2151 broods) hatchlings to fledge at different ambient temperatures (°C) during the nestling period. Predicted values (±95% CLs) come from GLMMs shown in Table 1. Selected temperatures correspond to approximately 10th, 50th and 90th percentiles of the distribution.

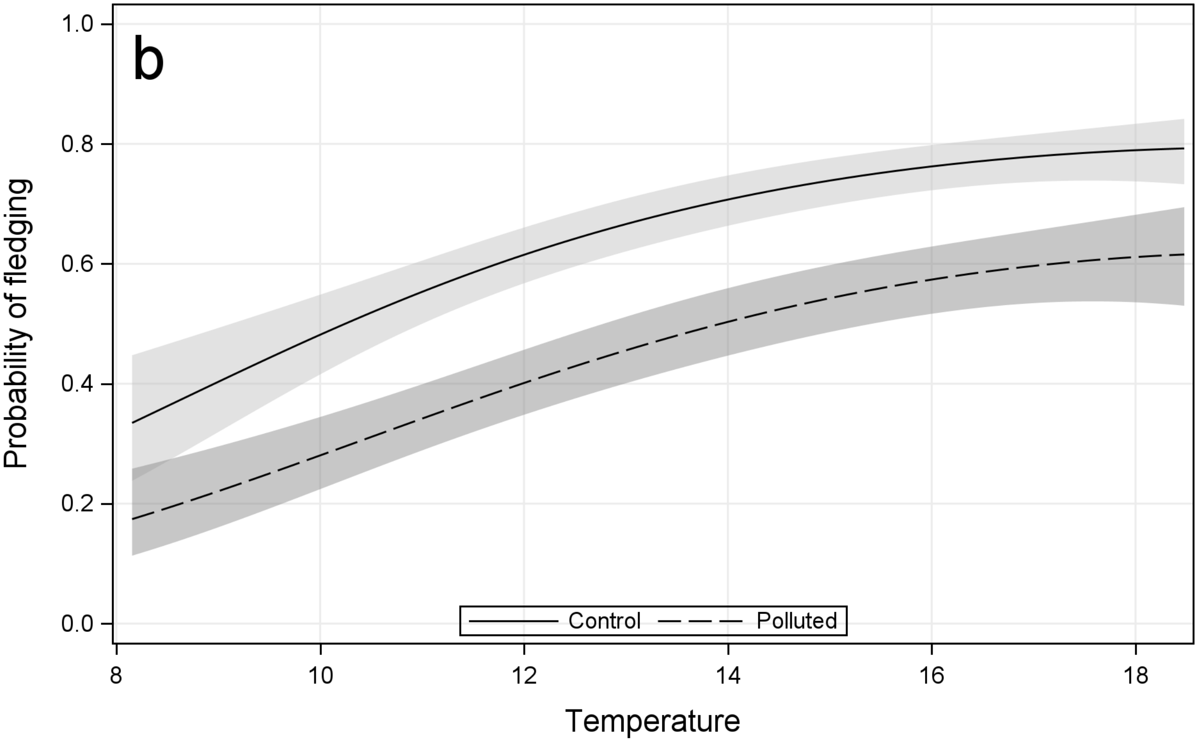
Figure 5. The effect of ambient temperature (°C) on nestling wing length residuals in (**a**) *F. hypoleuca* (n = 2609 broods) and (**b**) *P. major* (n = 1477 broods). Predicted wing length residual values (WLRs ±95% CLs) come from the LMMs shown in Table 2.

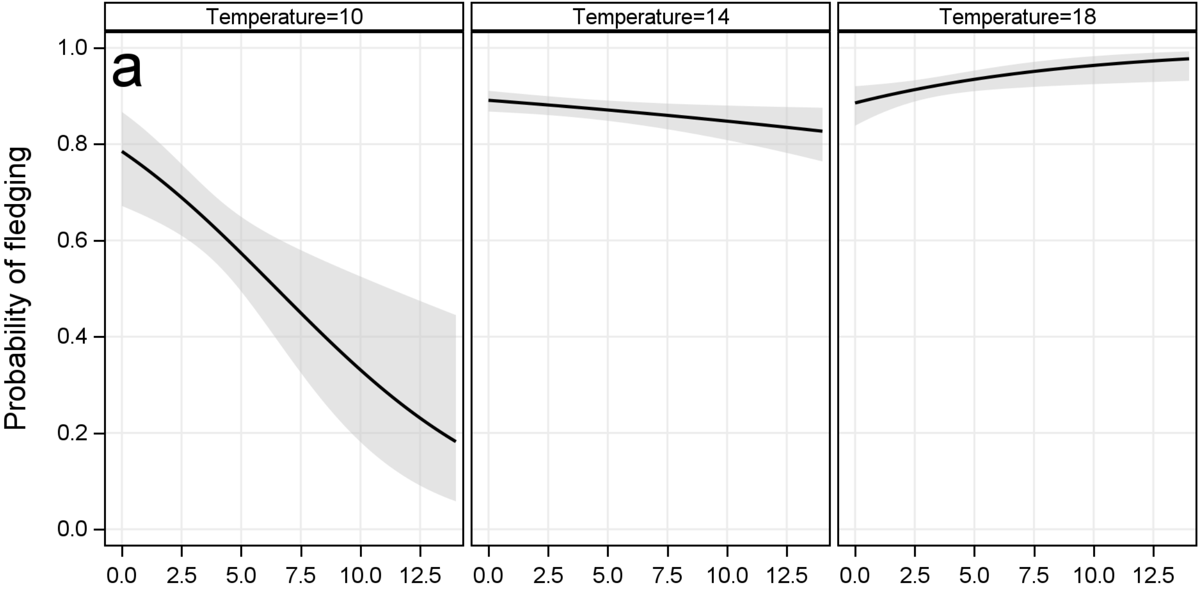

a
Probability of hatching
1.0
0.9
0.8
0.7
0.6
7.5
10.0
12.5
15.0
17.5
20.0
Control
Polluted

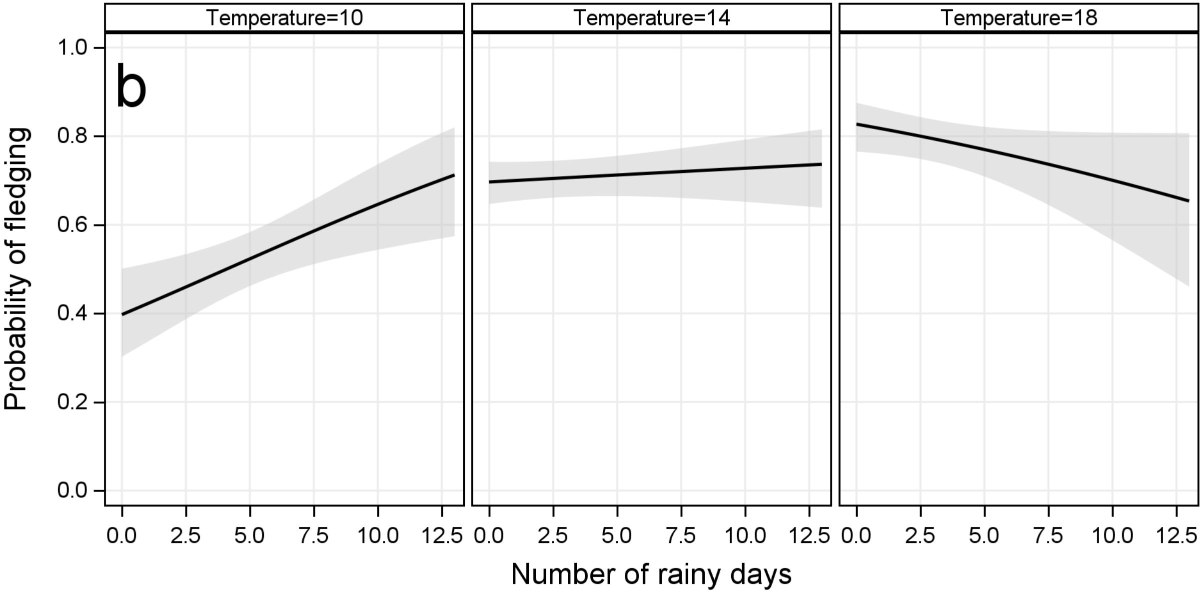

b
Probability of hatching
1.0
0.9
0.8
0.7
0.6
5
10
15
Temperature
Control
Polluted

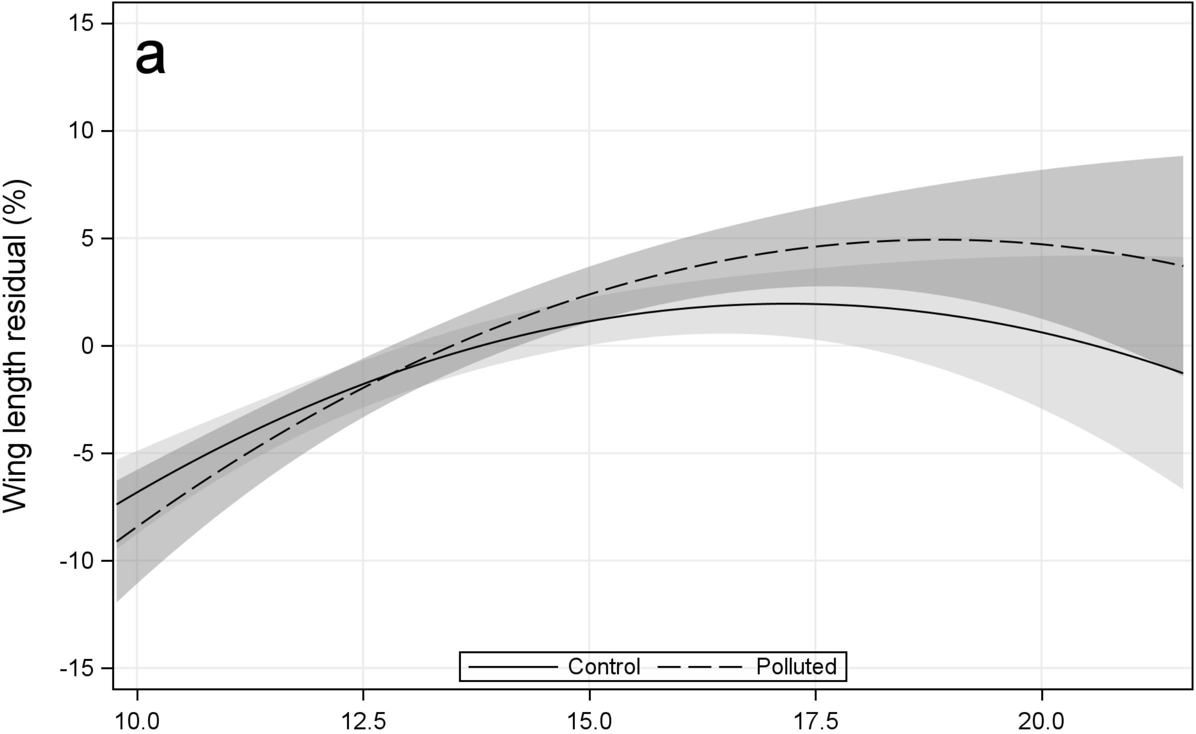

Temperature=10
Temperature=14
Temperature=18
Probability of hatching
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.0
2.5
5.0
7.5
10.0
12.5
Number of rainy days

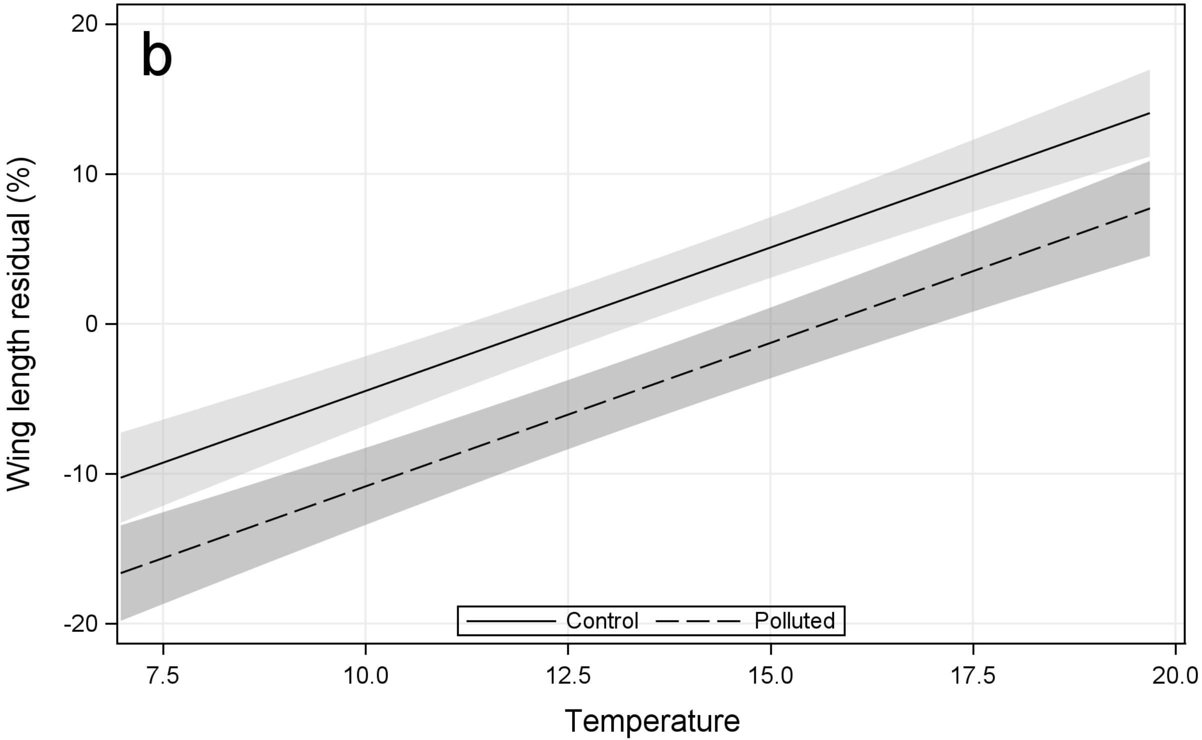

a
Probability of fledging
1.0
0.8
0.6
0.4
0.2
0.0
10.0
12.5
15.0
17.5
20.0
Control
Polluted


b
Probability of fledging
1.0
0.8
0.6
0.4
0.2
0.0
8
10
12
14
16
18
Temperature
Control
Polluted


a
Temperature=10
Temperature=14
Temperature=18
Probability of fledging
0.0
0.2
0.4
0.6
0.8
1.0
0.0
2.5
5.0
7.5
10.0
12.5


b
Temperature=10
Temperature=14
Temperature=18
Probability of fledging
1.0
0.8
0.6
0.4
0.2
0.0
0.0
2.5
5.0
7.5
10.0
12.5
Number of rainy days


a
Wing length residual (%)
15
10
5
0
-5
-10
-15
10.0
12.5
15.0
17.5
20.0
Control
Polluted


b
Wing length residual (%)
20
10
0
-10
-20
Temperature
7.5
10.0
12.5
15.0
17.5
20.0
Control
Polluted