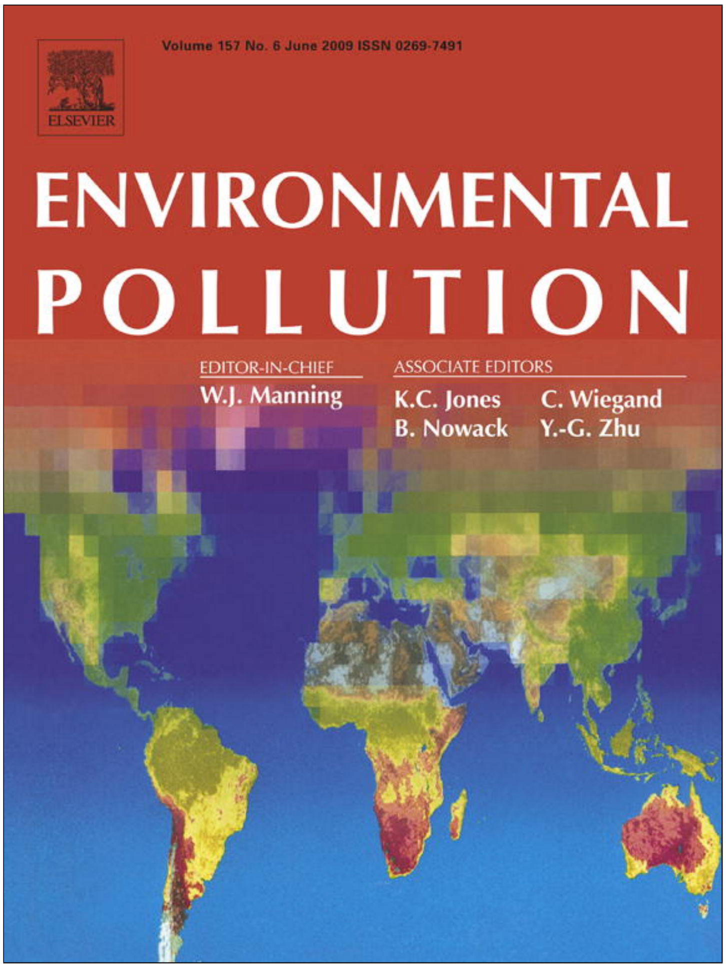
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Local survival of pied flycatcher males and females in a pollution gradient of a Cu smelter

T. Eeva [a,*], H. Hakkarainen [a], E. Belskii [b]

[a] Section of Ecology, University of Turku, FI-20014 Turku, Finland
[b] Institute of Plant and Animal Ecology, Russian Acad. Sci., 8th March street, 202, Ekaterinburg 620144, Russia

Female pied flycatchers (Ficedula hypoleuca) show decreased local survival around a copper smelter.

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ABSTRACT

Survival is one of the most central population measures when the effects of the pollution are studied in natural bird populations. However, only few studies have actually measured rigorous survival estimates on adult birds. In recent years there has been a methodological advance in survival analyses by mark-recapture models. We modelled local survival (including mortality and emigration) with the program MARK in a population of a small insectivorous passerine bird, the pied flycatcher (*Ficedula hypoleuca*), around a point source of heavy metals. The local survival of females in the polluted area was about 50% lower than in the other areas. Males, however, survived relatively well in the heavily polluted area, but showed somewhat lower survival in the moderately polluted area. Different pollution effects between two sexes might be due to pollution-related differences in reproductive effort in females and males, and/or more intensive uptake of heavy metals by laying females.

1. Introduction

Point sources of heavy metals, such as non-ferrous smelters, are known to pose a serious hazard for local breeding bird populations. Decreased breeding success of insectivorous passerines has been demonstrated at several smelter sites (Belskii et al., 1995a, 2005; Eeva and Lehikoinen, 1996, 2000; Janssens et al., 2003). Typically such studies report decreased clutch size, hatchling and nestling numbers and nestling survival, though the effects depend on study species and pollution load. Several studies have also shown decreased population densities and species richness of forest birds around smelter sites (Gilyazov, 1993; Kristín and Zilinec, 1997; Eeva et al., 2002; Belskii and Lyakhov, 2003). Heavy loads of sulphuric oxides and heavy metals have been shown to cause secondary effects on birds via changed food chains, such as decreased abundance of invertebrate food and limited Ca availability (Eeva et al., 1997, 2005; Eeva and Lehikoinen, 2004). Nestling stage is generally supposed to be the phase most affected by environmental stresses like pollution (Hoffman, 1995). It is also the phase most easily studied in birds, and, in migratory birds, the phase which is easiest to couple with certain environment. There is, however, much less information on pollution effects on survival of adult birds. This is partly due to the lack of long-term population data from polluted areas, but also due to problems to analyse long-term data sets with yearly variation in recapture rates.

In recent years there has been a methodological advance in analyses of adult survival by mark-recapture models that take into account the variation in recapture probabilities. By using such models in MARK software (White and Burnham, 1999) we modelled local survival (including mortality and emigration) of a small migratory insectivorous passerine bird, the pied flycatcher (*Ficedula hypoleuca*), around a Russian Cu smelter, a point source of heavy metals (Vorobeytchik et al., 1994). A few recent studies have suggested important effects of air pollution on the local survival of this species. *F. hypoleuca* females showed decreased local survival in a study around a Finnish Cu smelter, but there was no effect on another hole-breeding insectivore, the great tit (*Parus major*) (Eeva and Lehikoinen, 1998). Another study suggested that *F. hypoleuca* males showed, unexpectedly, increased local survival in a heavy metal polluted area, as compared to females in the polluted area or males in the unpolluted area (Eeva et al., 2006b). Long-term mark-recapture data collected around the Russian smelter gives a good opportunity to compare survival between the smelter sites, especially because heavy metal emission levels in the Russian study area are much higher than in any of the earlier studies.

* Corresponding author.
E-mail address: tapio.eeva@utu.fi (T. Eeva).

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2. Materials and methods

2.1. Study area and data collection

The data was collected during 1996–2007 in a pollution gradient of the Middle Ural copper smelter (56°51′N, 59°53′E) in Revda, Russia. Heavy metals (mainly Cu, Pb, Zn and Cd) and sulphuric oxides are the main pollutants of this large chemical metallurgy complex. The total emissions have decreased from 140,700 tons/year in 1989 to 95,700 tons/year in 1996 and 24,507 tons/year in 2007 (Vorobeytchik et al., 1994; Podust, 1997; Pakhalchak, 2008). High emission of dust causes considerable emission of heavy metals, especially lead, to surrounding forests. Study sites with nest boxes were located in three zones around the smelter: I heavily polluted zone (5 sites 1–2 km from the smelter), II moderately polluted zone (5 sites 4–8 km from the smelter) and III unpolluted zone (3 sites 16–27 km from the smelter). Forest stands in the vicinity of the smelter are sparser and contain more dead trees than the more distant sites. A more detailed description of habitat types is given by Belskii and Lyakhov (2003). A long-term pollution by metallic dust combined with sulphur dioxide has increased soil acidity and metal concentrations in the upper soil layer. For example, soil Cu concentrations decrease from zone I to zone III from 3770 to 862 to 87 μg/g dw, respectively (Belskii et al., 2005). Fledging success of *F. hypoleuca* is clearly decreased in the polluted area. During 1989–1993 the average number of fledglings was 2.0 (zone I), 4.6 (zone II) and 5.3 (zone III) while in 2000–2001 the figures were 2.8, 5.5 and 5.5 chicks, respectively (Belskii et al., 1995a, 2005).

Nest boxes were regularly checked to record the numbers of eggs, nestlings and fledglings. About 80–100% of breeding females and 30–90% of breeding males were yearly captured and marked with an aluminium ring. Adult birds were aged (1 year vs. ≥2 years) according to Karlsson et al. (1986), measured for their wing length (a measure of body size) and colour morph of males was scored according to the Drost's scale (Drost, 1936), scores varying in this population from 3 (dark) to 7 (grey).

2.2. Survival models

Survival analyses were performed using mark-recapture histories of 589 males and 815 females that recruited to the breeding population in 1996–2007. For modelling we used program MARK that enables separate estimation of survival and recapture rates (White and Burnham, 1999) based on the capture histories of a sample of marked individuals. Survival rate (*S*) describes the local survival of individuals, including emigration. Recapture rate (*P*), in turn, decreases with the number of individuals missed in the trapping process, and is taken into account when modelling estimates for *S*. To prevent a possible bias in recapture probabilities due to varying spatial distribution of study sites among distance zones, we omitted from all the analyses those 18 individuals (1.3% of all) that changed the study plot during the study period.

In both sexes, we first analyzed all 25 model combinations in which survival and recapture probability were allowed to vary or to be constant with respect to time (t) and/or to pollution zone (g). The individual models were ranked on the basis of Akaike's information criterion (AICc) to determine which models most parsimoniously fit the data (Akaike, 1973; Hurvich and Tsai, 1995; Burnham and Anderson, 1998). The model with the lowest AICc score was considered to be the best model, but any models that had AICc scores within two points of the best model were considered to be competitive with the best model (Burnham and Anderson, 1998; Cooch and White, 1999). The fit of our data to a general model, i.e. the model containing all the interactions ($S_{(g\,*\,t)}P_{(g\,*\,t)}$) was explored with contingency table tests in program RELEASE (tests T2 and T3) (see Burnham et al., 1987).

Finally, we examined whether parental quality in terms of age, wing length and plumage colour (males only) or breeding success influenced the survival parameters. All these parameters are known to depend on pollution level on the basis of earlier studies in the area (Belskii et al., 1995a; Belskii and Lyakhov, 2004). For this purpose, design matrix was modified by adding separately one of the variables to the most highly ranked model. Note that in program MARK only individual covariates are allowed and therefore we used mean values of an individual as individual covariates, except for age, where age at the first encounter was used as a covariate. The values of covariates were not available for all the individuals and the sample sizes in these analyses are consequently somewhat smaller than in the basic models. All the covariates were further tested for their differences among pollution zones with mixed linear models (SAS procedures GLIMMIX for age and MIXED for fledgling number, wing length and plumage colour) by using year as a random factor. Binary error distribution was used for modelling age distribution and normal error distribution for the other variables. Tukey's test was used to explore pairwise differences among the zones.

3. Results

3.1. Goodness of fit analyses

There was no overdispersion in the data, because the fit of our general model ($S_{(g\,*\,t)}P_{(g\,*\,t)}$) to the data was adequate: for females RELEASE test T2 ($\chi^2 = 5.23$, df = 11, $p = 0.92$), and test T3 ($\chi^2 = 23.2$, df = 36, $p = 0.95$). The data was adequate also for males: test T2 ($\chi^2 = 4.09$, df = 11, $p = 0.97$), and test T3 ($\chi^2 = 17.7$, df = 35, $p = 0.99$) (see Burnham et al., 1987).

3.2. Survival models

In females the best fit model ($S_{(g)}P_{(g\,+\,t)}$) included the zone effect (g) for both survival and recapture rate (Table 1). The best model also allowed recapture rate to vary annually (t) across the three distance zones (Table 1). The estimates from the best fit model showed that survival of females in the polluted zone I was about 50% lower than in the zones II and III (Fig. 1). On the basis of earlier studies it was known that fledgling numbers are low close to the Cu smelter (Belskii et al., 1995a, 2005). Fledgling number as a covariate further increased the fit of the model (LR-test between the nested models $S_{(g\,+\,\text{fledglings})}P_{(g\,+\,t)}$ vs. $S_{(g)}P_{(g\,+\,t)}$: $\chi^2 = 5.36$, df = 1, $p = 0.021$; ΔAICc = 3.28), because survival probability increased with the fledgling number ($\beta = 0.24$, SE = 0.10). The model including wing length as a covariate was not highly ranked, suggesting that female's survival probability was independent on its body size. The model including female age did not differ significantly from the most highly ranked model (LR-test $S_{(g)}P_{(g+t)}$ vs. $S_{(g\,+\,\text{age})}P_{(g\,+\,t)}$: $\chi^2 = 0.28$, df = 1, $p = 0.59$; ΔAICc = 1.79), suggesting that old females show a slightly higher (1.4%) local survival probability ($\beta = 0.091$, SE = 0.17). However, the majority of the variation in local survival among zones cannot be explained by age effect.

In males the best fit model ($S_{(g\,+\,t)}P$) showed that survival varied between the three different pollution zones and annually, whereas recapture rate was constant over time and space (Table 1). Males showed about 26% lower survival estimates in the moderately polluted zone II than in two other zones (Fig. 1). Fledgling number as a covariate did not increase the fit of the survival model of males. Furthermore, the models including wing length or plumage colour as a covariate were not highly ranked, suggesting that male's survival did not depend on its body size or colour morph. The model including male age did not significantly differ from the most highly ranked model (LR-test $S_{(g\,+\,t)}P$ vs. $S_{(g\,+\,\text{age}\,+\,t)}P$: $\chi^2 = 0.18$, df = 1, $p = 0.67$; ΔAICc = 1.91), suggesting that young males show a slightly (1.7%) higher local survival (β = −0.083, SE = 0.20). Therefore, the majority of the variation in local survival among zones cannot be explained by age effect in males either.

The fledgling numbers of marked birds were 30–40% lower in the most polluted zone I than in the other zones in data sets of both sexes, while the difference was not significant between zones II and III (Table 2). A larger proportion of breeding birds were young in the

Table 1
The most parsimonious survival models for females and males (*S* denotes survival, *P* denotes recapture probability), including model deviance, number of parameters (np) and Akaike's information criterion (AICc = deviance + 2np) and the difference in AICc compared to the most highly ranked model (ΔAICc). The letter t indicates time (i.e. annual variation) and g the zone-dependence (i.e. polluted, moderately polluted and unpolluted zone). The models in boldface, with lowest AICc, were used for interpretation of results.

Models	Deviance	Np	AICc	ΔAICc	AICc weight
Females					
$\mathbf{S_{(g)}P_{(g\,+\,t)}}$	**156.37**	**16**	**1137.33**	**0.00**	**0.81**
$S\,P_{(g+t)}$	164.37	14	1141.20	3.87	0.17
$S_{(t)}P_{(g)}$	167.23	14	1144.05	6.72	0.01
Males					
$\mathbf{S_{(g\,+\,t)}P}$	**134.87**	**14**	**986.91**	**0.00**	**0.52**
$S_{(t)}P_{(g)}$	136.95	14	988.99	2.08	0.19
$S_{(t)}P$	141.99	12	989.88	2.97	0.12

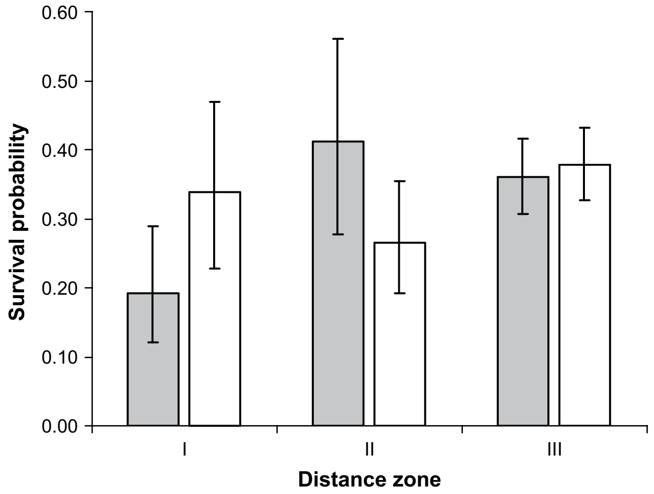

Fig. 1. Survival probabilities (±95% confidence limits) of *F. hypoleuca* females (grey bars; estimates derived from the model $S_{(g)}P_{(g+t)}$) and males (white bars, estimates derived from the model $S_{(g)}P$) at three distance zones from the Cu smelter.

most polluted zone than in the two other zones for both sexes (Table 2). Both females and males were also smaller (shorter winged) in the zone I than in zones II and III (Table 2). Furthermore, males were lighter coloured in the zone I (median score = 6) than in the other zones (median score = 5 for both zones; Table 2). A great deal of the differences in wing length and male colour is explained by age. When age was added in the models the zone effect was still significant for female wing length ($F_{2,781} = 4.4$, $p = 0.012$) and male wing length ($F_{2,572} = 5.4$, $p = 0.0047$), but not for male colour ($F_{2,558} = 2.2$, $p = 0.11$). The fledgling number of young females was 0.5 fledglings smaller than that of old females ($F_{1,688} = 17.3$, $p < 0.0001$), but zone effect still remained strong ($F_{2,695} = 96.8$, $p < 0.0001$) after including age into the model. Male age did not significantly explain the fledgling number ($F_{1,527} = 0.23$, $p = 0.63$).

4. Discussion

The local survival of *F. hypoleuca* females was decreased in the heavily polluted area around the Revda Cu smelter while males seemed to survive relatively well in the polluted area. The differences in fledging production, age, body size or male plumage colour could not explain the differences in survival among the pollution zones. In Revda, heavy metal emissions were very high during the study period. For example, Revda smelter emitted 170 tons of lead in 2002 (Lassen et al., 2005). High emission levels in Revda are likely to explain the stronger negative effect on female survival as compared to earlier studies (Eeva and Lehikoinen, 1998; Eeva et al., 2006b). The negative effect on survival may be due to direct toxic effects of heavy metals (Eeva and Lehikoinen, 2004), or indirect effects, e.g. via changes in food availability (Eeva et al., 1997) or population structure (Eeva et al., 2006a). High emission levels are also reflected in relatively poor breeding success in the polluted sites near the Revda smelter (Belskii et al., 1995a,b, 2005; Bezel et al., 1998). For example, the average fledgling number in the whole population of the polluted area in Revda was 2.8 in 2000–2001, while the corresponding figure was 5.5 in the unpolluted area (Belskii et al., 2005). In our data set the number of fledglings was somewhat higher (see Table 2) because parents of the most unsuccessful nests (i.e. those that fail at early phases of breeding) may remain untrapped more often than those of more successful nests.

The local survival probability (±SE) of *F. hypoleuca* males was relatively high (34% ±6.2) in the polluted area of Revda. Surprisingly, male survival was somewhat lower in the moderately polluted zone II than in the most distant zone III. A possible reason to this might be a relatively high occupation rate (71%) of nest boxes in two study sites in the zone II, which likely indicates increased competition for nest holes among males. High competition might lead to decreased local survival probability among males. Male age distribution, size, colour morph or fledgling production in zone II were not different from the zone III (Table 2). High female survival and fledging success further suggest that food resources should be relatively good in the zone II.

Studies on the effects of air pollution on survival of adult birds are scarce. Local survival of *F. hypoleuca* has been studied around an another Cu smelter in Harjavalta, Finland (Eeva and Lehikoinen, 1998; Eeva et al., 2006b). In the beginning of 1990s local survival of females was decreased in this heavy metal polluted area, but along with strongly reduced emissions the female survival has approached the level of an unpolluted control area towards the end of 1990s. For example, particulate yearly lead emissions from Harjavalta smelter have decreased from 50 tons in 1991 to 0.4 tons in 2002. Simultaneously, heavy metal residues in birds have decreased and fledgling numbers have increased (Eeva and Lehikoinen, 2000). Like in Revda, males survived well (42% ±4.0) in the polluted area around the Harjavalta smelter (Eeva et al., 2006b). Studies at both locations suggest that the effect of pollution on local survival is sex-dependent, females being affected more severely by heavy metal pollution.

The reasons for sex-dependent pollution effects are unknown, but we suggest here some ideas for further studies. In *F. hypoleuca*, female alone is responsible for nest-building, egg production, incubation and brooding, which apparently cause reproductive costs (e.g. Ilmonen et al., 2002). Therefore, females might be more susceptible to negative health effects of pollution stress due to their

Table 2
The average number of fledglings, proportions of young (1 yr) breeding females and males, average wing length and average colour morph of males according to Drost's scale (smaller value means darker) in three distance zones around the Cu smelter. Tukey's test for pairwise differences: means with the same letter are not significantly different.

	Mean (±SE)/Proportion						
	n	Zone I	Zone II	Zone III	df	*F*	*p*
Fledgling number (for females)[a]	731	3.09 (0.17)a	5.23 (0.12)b	5.50 (0.07)b	2,709	112.6	<0.0001
Fledgling number (for males)[a]	539	3.94 (0.23)a	5.55 (0.12)b	5.70 (0.06)b	2,534	45.9	<0.0001
Proportion of young females (%)[b]	790	61.7a [53.2]	35.9b [30.3]	39.7b [30.8]	2,776	10.9	<0.0001
Proportion of young males (%)[b]	543	45.8a [36.0]	25.5b [20.4]	29.7b [21.3]	2,529	4.16	0.016
Female wing length (mm)[a]	805	79.5 (0.13)a	79.9 (0.11)b	80.1 (0.06)b	2,800	10.5	<0.0001
Male wing length (mm)[a]	592	81.1 (0.21)a	82.0 (0.14)b	82.0 (0.08)b	2,586	9.84	<0.0001
Male colour morph in Drost's scale[a]	578	5.51 (0.14)a	5.04 (0.10)b	5.04 (0.06)b	2,562	4.97	0.0072

[a] A mixed linear model with normal error distribution and year as a random factor.
[b] A mixed linear model with binary error distribution and year as a random factor. Note that these covariate values refer to the age at the first encounter. The figures in parentheses give real proportions of young birds in the whole data set ($n_{♀♀} = 990$; $n_{♂♂} = 733$).

higher reproductive effort as compared to males. Furthermore, many males in the impact zone were observed to became passive (did not take part in feeding nestlings) towards the end of nesting period and sometimes they disappeared before nestlings fledged. The proportion of nests without a male during the nestling period was almost three times higher in the heavily polluted area than in the unpolluted area (Zone I: 20.3%; Zone II: 14.1%; Zone III: 7.5%; E. Belskii, unpublished data). Therefore, males might partly avoid the pollution stress by withdrawing the breeding, and would thus further increase females' load at polluted breeding sites where also food resources may be limited. Furthermore, during egg laying females need to collect high amount of calcium-rich food for egg shell formation (Eeva and Lehikoinen, 2004). Together with Ca they are likely to accumulate heavy metals, especially lead (Goyer, 1997). More intensive accumulation of heavy metals to breeding females would mean that detrimental effects would first manifest in this sex. Snoeijs et al. (2005) showed further that lead exposure impaired antibody production in non-breeding female zebra finches (*Taeniopygia guttata*) while such an effect was not found in males.

The differences in local survival probabilities might also reflect different population age structure and/or breeding dispersal. In Revda population, proportions of young females and males were higher in the heavily polluted than in moderately polluted or unpolluted zones. Such a difference could be produced by non-random settlement of young and old individuals to polluted and unpolluted environments (Eeva et al., 2006a). Generally, *F. hypoleuca* males are clearly more site tenacious than females and older birds of both sexes are supposed to move shorter distances between years than young birds (Lundberg and Alatalo, 1992). A high tendency of young females to disperse to less polluted areas (e.g. as a response to low breeding success) would produce similar survival pattern as we observed. However, although age seemed to explain some of the variation in survival probabilities in both sexes, adding age to the survival models did not remove a much stronger effect of distance zone. Alternatively, poor breeding success could increase breeding dispersal of females independent of age. In accordance with this, we found a positive association between the local survival of females and their fledgling production, while such an effect was not observed in males. Studies in Harjavalta, however, suggest that in *F. hypoleuca* less productive individuals in both sexes tend to disperse as far as well producing individuals (Eeva et al., 2008), independently of pollution levels. Much higher pollution levels in Revda might, however, produce a stronger success-related effect on female dispersal. A need to disperse from a breeding area may also be associated with other factors than fledgling production, e.g. with the degree of physiological stress and/or pollution-related hormonal changes.

The Revda and Harjavalta populations also seem to differ in their local female survival even between the unpolluted sites, survival probabilities in Harjavalta (21% $\pm$5.2) being generally much lower than those in Revda (36% $\pm$2.8). We don't know the reason for this inter-population variation, but for example different breeding dispersal distances in two populations could produce such a difference. Birds were trapped more efficiently in Revda than in Harjavalta, but our models correct survival estimates by the variation in recapture probabilities. The between-site differences in survival were smaller in males but to the same direction (Harjavalta: 31% $\pm$3.9; Revda 38% $\pm$2.6).

5. Conclusion

The local survival of *F. hypoleuca* females is decreased in the heavily polluted area around the Revda Cu smelter while males seem to survive relatively well in the polluted area. The observed differences in fledging production, age distribution, body size and male plumage colour could not explain the differences in survival among the pollution zones. Possible explanations for decreased local survival of females in the polluted area could be pollution-related differences in reproductive effort between females and males and/or more intensive accumulation of heavy metals to breeding females. However, further studies are needed to confirm the mechanisms leading to this kind of pollution-related sex-specific local survival.

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