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Environmental pollution has sex-dependent effects on local survival

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Environmental pollutants cause a potential hazard for survival in free-living animal populations. We modelled local survival (including emigration) by using individual mark–recapture histories of males and females in a population of a small insectivorous passerine bird, the pied flycatcher (*Ficedula hypoleuca*) living around a point source of heavy metals (copper smelter). Local survival of *F. hypoleuca* females did not differ between polluted and unpolluted environments. Males, however, showed a one-third higher local-survival probability in the polluted area. Low fledgling production was generally associated with decreased local survival, but males in the polluted area showed relatively high local survival, irrespective of their fledgling number. A possible explanation of higher local survival of males in the polluted area could be a pollution-induced change in hormone (e.g. corticosterone or testosterone) levels of males. It could make them to invest more on their own survival or affect the hormonal control of breeding dispersal. The local survival of males decreased in the polluted area over the study period along with the simultaneous decrease in heavy metal emissions. This temporal trend is in agreement with the stress hormone hypothesis.

Keywords: air pollution; breeding dispersal; *Ficedula hypoleuca*; heavy metals; reproduction; survival models

1. INTRODUCTION

Environmental pollutants are a potential hazard for survival in free-living animal populations (Fry 1995; Keith & Bruggers 1998). Large amounts of pollutants (e.g. pesticides) have acute effects on survival, due to immediate increased mortality at sites of exposure (Blus & Henny 1997; Fleischli *et al.* 2004). It is not, however, known whether constant environmental pollution has delayed effects on individual survival later in life. These delayed effects may arise due to the accumulation of toxic compounds in body tissues or due to stress, e.g. as a result of limited resources for reproduction (Graveland & Drent 1997; Eeva & Lehikoinen 2004). Individuals may also show increased breeding dispersal from polluted and often from unproductive territories (Greenwood & Harvey 1982).

The electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2006.0443 or via http://www.journals.royalsoc.ac.uk.

We modelled local survival (including mortality and emigration) in a population of a small insectivorous passerine bird, the pied flycatcher (*Ficedula hypoleuca*), around a copper smelter, a point source of heavy metals. Our earlier studies have shown decreased breeding success in this species near the pollution source due to lower quantity and quality of food (Eeva & Lehikoinen 1996). Increased heavy metal content in nestling diet leads to poor fledgling production by interfering with calcium, a limited resource for breeding in the polluted area (Eeva & Lehikoinen 2004). Since local survival of parents may be related to their reproductive output, e.g. via trade-offs between reproduction and survival or via changed breeding dispersal, we also modelled the possible effect of fledgling number on local survival probabilities of males and females. We further tested *a posteriori* whether local survival of males is affected by relaxed competition over nest holes in a polluted area, where nest-box occupancy is lower than in the unpolluted area (Eeva *et al.* 1997b).

2. MATERIAL AND METHODS

(a) *Study area*

The data were collected in 1991–2000 around a copper smelter ($61°20'$ N, $22°10'$ E) in southwestern Finland. Sulphuric oxides and heavy metals (especially Cu, Zn, Ni, Pb and As) are common pollutants in the area (Kiikkilä 2003). Elevated heavy metal concentrations occur in the polluted area due to current and historical deposition, and metal contents decrease exponentially with increasing distance to the smelter, approaching background levels at sites more than 5 km from it (Eeva & Lehikoinen 1996). Heavy metal and SO_2 emissions from the smelter decreased considerably during 1990s (see electronic supplementary material). At the same time, heavy metal levels in *F. hypoleuca* nestlings have decreased with a simultaneous increase in breeding success (Eeva & Lehikoinen 2000).

Twenty-two study sites, each with 30–50 nest boxes, were established in the pollution gradient in three main directions (southwest, southeast and northwest), in a range of 0.5–74 km from the smelter. The number of active sites varied in different years and annually 540–802 nest boxes were checked. We captured and ringed males and females from nest boxes during the incubation and nestling periods. To compare the survival in different parts of the pollution gradient, we split the data in two parts: the zone less than 5 km from the pollution source (median 1.9 km) is hereafter called 'polluted', whereas the zone greater than 5 km from the source (median 10.3 km) is called 'unpolluted'.

(b) *Survival analyses*

Survival analyses were performed using the mark–recapture histories of 637 males and 1597 females that were recruited to the breeding population in 1991–2000. We used program MARK that enables the separate estimation of survival and recapture rates (White & Burnham 1999). 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. To prevent a possible bias in recapture probabilities due to different sizes of the study areas, we omitted from all analyses those 22 individuals (1% of all) that changed the study plot under the study period.

In both the sexes, we analysed all of the 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 zone (g). The individual models were ranked on the basis of Akaike's information criterion, AIC (Burnham & Anderson 1998). The fit of our data to a general model (S_{gt}, P_{gt}) was explored with contingency table tests in program RELEASE (tests 2 and 3; see Burnham *et al.* 1987). It was adequate for males, but not for females, suggesting some over-dispersion in the data. Therefore, for females we used ĉ corrected AICc values (QAICc) in our analyses (Burnham *et al.* 1987). When ΔAICc (i.e. the difference from the best fitting model) is less than 2, both models have approximately equal support in the data. If ΔAICc is greater than 2, there is a considerable support for a real difference between the models.

To explore the association between survival and fledgling production, we modelled the combined data of males and females

Table 1. The most parsimonious survival models for males and females (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 versus non-polluted zone). The models in boldface, with lowest AICc, were used for interpretation of results.

models	deviance	np	AICc	ΔAICc	cumulative weight
males					
S_{gt}, P	**792.15**	**16**	**824.88**	**0.00**	**0.62**
S_{gt}, P_g	791.97	17	826.79	1.91	0.86
S_{gt}, P_t	786.28	21	829.53	4.64	0.92
females[a]					
S, P	**48.92**	**2**	**351.94**	**0.00**	**0.49**
S_g, P	48.47	3	353.49	1.55	0.71
S, P_g	48.83	3	353.85	1.91	0.90

[a] For females we used ĉ corrected AICc values (QAICc), see § 2b.

with generalized linear mixed models (GLMM), which allowed more flexible models, including continuous variables, clustering factors and three-way interactions (GENMOD procedure of SAS, type 3 test). We modelled the probability of an individual bird breeding in the same study plot in later years (0 = not captured later; 1 = captured later). Each individual was used only once in the analyses, so that survival probability from first to second capture was modelled. The independent variables were zone, sex and fledgling number with all interaction terms. Since the same nest boxes were used many times in our long-term data, we introduced nest box as a clustering (repeated) factor in our analysis. Fledgling number refers to the number of fledglings in the brood where a bird was captured for the first time. The model fitted the data well (dispersion parameter = 0.6). We first included also age at first breeding and body mass in our model, but these were omitted as non-significant factors (age: $\chi_1^2 = 2.1$, $p = 0.15$, $n = 2036$; body mass: $\chi_1^2 = 0.03$, $p = 0.86$, $n = 2036$). Age distributions of males (young in polluted versus unpolluted area: 44 and 45%), as well as of females (48 and 43%, respectively) were very similar in two zones.

3. RESULTS

All the highest ranking models for males incorporated the zone effect (g) with time variation (t) in survival (table 1). Survival probability ($\pm$s.e.) of males was significantly higher in the polluted ($42\% \pm 4.0$) than in the unpolluted ($31\% \pm 3.9$) zone (LRT-test between the highest ranking and reduced model: $\chi_6^2 = 26.0$, $p = 0.0002$). In females, no difference between the zones was found ($18\% \pm 4.9$ versus $21\% \pm 5.2$, respectively), i.e. the most parsimonious model did not include zone effect (g) on survival (table 1). Recapture rates based on top models were independent of zone and time variation in both sexes (table 1).

In the GLMM, a three-way interaction between zone, sex and fledging number ($\chi_1^2 = 3.76$, $p = 0.05$, $n = 2234$) indicated that males and females responded differently to variation in fledgling numbers in the two zones: while males and females in the unpolluted area and females in the polluted area showed decreased local survival when their fledgling number was low, this pattern was not observed in males in the polluted area (figure 1). The local survival probability of males that failed to produce any fledglings was seven times
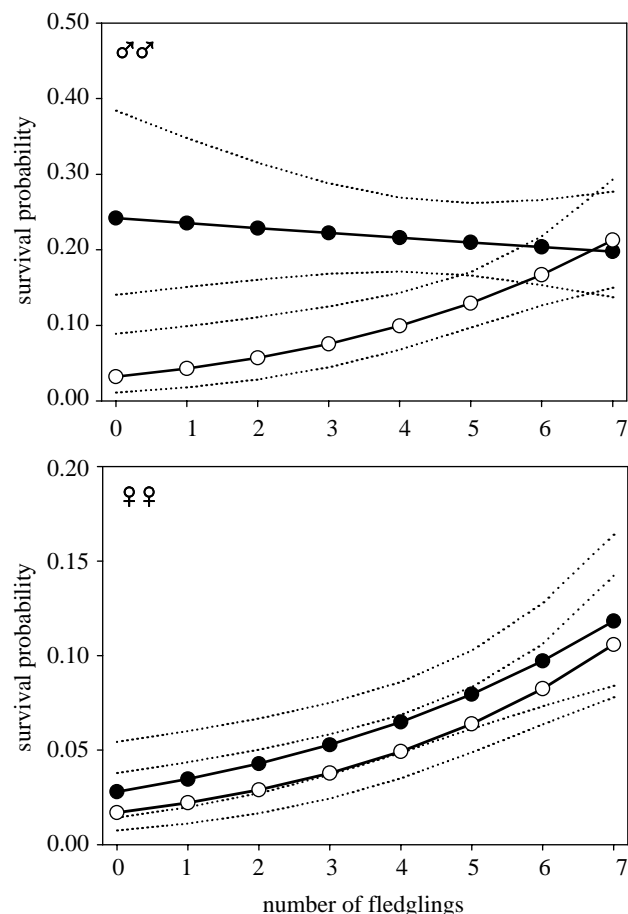

Figure 1. Survival probabilities ($\pm 95\%$ CI) of male and female pied flycatchers in polluted (filled circle) and unpolluted (open circle) areas in relation to number of fledglings produced at the first-breeding attempt.

higher in the polluted than in the unpolluted area (figure 1). When the analysis was done separately for the two zones, there was an interaction between sex and number of fledglings in the polluted area ($\chi_1^2 = 7.03$, $p = 0.008$), but not in the unpolluted area ($\chi_1^2 = 0.18$, $p = 0.68$).

To explore how consistent the observed pattern was in time, we modelled the data on males by adding year to the model (fledgling number, year, fledgling number $\times$ year). In the polluted area, local survival of males decreased over the study period (year: $\chi_1^2 = 7.23$, $p = 0.0072$; figure 2) and there was a temporal change in the relationship between fledgling number and local survival (interaction: $\chi_1^2 = 3.88$, $p = 0.049$). In the unpolluted area no temporal trends were found (year: $\chi_1^2 = 0.25$, $p = 0.62$; interaction: $\chi_1^2 = 0.28$, $p = 0.60$; figure 2).

The data on males were further modelled to test *a posteriori* if their higher survival in the polluted area could be explained by relaxed competition over nest holes in the polluted area where a greater proportion (43%) of nest boxes remain unoccupied than in the unpolluted area (33%). The yearly number of empty nest boxes at each study plot was introduced to the model as a covariate (i.e. zone, fledgling number, zone $\times$ fledgling number, empty nest boxes, zone $\times$ empty boxes). The number of empty nest boxes was positively associated with males' survival probability ($\chi_1^2 = 9.40$, $p = 0.0022$) and this effect was similar in
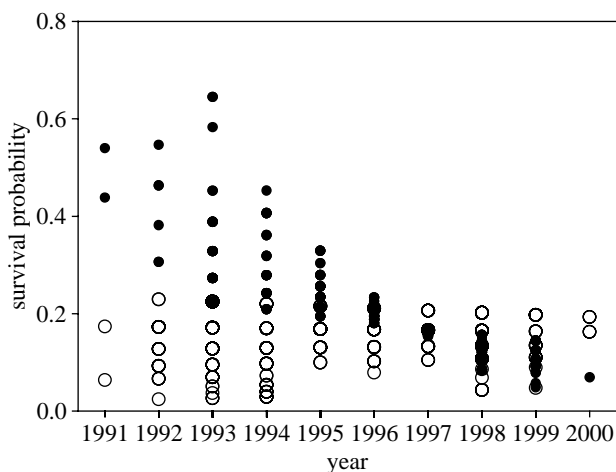
Figure 2. Survival probabilities of pied flycatcher males in polluted (filled circle; $n=288$) and unpolluted (open circle; $n=350$) areas in relation to time (note that dots overlap). The probabilities were estimated with a model also including fledgling number.

two zones (interaction: $\chi^2_1=0.12$, $p=0.73$). However, the interaction between zone and fledgling number still remained strong ($\chi^2_1=7.17$, $p=0.0074$) when the number of empty nest boxes was controlled for. Therefore, it cannot be wholly explained by differences in nest-box occupancy levels.

4. DISCUSSION

While low fledgling production was associated with decreased local survival in males in the unpolluted area and in females in both areas, males in the polluted area showed relatively high local survival, irrespective of their fledgling number. Differences in local survival may be due to differences in mortality or breeding dispersal. Birds are known to be more likely to disperse from their breeding sites if their breeding fails or the fledgling production is low (Greenwood & Harvey 1982). Our data showed this general pattern for females in the both study areas and for males in the unpolluted area. The question is, why males of the polluted area are more likely to return to their breeding site after an unsuccessful breeding than males in the unpolluted area? A higher frequency of empty nest boxes in the polluted area cannot explain the observed pattern. We hypothesize that environmental pollution might produce different hormonal responses in males and females. For example, if pollution stress increases corticosterone levels in males, they might redirect their behaviour towards their own survival (Silverin 1990). Alternatively, heavy metal pollution might directly affect the hormonal (e.g. testosterone or corticosterone) control of territoriality or breeding dispersal (Silverin 1998).

Heavy metal exposure and concentrations in birds' tissues have decreased in our study area considerably during the study period (Eeva & Lehikoinen 2000). The stress hormone hypothesis predicts that the local survival of males should, paradoxically, decrease in the polluted area when heavy metal exposure decreases. In accordance with this, we found a decreasing temporal trend in male survival in a

polluted area during 1990s, while no temporal change was observed in the unpolluted area. On the basis of our results the stress hormone hypothesis should be experimentally tested in future.

Blus, L. J. & Henny, C. J. 1997 Field studies on pesticides and birds: unexpected and unique relations. *Ecol. Appl.* 7, 1125–1132.

Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference: a practical information-theoretic approach.* New York, NY: Springer.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. & Pollock, K. H. 1987 Design and analysis methods for fish survival experiments based on release–recapture. *Am. Fish. Soc. Monogr.* 5, 1–437.

Eeva, T. & Lehikoinen, E. 1996 Growth and mortality of nestling great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) in a heavy metal pollution gradient. *Oecologia* 108, 631–639. (doi:10.1007/BF00329036)

Eeva, T. & Lehikoinen, E. 2000 Improved breeding success in forest passerines after decreased emissions of heavy metals. *Nature* 403, 851–852. (doi:10.1038/35002672)

Eeva, T. & Lehikoinen, E. 2004 Rich calcium availability diminishes heavy metal toxicity in Pied Flycatcher. *Funct. Ecol.* 18, 548–553. (doi:10.1111/j.0269-8463.2004.00875.x)

Eeva, T., Lehikoinen, E. & Sunell, C. 1997 The quality of pied flycatcher (*Ficedula hypoleuca*) and great tit (*Parus major*) females in an air pollution gradient. *Ann. Zool. Fenn.* 34, 61–71.

Fleischli, M. A., Franson, J. C., Thomas, N. J., Finley, D. L. & Riley, W. 2004 Avian mortality events in the United States caused by anticholinesterase pesticides: a retrospective summary of National Wildlife Health Center records from 1980 to 2000. *Arch. Environ. Contam. Toxicol.* 46, 542–550. (doi:10.1007/s00244-003-3065-y)

Fry, D. M. 1995 Reproductive effects in birds exposed to pesticides and industrial chemicals. *Environ. Health Persp.* 103, 165–171.

Graveland, J. & Drent, R. H. 1997 Calcium availability limits breeding success of passerines on poor soils. *J. Anim. Ecol.* 66, 279–288.

Greenwood, P. J. & Harvey, P. H. 1982 The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* 13, 1–21. (doi:10.1146/annurev.es.13.110182.000245)

Keith, J. O. & Bruggers, R. L. 1998 Review of hazards to raptors from pest control in Sahelian Africa. *J. Raptor Res.* 32, 151–158.

Kiikkilä, O. 2003 Heavy-metal pollution and remediation of forest soil around the Harjavalta Cu–Ni smelter, in SW Finland. *Silva Fenn.* 37, 399–415.

Silverin, B. 1990 Testosterone and corticosterone and their relation to territorial and parental behavior in the pied flycatcher. In *Hormones, brain and behaviour in vertebrates. 2. Behavioural activation in males and females—social interaction and reproductive endocrinology* (ed. J. Balthazart), pp. 129–142. Basel, Switzerland: Karger.

Silverin, B. 1998 Territorial behaviour and hormones of pied flycatchers in optimal and suboptimal habitats. *Anim. Behav.* 56, 811–818. (doi:10.1006/anbe.1998.0823)

White, G. C. & Burnham, K. P. 1999 Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, 120–138.