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Heavy metal pollution affects dawn singing behaviour in a small passerine bird

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Abstract Although several studies have suggested that behavioural measures may be more comprehensive than other biomarkers for indicating an organism's health or welfare, this has rarely been investigated in free-living terrestrial vertebrates. Here we examine the expression of dawn singing behaviour in a free-living small songbird in relation to environmental pollution. We compared the singing behaviour of male great tits *Parus major* inhabiting an area extremely polluted with heavy metals with that of males inhabiting areas of low(er) pollution (at 4 and 20 km distance from the pollution source). Males at the most polluted site had a significantly smaller repertoire size than males at the two other sites. They also produced a significantly lower total amount of song during the dawn chorus than the males at a distance of 4 km from the pollution source. Our results, although non-experimental and obtained in field conditions, strongly suggest that heavy metal pollution might affect the expression of singing behaviour. Taking into account that previous studies were not able to detect clear, straightforward differences between the health of great tits at the most polluted site and at 4 km distance from the pollution source, our results suggest that the singing behaviour of great tits may be a useful indicator of environmental stress at the population level.

Keywords Biomarker · Contaminant exposure · Developmental stress · Repertoire size · Singing behaviour

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Introduction

Human-altered environments might change the communication signals of wild birds as shown by Slabbekoorn and Peet (2003), who recently reported that birds sing at higher pitch in urban noise. Apart from noise pollution, other sources have been releasing pollutants into the environment because of technological progress and industrialisation. These pollutants can alter life history phenotypes of organisms indirectly by altering their operative environments (e.g. resource availability, availability of mates, predation risk) and/or directly by altering the development or physiology of the organism itself (Congdon et al. 2001). In early life, developmental stress can have a deleterious effect on neural development which may affect behaviour, life history strategies and/or the development of secondary sexual signals (Nowicki et al. 1998; Buchanan 2000). During adult life, the additional costs from continued interactions with toxins may result in reallocation of energy expenditures so that resource allocation strategies become modified, reflecting changes in energy assimilation and energy demands (Buchanan et al. 1999; Congdon et al. 2001).

Birdsong is one of the best-studied topics in animal communication and its expression depends on learning as well as on genetic and other environmental factors (see Buchanan et al. 2004). Recently, evidence has come to light that showed that a secondary sexual signal like song is linked to physiological stress. Food deprivation has been shown to influence European starlings' *Sturnus vulgaris* song output: fledglings with ad libitum food supply sang more and longer song bouts when fully grown than fledglings with limited food supply (Buchanan et al. 2003). Food deprivation early in life has also been shown to have a detrimental effect on nestling growth rate, song complexity and song motif duration in adulthood in zebra finches *Taeniopygia guttata* (Spencer et al. 2003). In the sedge warbler *Acrocephalus schoenobaenus*, parasitized males had significantly smaller repertoire sizes than non-parasitized males (Buchanan et al. 1999) and injecting collared flycatchers *Ficedula albicollis* with sheep red blood cells (challenge of the immune system) resulted in a decrease in song rate (Garamszegi et al. 2004). These findings are consistent with the developmental stress hypothesis (Nowicki et al. 1998, 2002a), which proposed that learned features of song can serve as reliable indicators of male quality because the brain structures underlying song learning and production develop early in life when young birds are likely to experience developmental stress. So according to this hypothesis, singing males express variation in the magnitude of stress they experienced during development and how well they responded to this stress with respect to brain development. Therefore, song may provide reliable information about male quality for female mate choice or for male–male competition (Searcy and Andersson 1986; Catchpole and Slater 1995; Nowicki et al. 1998, 2002a; Ten Cate et al. 2002). However, an important factor often overlooked in regard to physiological stress is the role of environmental pollution and its effect on behavioural strategies (see Wingfield 2003) or on the expression of secondary sexual signals. For example, Eeva et al. (1998) showed that air pollution faded the plumage of great tits *Parus major*, which may have important implications for survival and mate choice. In this study, we investigated another secondary sexual signal in great tits in relation to environmental pollution.

We compared the singing behaviour of male great tits inhabiting an area seriously polluted with heavy metals with that of males inhabiting areas of low pollution (Fig. 1). Heavy metals are frequent waste products of industrial and agricultural processes (Depledge et al. 1993). They enter the food chain via air, water, soil and biota and their accumulation increases at higher levels of the food chain (Burger 1993). Heavy metals can have harmful effects on development, behaviour and intelligence both in animals and humans (Finkelstein et al. 1998). For instance, substantial literature reports show effects ranging from subtle behavioural and biochemical changes to memory and learning deficits in children and primates as a consequence of lead exposure (Finkelstein et al. 1998). Most of these studies were carried out in laboratory conditions and results are often difficult to extrapolate to free-living organisms. In this study, we show that the amount of song produced and the song complexity (quantified as repertoire size) of wild birds inhabiting a heavily polluted area are significantly lower than in birds inhabiting areas of low pollution, suggesting that pollution might negatively affect the singing behaviour.

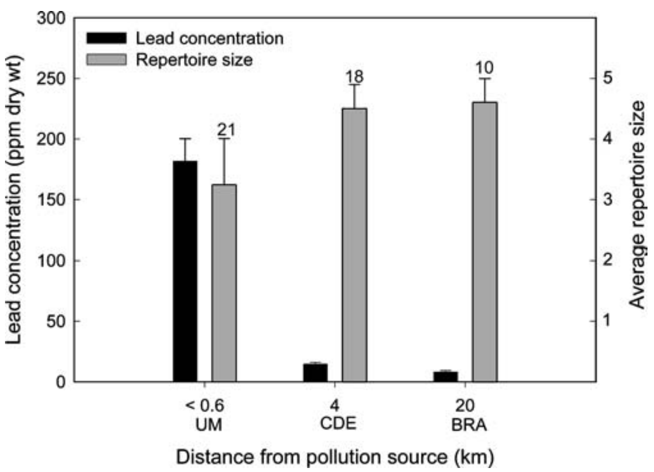

Fig. 1 Average repertoire size of male great tits in relation to distance from pollution source combined with the lead concentrations (ppm dry weight) in the feathers of great tits found in an earlier study from Janssens et al. (2001) ±SE. Repertoire size for BRA was taken from a study from Lambrechts and Dhondt (1987). *Numbers* refer to the number of individuals recorded

Materials and methods

Study species and study sites

Great tits are common monogamous territorial passerines which breed in secondary holes and artificial nest boxes in all types of wooded areas throughout Europe and parts of Asia and North Africa (Cramp and Perrins 1993). Before and during egg laying, male great tits sing vigorously in the vicinity of their female's nest hole at dawn. A peak of song (dawn chorus) occurs between the waking time of the male and the emergence of the female from the roosting hole (Mace 1987; Cramp and Perrins 1993). In great tits, male quality is reflected in song: a number of studies showed strong correlations between repertoire size and strophe length and various aspects of male fitness and female preferences (McGregor et al. 1981; Lambrechts and Dhondt 1986, 1987; Baker et al. 1986). In addition, the amount of song produced during a dawn chorus has been shown to be related to male quality in other tit species as well (Kempenaers et al. 1997; Otter et al. 1997).

Study sites are situated in Flanders (Belgium), one of the most industrialised and populated regions of the world. The heavily polluted site (UM) is situated in the immediate vicinity of a large metallurgic smelter (0–600 m), which is the most extensively heavy metal air-emitting point source in Flanders (Verbruggen 1994). A less polluted site (CDE; former UIA) is situated 4 km eastwards from the pollution source. Results of both study sites were compared to earlier findings from another site in Flanders (BRA), 20 km northeast from the smelter with very limited pollution (Lambrechts and Dhondt 1987; Janssens et al. 2001; Fig. 1). Lead, copper, cadmium, arsenic and zinc are common pollutants in UM and several studies have shown that lead and cadmium concentrations in the feathers and eggs of tits that reside in the vicinity of the smelter are among the highest reported in literature (Dauwe et al. 2000; Janssens et al. 2001, 2002). In UM for example, lead and arsenic concentrations in great tit feathers are 16 and 26 times higher in adults and 10 and 29 times higher in nestlings compared to concentrations in CDE (Janssens et al. 2001; Janssens et al. 2002). These metal concentrations are strikingly higher than those reported to cause negative effects on the health and reproduction of birds (Burger 1993).

Recordings

Dawn choruses of free-living male great tits were recorded during their female's egg-laying stage in UM ($n = 21$) and CDE ($n = 18$) between March 31 and April 26 in 2001. Each male was recorded only once and 15 males in UM and CDE were recorded on the same date. These sites represent a similar habitat type (deciduous park areas; see Dauwe et al. 2004) and have been provided with nest boxes since 1996 (CDE) and 1997 (UM). Nest boxes were checked every 2 days to quantify breeding status. The recordings were made before and during sunrise (between 05.00 h and 08.00 h) and a dawn chorus was considered to be complete when all vocalizations were recorded between the male's waking time and the female's emergence from the nest box. Although until now, it has not been tested unambiguously whether male great tits sing their entire repertoire during one dawn chorus, Snoeijs (2004) showed that the repeatability of repertoire size is highly significant in males that have been recorded twice within the same fertile period of the female or that have been recorded in separate years (see also Van Duyse 2004). Recordings were made using a Sennheiser ME 67 shotgun microphone connected to a portable SONY MZ-R700 Minidisc Recorder. All recordings were digitised and spectograms analysed using the AVISOFT Saslab pro software (20 kHz sampling rate; antialiasing filter; Hamming window type) and a ESS AudioDrive Record (1000) 4.7 soundcard (16 bit). We determined three different song characteristics: repertoire size (number of different song types), amount of song (sum of all strophe lengths in seconds) and mean strophe length (of all song types in the repertoire in seconds; Fig. 2). Males were individually marked with colour rings and aged (first-year vs. older birds, see Svensson 1984). We were not able to catch and age two males in UM, which accounts for the differences in sample size. The proportion first-year birds in UM (5 out of 19) and CDE (6 out of 18) did not differ (Fisher Exact Test, $P > 0.7$). For BRA, repertoire size was taken from a study of Lambrechts and Dhondt (1987), who quantified repertoire size from spontaneous song recordings made from March to May in 1983 of 10 different males. All males reached an

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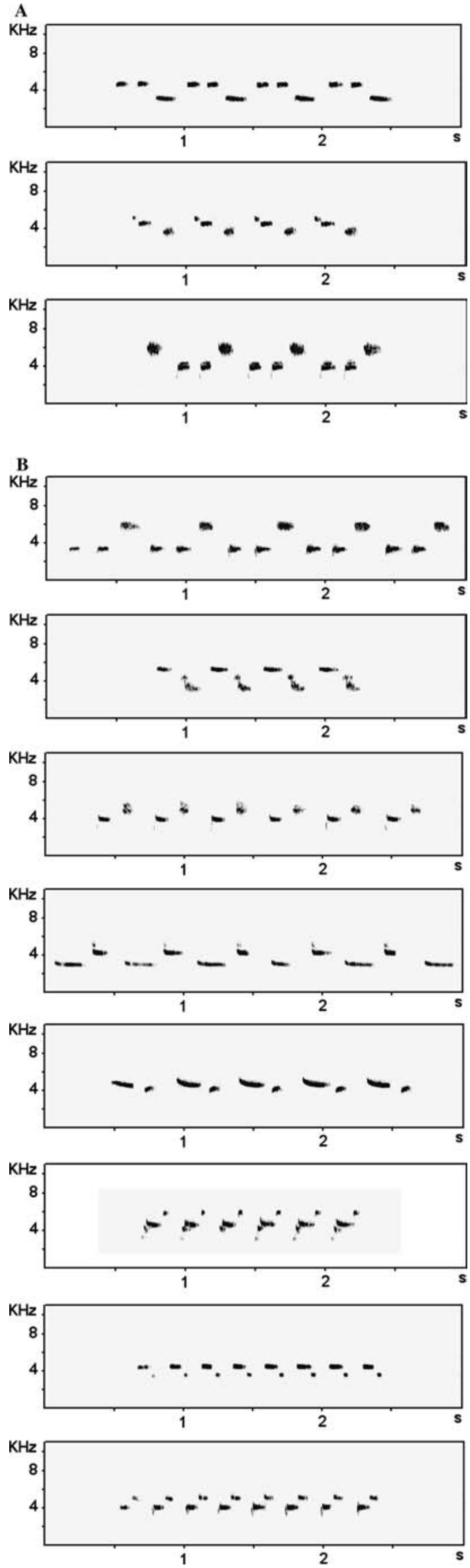

Fig. 2 Sonograms of the song types sung during the dawn chorus of a male great tit recorded in UM with a repertoire size of 3 (**A**) and of a male recorded in CDE with a repertoire size of 8 (**B**). Great tits usually sing several strophes of the same song type before switching to another song type. Both dawn choruses have been recorded during the egg-laying period of the female in comparable weather conditions

asymptote when the cumulative number of song types was plotted against recording time, suggesting that the observed repertoire size in this study was a good measure of actual repertoire size.

Statistical analysis

Statistical analyses were performed using Statistica (Statsoft Inc. 1994) and SAS (SAS Institute 1999–2000) statistical software. To approximate normal distribution, repertoire size and the amount of song have been log-transformed. Song characteristics were tested for mean differences among age classes and study sites using a two-way analysis of variance (ANOVA). Age was included in the model since survival has been suggested to be correlated to repertoire size and strophe length (Lambrechts and Dhondt 1986). The interaction between age class and study site was also investigated. Interactions and non-significant effects were excluded from the model using a backward deletion procedure. A sequential Bonferroni correction was applied to control for multiple comparisons (P_a; Rice 1989). Numbers given are means ± SE.

Results

All two-way interactions were not significant and thus, excluded from the model. Study site was the most important main factor influencing the amount of song produced during the dawn chorus and repertoire size of great tits. Great tits inhabiting the heavily polluted site (UM) sang significantly less than those in CDE (491.59 ± 50.04 s in UM, 738.91 ± 82.83 s in CDE; $F_{2,35}$ = 3118.24, $P_a < 0.001$). Repertoire size at the heavily polluted site (UM) was also significantly lower than at CDE (3.24 ± 0.19 in UM, 4.5 ± 0.40 in CDE; $F_{1,34}$ = 8.64, $P_a < 0.02$; Fig. 1). In UM, repertoire size ranged from 2 to 4 song types, while repertoire size in CDE ranged from 2 to 8 song types. Time spent singing was no confounding variable since it was not correlated with repertoire size in UM and CDE (r = 0.17, $P > 0.1$ and r = 0.42, $P > 0.05$, respectively). Repertoire size was also age-dependent, with older birds having a significantly higher repertoire size than first-year birds (3.27 ± 0.36 in first-year birds, 4.11 ± 0.28 in older birds; $F_{1,34}$ = 5.53, $P_a < 0.05$). Older birds also sang significantly longer strophes than first-year birds (2.10 ± 0.13 s in first-year birds, 2.54 ± 0.10 s in older birds, $F_{2,35}$ = 482.08, $P_a < 0.001$) but strophe length did not differ between UM and CDE (2.39 ± 0.12 s in UM, 2.45 ± 0.11 s in CDE, $F_{1,34}$ = 0.81, $P > 0.1$). Average repertoire size at BRA equalled 4.60 ± 0.13, which was significantly higher than repertoire size in UM (ANOVA, Tukey Kramer Multiple Comparisons test: q = 4.19, $P < 0.05$), while repertoire size in CDE and BRA did not differ significantly (ANOVA, Tukey Kramer Multiple Comparisons test: q = 0.27, $P > 0.05$).

Discussion

Study site and age were important main effects influencing the great tit song characteristics under study except strophe length. Male great tits inhabiting the heavily polluted site sang significantly less (almost 35%) and had a significantly lower repertoire size (almost 30%) than males only 4 km away from the smelter. Repertoire size at 4 and 20 km distance from the pollution source did not differ significantly. Although we cannot exclude that other factors or other pollutants can also be part of the cause of this lower repertoire size and smaller amount of song at the heavily polluted site, our results indicate that exposure to heavy metals might have an impact on the singing behaviour of songbirds. A large scale study in many populations exposed to different levels of heavy metal pollution is now required to fully support this hypothesis and experiments are needed to investigate whether pollution acts directly through interference of song development or indirectly by changing the avian operative environment. The age dependence of repertoire size and strophe length supports the findings from Lambrechts and Dhondt (1986) that these characteristics reflect male quality in great tits. Older males had higher repertoire sizes and longer strophes than first-year males, which is in accordance with earlier findings that males with larger repertoires and longer strophes survive better since strophe length and repertoire size do not change with age (e.g. McGregor et al. 1981; Lambrechts and Dhondt 1986). Hence, repertoire size and strophe length are reliable indicators of male quality. At present, it is unclear why repertoire size and amount of song are significantly different at the polluted site while strophe length is not. A possible explanation may be that the neural government of repertoire size and strophe length may involve different mechanisms that may require independent brain space (Garamszegi and Eens 2004).

Singing behaviour, operative environment and development and physiology of great tits

Song output can be regarded as a reflection of the male's present condition because singing incurs costs in time and energy regardless of what is sung (see also Otter et al. 1997; Gil and Gahr 2002). The smaller amount of song produced during the dawn chorus in UM might be an indirect result of lower food quality or quantity, reflecting a change in the operative environment of great tits, as was shown in European starlings and zebra finches (Buchanan et al. 2003; Spencer et al. 2003). Clear evidence of a link between food and metal-intake comes from a recent study of Dauwe et al. (2004) that reported significant higher metal concentrations in caterpillars (the main food source for great tit nestlings) collected at the site closest to the smelter compared to the site at 4 km distance in the same pollution gradient as ours.

These authors also provided clear significant positive correlations of lead and arsenic concentrations in caterpillars, great tit nestling excreta and great tit nestling feathers. Investigations of body condition and tarsus length in nestlings and adults and immune responsiveness and haematocrit levels in adult great tits however, did not show an apparent difference between UM and CDE (Janssens et al. 2003; Janssens 2003; Snoeijs et al. 2004). Together with our finding that strophe length did not differ between both sites, this suggests that assortative settlement, i.e. that only low quality great tits establish a territory near the pollution source, is not very probable. Otherwise, environmental pollution might influence song production imposing constraints on the available time and energy budget that can be used for vocal activity. For instance, at the heavily polluted site, more time may be required to forage in order to maintain body condition thereby decreasing the time available for singing and/or song learning.

A male's ability to invest in brain tissue has been suggested to be an important physiological mechanism that links repertoire size to male quality (Garamszegi and Eens 2004; Podos et al. 2004). Since repertoire size is a reflection of song development (Catchpole 1996; Nowicki et al. 1998, 2002a, 2002b), the lower repertoire size at the polluted site might reflect a direct neurotoxic effect of particular heavy metals which may interfere with song system development or song learning. Brain tissue is costly to produce and maintain, so it is likely that only high quality males can meet the neurological demands required for a large song repertoire (see Garamszegi and Eens 2004; Podos et al. 2004). Since these costs are likely to be highest during development, exposure to a heavy metal such as lead, can cause severe learning and memory deficits (Finkelstein et al. 1998) because lead poisoning exerts its most severe consequences during development due to the intense cellular proliferation, differentiation and synaptogenesis in the developing brain (Burdette and Goldstein 1986). Since lead and arsenic concentrations in food, nestling excreta and nestling feathers are significantly correlated (Dauwe et al. 2004) and these metal concentrations are significantly site-dependent, our findings strongly suggest that residing in a heavily polluted site apparently bears no consequence on great tit health (see above-mentioned studies) but is mainly reflected through a cognitive behavioural trait such as birdsong. To our knowledge, our results show for the first time that pollution might impose a heavy strain on song output in a free-living passerine. This should be taken into account when studying birdsong.

Conclusion

So far, metals have only been considered as a contributing factor influencing avian survival and reproduction (Eeva and Lehikoinen 2000; Larison et al. 2000). However, if birdsong provides reliable information about male quality for female mate choice as suggested by Nowicki et al. (2002a, 2002b), heavy metal pollution might influence sexual selection, for example, by altering breeding behaviour (e.g. female preferences, extra pair copulations). This might have important implications when studying secondary sexual signals (like song for instance) in urban regions because of the mosaic-like pattern of metal pollution, a factor often overlooked when investigating sexual selection or the function or evolution of secondary sexual signals.

Behaviour is suggested to be a more useful indicator or biomarker than standard assays in laboratory conditions because the harmful effects of pollutants sometimes become only noticeable in natural ecological conditions, such as social stress or infections (see review of Zala and Penn 2004). These authors also pointed out that behaviour is the outcome or endpoint of many compound developmental and physiological processes, so it should provide a more inclusive measure than one or a few chemical, physical or morphological parameters. Hence, our results support the conclusion of Zala and Penn (2004) that behaviour might provide a useful indicator for detecting harmful chemical pollutants and that at this point, more integration between behavioural ecology and toxicology is badly needed to determine how pollutants affect all living organisms outside the laboratory. As shown here, pollution might have the potential to influence songbirds' singing behaviour in the wild by diminishing the amount of song produced as well as the complexity of song. So, it seems that the prophecy of Silent Spring (Carson 1962) becomes more actual than ever.

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