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Variation in personality traits across a metal pollution gradient in a free-living songbird

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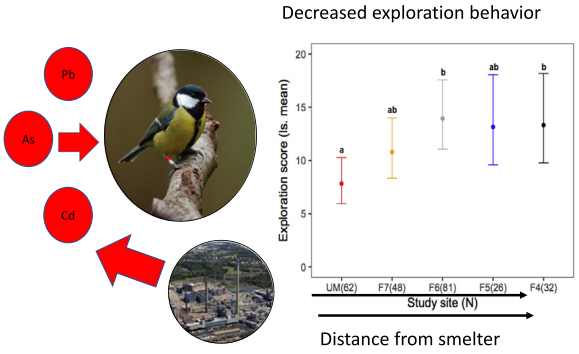
HIGHLIGHTS

- Exposure to contaminants may affect animal personality traits.
- Exploration, aggression and nest defense were measured across a metal pollution gradient.
- Exploration was slower at the most polluted site, perhaps reflecting neurological effects.
- Territorial aggression and nest defense were unrelated to proximity to the pollution source.
- Slower exploration behavior in metal exposed individuals could negatively affect fitness.

GRAPHICAL ABSTRACT



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ABSTRACT

Anthropogenic contaminants could alter traits central to animal behavioral types, or personalities, including aggressiveness, boldness and activity level. Lead and other toxic metals are persistent inorganic pollutants that affect organisms worldwide. Metal exposure can alter behavior by affecting neurology, endocrinology, and health. However, the direction and magnitude of the behavioral effects of metal exposure remain equivocal. Moreover, the degree to which metal exposure simultaneously affects suites of correlated behavioral traits (behavioral syndromes) that are controlled by common mechanisms remains unclear, with most studies focusing on single behaviors. Using a model species for personality variation, the great tit (*Parus major*), we explored differences in multiple behavioral traits across a pollution gradient where levels of metals, especially lead and cadmium, are elevated close to a smelter. We employed the novel environment exploration test, a proxy for variation in personality type, and also measured territorial aggressiveness and nest defense behavior. At polluted sites birds of both sexes displayed slower exploration behavior, which could reflect impaired neurological or physiological function. Territorial aggression and nest defense behavior were individually consistent, but did not vary with proximity to the smelter, suggesting that metal exposure does not concurrently affect exploration and aggression. Rather, exploration behavior appears more sensitive to metal pollution. Effects of metal pollution on exploration behavior, a key animal personality trait, could have critical effects on fitness.

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1. Introduction

Organisms are exposed to an array of anthropogenic contaminants, which can have cascading effects on physiological and neurological systems, individual fitness and population viability (Burger and Gochfeld, 2000; Carere et al., 2010a; Peterson et al., 2017). Metal pollution is a worldwide biological problem, which continues to have lethal and sublethal effects on organisms, despite increasing government regulations. Lead and other toxic metals are persistent inorganic pollutants, which can remain in the environment and affect organisms long after remedial policies have been adopted to reduce emissions (Ercal et al., 2001; Tchounwou et al., 2012; Vermeulen et al., 2015).

A shortage of studies exists regarding the sublethal behavioral ramifications of exposure to pollutants, including toxic metals, despite growing evidence that the neurotoxic and health effects of contaminants can have behavioral implications (Peakall, 1996; Burger and Gochfeld, 2000; Dell'Omo, 2002; Brodin et al., 2013; Kobiela et al., 2015; Ecke et al., 2017; Peterson et al., 2017). Studies predominantly focused on humans and laboratory animals indicate that exposure to metals, particularly lead, can impair learning, memory and performance in cognitive tasks (Koller et al., 2004; Liu et al., 2014; Engstrom et al., 2017). In addition, there is some evidence that exposure to contaminants (Brodin et al., 2013), including metals (Janssens et al., 2003a; White and Briffa, 2017), can affect behavioral traits central to animal behavioral types, or personalities. Animal personalities are defined by consistent inter-individual variation in behavioral traits such as aggressiveness, risk-taking and activity levels, and can have important effects on fitness (Dall et al., 2004; Dingemanse et al., 2004; Smith and Blumstein, 2008). Rather than being one-dimensional, personalities can consist of suites of correlated traits, referred to as behavioral syndromes (Sih et al., 2004). For instance, consistently more aggressive individuals are often also less risk-adverse and have higher activity levels. This co-occurring suite of traits is characterized by bold-shy and aggressive-passive behavioral continuums, with the bold-aggressive personality type potentially associated with a life-history strategy that favors early reproduction over survivorship (Wolf et al., 2007; Dingemanse and Wolf, 2010). Behavioral traits associated with personalities often have a heritable, genetic component (Drent et al., 2003; van Oers et al., 2004), but can also be affected by permanent environment effects (Quinn et al., 2009; Nicolaus et al., 2012) and state-dependent behavioral dynamics (Dall et al., 2004; Sih et al., 2015), which may be altered by exposure to contaminants (Montiglio and Royauté, 2014).

Past studies have yielded conflicting results regarding how metal exposure affects behavioral traits along the continuums described above. For instance, humans (Nevin, 2000) and golden hamsters (*Mesocricetus auratus*) (Deville, 1999) exposed to lead during development show increases in aggressiveness, and some studies in humans also report that metal (cadmium, lead) exposure increases testosterone, which could elevate aggressiveness and boldness (Zeng et al., 2002; Meeker et al., 2010). In contrast, aggressive behavior is reduced in two species of crabs exposed to copper (Dissanayake et al., 2009; White et al., 2013), and zebra finches (*Taeniopygia guttata*) exposed to mercury become more risk-adverse (Kobiela et al., 2015), perhaps reflecting neurotoxic effects on fearfulness. In a variety of species, activity level also declines with metal exposure, perhaps reflecting poor health (Cheung et al., 2002; Ecke et al., 2017). Toxic metal exposure can reduce survivorship (Alissa and Ferns, 2011; Hallinger et al., 2011), and increases in aggressiveness and boldness with metal exposure could thus represent a shift in life-history strategy to promote early reproduction (Bélanger-Deschênes et al., 2013; Sih et al., 2015). However, either increases or decreases in the expression of behavioral traits could also reflect neurological and physiological changes that impair normal behavioral regulation.

If suites of behaviors are controlled by common mechanisms, these traits could be simultaneously affected by metal exposure, potentially magnifying behavioral syndromes in exposed populations (Brodin et al., 2013). On the other hand, if certain behavioral traits are more sensitive to metal exposure than others, exposure could disrupt behavioral syndromes relative to non-exposed populations (Swaddle et al., 2017). However, most studies focus on single behavioral traits, often within a single sex (e.g. aggression in males, Janssens et al., 2003a; White et al., 2013), leaving these hypotheses largely unexplored.

We used a model species for the study of personality types, the great tit (*Parus major*), to investigate behavioral ramifications of metal exposure. Great tits exhibit distinct personality types, with birds that rapidly explore a novel environment (fast explorers) also displaying boldness in the presence of novel objects (van Oers et al., 2004), high levels of aggressiveness (Verbeek et al., 1996; Carere et al., 2005; Thys et al., 2017), and low glucocorticoid stress responses (Carere et al., 2003; Baugh et al., 2017). Thus, fast explorers generally display a bold-aggressive personality type, whereas slow explorers are shy and non-aggressive. A few recent studies in great tits have linked urbanization to personality type, and specifically suggest that urbanization is associated with increased boldness and fast exploration behavior (Charmantier et al., 2017; Riyahi et al., 2017; Sprau and Dingemanse, 2017). However, despite growing interest in the effects of urbanization on personality type, very few studies have examined how personality traits vary along known pollution gradients. Those studies that have pursued such examinations suffer from methodological limitations, including small sample sizes and a focus on single behavioral traits (e.g. Janssens et al., 2003a), whereas animal personalities are multidimensional and potentially characterized by a diverse array of interrelated traits (Koski, 2014).

We explored whether metal exposure concurrently affects multiple animal personality traits and the correlations between these traits in great tits of both sexes, using five great tit populations located across a well-characterized metal pollution gradient, which emanates from the Umicore smelter and refinery facility, located south of Antwerp, Belgium (Fig. 1). Past research has established that pollution from the Umicore facility causes metal exposure in great tits (Janssens et al., 2001; Van Parys et al., 2008; Vermeulen et al., 2015), with lead and cadmium levels in kidneys being respectively >150 and 5 times higher close to the smelter than farther away (Van Parys et al., 2008). Exposure in liver tissue is similarly highly elevated close to the smelter (Van Parys et al., 2008). A previous study comparing aggressive behavior between the most and least polluted study sites tentatively suggested higher aggressiveness in birds breeding close to the Umicore smelter (Janssens et al., 2003a), but relied on much smaller sample sizes than the current study. To characterize personality traits across the pollution gradient, we measured novel environment exploration and territorial aggression. Moreover, we also measured female aggressiveness during nest defense as an important aspect of parental investment (Barash, 1975; Montgomerie and Weatherhead, 1988). To establish individual consistency in behavior and the existence of personality types, we tested the repeatability of territorial aggression and nest defense behaviors. We did not measure the repeatability of exploration behavior at sites across the pollution gradient because of logistical constraints, but exploration behavior is repeatable at our intensively monitored and centrally located study population (Thys et al., 2017), and in other European study populations of great tits (Dingemanse et al., 2012; Stuber et al., 2013). Based on past work along the pollution gradient (Janssens et al., 2003a), we predicted that aggression might increase with proximity to the pollution source and that exploration behavior might increase in parallel. Our study informs how behavioral changes could affect population integrity in metal polluted areas, while also providing insights to behavioral researchers seeking to understand the mechanisms underlying individual variation in behavior.

2. Methods

2.1. Study system

We conducted our study in 2017, using five populations of great tits located along the metal pollution gradient produced by the Umicore