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Signs of adaptation to trace metal contamination in a common urban bird

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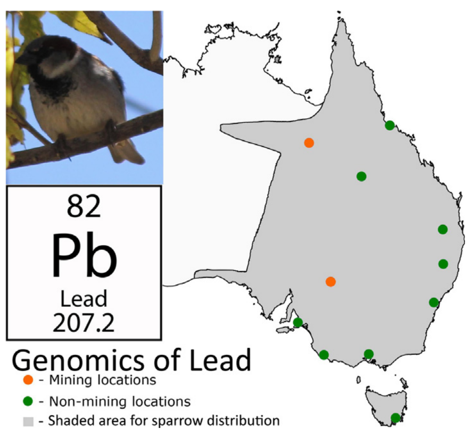
HIGHLIGHTS

- Trace metal contamination can have negative impacts and we lack evidence to show if species can adapt to these stressors.
- Using Genomic data and estimates of lead contamination we find that selection could be helping this invasive species adapt.
- Several of our candidate genes have links to lead and show changes in their expression levels with exposure to lead.

GRAPHICAL ABSTRACT



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ABSTRACT

Metals and metalloids at elevated concentrations can be toxic to both humans and wildlife. In particular, lead exposure can act as a stressor to wildlife and cause negative effects on fitness. Any ability to adapt to stress caused by the negative effects of trace metal exposure would be beneficial for species living in contaminated environments. However, mechanisms for responding adaptively to metal contamination are not fully understood in free-living organisms. The Australian populations of the house sparrow (*Passer domesticus*) provides an excellent opportunity to study potential adaptation to environmental lead contamination because they have a commensal relationship with humans and are distributed broadly across Australian settlements including many long-term mining and smelting communities. To examine the potential for an evolutionary response to long-term lead exposure, we collected genomic SNP data using the house sparrow 200 K SNP array, from 11 localities across the Australian distribution including two mining sites (Broken Hill and Mount Isa, which are two genetically independent populations) that have well-established elevated levels of lead contamination as well as trace metals and metalloids. We contrast these known contaminated locations to other lesser-contaminated environments. Using an ecological association genome scan method to identify genomic differentiation associated with estimates of lead contamination we identified 60 outlier loci across three tests. A total of 39 genes were found to be physically linked (within 20 kbps) of all outliers in the house sparrow reference genome. The linked candidate genes included 12 genes relevant to lead exposure, such as two metal transporters that can transport metals

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including lead and zinc across cell membranes. These candidate genes provide targets for follow up experiments comparing resilience to lead exposure between populations exposed to varied levels of lead contamination.

1. Introduction

Environmental contaminants such as lead and other trace metals pose of significant risk of harm for humans and wildlife when found in high concentrations (Peterson et al., 2017; Ray et al., 2014). The effects of exposure to trace metal contaminants on health has led to a large body of research aimed towards understanding how humans and other species respond to exposures from their environment (Lanphear, 2015; Lanphear et al., 2005; Lattin et al., 2014; Li et al., 2017; Pierron et al., 2011; Varian-Ramos et al., 2014). These contaminants are not always lethal and can have subtle negative effects on health. For example, the accumulation of metals inside individuals living in contaminated environments is known to be a stressor for animals (Lattin et al., 2014; Romero and Wikelski, 2001; Wikelski et al., 2002). Environmental stressors can cause physiological responses that have negative effects on fitness and reproduction (Cyr and Romero, 2007; Romero, 2004). The adverse effects of metal-related stress on fitness has been shown to be a threatening process due to the loss of fitness causing population decline (Wikelski and Cooke, 2006). Beneficial physiological responses to stressors can also alleviate the negative effects of stress. In response to the negative effects of stress on fitness there should be positive selection for adaptations that reduce the impact of exposure in contaminated environments. A recent example of such selection was found in killifish (*Fundulus heteroclitus*) in response to pollution, using whole genome resequencing and transcriptomics they found convergent selection on the aryl hydrocarbon receptor–based signalling pathways (Reid et al., 2016). However, examples of this kind are limited and studying adaptation in urban environments is a growing field of research (Johnson and Munshi-South, 2017).

One of the most studied metal contaminants is lead (Pb) because of its toxicity and its known adverse impacts on human health (Lanphear, 2015; National Toxicology Program, 2012). Environmental lead in aerosols, dusts and soils, among other things, are elevated in most global urban city environments due to the former massive emissions of lead from industrial sources with a majority coming from leaded petrol combustion (Kristensen, 2015; Kristensen et al., 2017; Laidlaw et al., 2017; Mielke et al., 2011; Olszowy et al., 1995; Rouillon et al., 2017). These industrial emissions and depositions remain present and bioavailable in the environment (Laidlaw et al., 2017; Mackay et al., 2013) and consequently present a risk of harm to a range of organisms living in urban environments. In Australia, there are a number of locations that have a protracted history of environmental lead emission from lead mining and smelting practices, as well as other trace metals such as cadmium and zinc (Dong et al., 2015; Kristensen and Taylor, 2016; Mackay et al., 2013; Taylor et al., 2010; Taylor et al., 2014b). Environmental exposures in lead producing communities as well as those impacted by former leaded petrol depositions are typically via the ingestion of soils and dusts (Gulson et al., 2014). Unlike dust, soil metal concentrations have national guidelines values promulgated under the NEPM (2013). The most relevant soil lead value is the health investigation level guideline of 300 mg/kg NEPM (2013), which is applied to residential dwellings and to ensure blood lead levels remain below 7.5 μg/dL. However, it is well-accepted that there is no safe lower threshold for blood lead exposure (Lanphear et al., 2005) and that blood leads as at 2 μg/dL or lower are considered harmful to human health (National Toxicology Program, 2012). Therefore, we use the lowest acceptable upper limit of 300 mg/kg for soil lead provided in the NEPM (2013) as a benchmark for assessing the level of contamination seen at our study sites.

Describing how species adapt to trace metal contamination should be a priority for understanding and managing urban ecosystems. The house sparrow's (*Passer domesticus*) introduction to Australia provides a good opportunity for studying adaptation to contaminated urban environments in a common species due to its broad distribution with recently established and isolated populations including lead-contaminated sites. The house sparrow is an obligate commensal species with humans and are typically constrained to urban and rural environments (Anderson, 2006). Sparrows also have sedentary populations with moderate genetic population structure and relatively low gene flow (Jensen et al., 2013; Kekkonen et al., 2011), and this is also true for populations living in broadly spaced human settlements across Australia (Andrew et al., 2017). The invasion of the house sparrow to different mining communities provides an opportunity to observe genetic adaptation to lead contamination through genetic differentiation that is associated with levels of lead contamination. Any selection that has have taken place would have happened over a relative short time frame. For example, sparrows have been present in the mining communities of Broken Hill (New South Wales) and Mount Isa (Queensland) for approximately 100 and 50 years respectively (Andrew and Griffith, 2016). Long term mining practices, and relatively high levels of contamination have potentially allowed for selection to take place over dozens of generations (50 and 25 in the two locations respectively, assuming a generation time of approx. two years [Jensen et al., 2013]) to ameliorate the deleterious effects of lead and/or trace metal contamination on fitness. Through previous descriptions of genetic population structure we know these two locations have independent populations (Andrew et al., 2017), and to an extent they are genetically independent replicates in which selection can occur in parallel.

There are many potential physiological mechanisms sparrows could employ to adaptively respond to lead contamination in their environment. Lead (Pb) is not essential to life and is a non-biodegradable element, meaning there are no efficient pathways for it to be metabolized and eliminated, thus it tends to accumulate in the different organs and tissues of individuals exposed to lead (Peakall and Burger, 2003). The first line of defence for species would be through reducing the unintentional uptake of lead into the body through external surfaces like the respiratory system (Ribeiro et al., 2014), the alimentary canal (Madigosky et al., 1991), or the inner ear (Ding et al., 2014). Another suggested trait involved in adapting to lead contamination is increased exclusion through the accumulation of lead in the kidneys and other tissues to reduce the amount lead bioavailable in the body (Ribeiro et al., 2014). Lead is also known to be a stressor to the endoplasmic reticulum of cells, affecting protein production, however this effect can also be countered through different molecular pathways that remove misfolded proteins (Qian and Tiffany-Castiglioni, 2003; Shinkai et al., 2010). Alternatively, sparrows could also respond to lead by trying to avoid contamination through behavioural modifications that reduce exposure.

We have collected genomic data from 11 house sparrow populations across Australia including the mining locations of Broken Hill and Mount Isa, using a 200 K SNP array (Lundregan et al., 2018). This is an observational study, in which we aim to explore genetic differentiation across loci that is related to geographical variation in lead contamination. We are particularly interested in the contrast between the heavily contaminated locations of Broken Hill and Mount Isa, and the other nine populations. We predict that some of the loci that are significantly associated with lead contamination in our analyses will be physically linked