



Risk-taking behaviours in zebra finches affected by mercury exposure



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The trade-off between starvation and predation risk is of paramount importance to songbirds and many other small organisms. A contaminant with metabolic or neurological effects may hinder a bird's ability to manage these ecological risks, which are contingent on metabolic state and require cognitive assessments. Methylmercury (MeHg) is a ubiquitous pollutant that is associated with neurotoxicity, reproductive failure, altered behaviour and increased mortality in aquatic organisms. It was recently discovered that MeHg can enter terrestrial food webs and affect songbirds that eat contaminated invertebrates. Research on behavioural effects of environmentally relevant doses of MeHg in songbirds is a conservation priority as this pollutant is widespread, poorly regulated, increasing and understudied in terms of sublethal effects such as abnormal behaviours. To help close this knowledge gap, we examined how MeHg affects behavioural strategies in captive zebra finches, *Taeniopygia guttata*. We quantified the birds' responses to risk by measuring regulation of body mass, vigilance behaviour, willingness to move away from dense cover in search of food and reluctance to return to foraging after a disturbance. Dosed and undosed birds were placed in an experimental arena and were videorecorded over 3 days of increasing perception of predation risk. We found that MeHg-exposed birds, compared to control birds, (1) lost significantly more mass and (2) waited significantly longer to forage under the highest predation risk. Our results indicate that MeHg-exposed birds may react more strongly to threat of predation and thereby increase their risk of starvation. To our knowledge this is the first mechanistic study of how a pervasive pollutant may alter optimal decision making, and therefore potentially survival, in songbirds. © 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Foraging and antipredator vigilance are often mutually exclusive activities, thus most animals experience a trade-off between the risk of starvation and the risk of predation (Houston, McNamara, & Hutchinson, 1993; Lima & Dill, 1990). While this trade-off is an important determinant of behaviour in most animals, it has been extensively examined in small songbirds because they are vulnerable to many predators and have high costs of metabolic regulation and fat storage (Blem, 1990; Witter & Cuthill, 1993). For example, birds with more stored fat have a harder time escaping from predators (Witter, Cuthill, & Bonser, 1994), so, in response to increased predation risk, birds adaptively lower their body mass (Gentle & Gosler, 2001; Lilliendahl, 1997). If a bird does not eat enough, however, it can easily use up its fat reserves and may starve in a day or two (Ketterson & King, 1977).

There are three behaviours that a songbird can use to minimize its risk of predation. First, vigilance rate, or how often an individual lifts its head from foraging to scan for potential predators, influences detection of an incoming threat (Hart & Lendrem, 1984; Lima & Bednekoff, 1999). Second, time and distance away from protective cover, such as dense brush, increases a bird's likelihood of succumbing to predatory attack (Lima & Dill, 1990). Finally, reluctance to resume foraging after being disturbed by a potential predator (i.e. latency to forage) indicates a bird's willingness to expose itself to predation risk in order to eat (Seress, Bókony, Heszberger, & Liker, 2011). Under increased threat of predation, birds tend to increase their time spent vigilant, increase their time in protective cover and increase their latency to forage after disturbance (Lima & Dill, 1990). These behavioural changes all lead to a reduction in body mass in the short term, although birds may adaptively increase fat stores in the longer term to compensate (Witter, Swaddle, & Cuthill, 1995).

While behavioural trade-offs such as that between vigilance and foraging have been well studied, we know little about how these trade-offs may be affected by neurotoxins, specifically those that are environmental pollutants. Many such pollutants have been

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implicated in avian population declines, acute mortality events and sublethal effects on reproduction and behaviour (Mineau & Whiteside, 2013). Mercury is one well-known contaminant that is projected to increase globally due to fossil fuel combustion (Wang, Shen, & Ma, 2000), artisanal gold mining (Van Straaten, 2000) and climate change (Hooper et al., 2013). When elemental mercury enters water, it is methylated by sulphur-reducing bacteria (Boening, 2000) and forms methylmercury (MeHg). This organic form of mercury is more dangerous to organisms because of its ability to cross the intestinal wall and blood-brain barrier, making it a potent neurotoxin with effects throughout the central nervous system (Scheuhammer, 1987; Wolfe, Schwarzbach, & Sulaiman, 1998). Given that MeHg affects brain development and cognitive performance, there are most likely many understudied consequences on the development and expression of behaviour. MeHg has long been recognized as a teratogen (e.g. Harada, 1978), so there are pronounced effects of both short-term exposure during embryonic development and chronic adult exposure to bioaccumulated MeHg (Wolfe et al., 1998).

Because mercury methylation occurs in aquatic ecosystems, much attention has been paid to its effects on aquatic organisms, especially large predatory fish and piscivorous mammals and birds (Scheuhammer, Meyer, Sandheinrich, & Murray, 2007). It has recently been discovered, however, that methylmercury can enter terrestrial food webs and accumulate in songbirds (Cristol et al., 2008; Rimmer, Miller, McFarland, Taylor, & Faccio, 2010). As in aquatic taxa, environmental mercury has sublethal effects on songbird reproduction (Bouland, White, Lonabaugh, Varian-Ramos, & Cristol, 2012; Hallinger & Cristol, 2011; Varian-Ramos, Swaddle, & Cristol, 2013), endocrine physiology (Wada, Cristol, McNabb, & Hopkins, 2009) and immune competence (Hawley, Hallinger, & Cristol, 2009; Lewis, Cristol, Swaddle, Varian-Ramos, & Zwollo, 2013). While behavioural end points have become routine for ecotoxicologists (e.g. Blocker & Ophir, 2013; Walker, 2003), animal behaviourists have been slow to conduct robust experiments quantifying effects of pollutants on behaviours (Clotfelter, Bell, & Levering, 2004; Montiglio & Royauté, 2014; but see Bean et al., 2014). Furthermore, it is important for behavioural ecologists to recognize that ubiquitous and persistent environmental contaminants, such as MeHg, are likely present in many study populations and could influence the results of basic behavioural studies.

We examined the effect of lifelong sublethal dietary MeHg exposure on the trade-off between starvation and predation risk in a model songbird, the zebra finch, *Taeniopygia guttata*. Because of the various effects of MeHg on animals, we had two competing hypotheses. First, MeHg could increase a bird's risk of predation by causing aberrant antipredator behaviours (as shown in fish, e.g. Webber & Haines, 2003) or affecting their senses (i.e. vision and hearing, as shown in primates: Burbacher, Grant, Mayfield, Gilbert, & Rice, 2005; Rice & Gilbert, 1992), and, therefore, their ability to detect and assess risk. Alternatively, MeHg could increase a bird's risk of starvation through several possible mechanisms. Birds dosed with mercury have been shown to have a reduced appetite, and therefore may have a reduced motivation to forage (Bouton, Frederick, Spalding, & McGill, 1999); there is also some evidence that mercury may affect foraging efficiency (Adams & Frederick, 2008). In addition, MeHg may cause birds to be hypersensitive to a perceived predatory threat (Heinz, 1979) and overreact to stimuli by increasing their latency to forage and losing more body mass than undosed birds. If mercury affects a bird's perceived predation risk, we predicted that MeHg-dosed birds would spend less time in cover, be less vigilant, not wait as long to forage and be heavier compared to controls. However, if mercury causes an increased starvation risk, we predicted that MeHg-dosed birds would spend more time in cover, be more vigilant, wait longer to forage and lose

more body mass in response to a predatory threat compared to control birds.

METHODS

We conducted this experiment in an aviary with captive-bred zebra finches exposed to chronic sublethal dietary MeHg from the embryo stage through the rest of their lives. Control birds were hatched and raised by parents receiving no MeHg, while the MeHg-treated subjects were raised by parents receiving a diet of 1.2 µg/g MeHg-cysteine (wet weight, equivalent to 1.39 µg/g dry weight) for 10 weeks before they were allowed to breed. This mercury level simulates exposure of wild songbirds at a highly contaminated industrial site (see Varian-Ramos, Swaddle, & Cristol, 2014). At such a site, exposure would begin as an embryo, because females deposit MeHg into their eggs (Wolfe et al., 1998), and continue as a nestling, because parents provision them with contaminated food. Developmental exposure to neurotoxins typically has more impact than exposure later in life (Harada, 1978). To achieve proper MeHg concentration in the diet, an aqueous MeHg-cysteine solution was added to commercial zebra finch food (ZuPreem FruitBlend) and homogenized as described in Lewis et al. (2013). Food was tested on a direct mercury analyser (DMA-80; Milestone, Shelton, CT, U.S.A.) to ensure that total mercury concentrations were within 10% of 1.2 µg/g (or contained no detectable mercury in the case of control food, which was mixed only with aqueous cysteine).

We tested young adult female finches between 100 and 200 days old that had been maintained on the same diet as their parents ($N = 20$ in the embryonically and chronically exposed 1.2 µg/g MeHg treatment; $N = 20$ controls). Birds were housed in groups of four in $75 \times 45 \times 45$ cm wire enclosures ('home cages') with ad libitum food and water until trials. Because zebra finches are highly social (Zann, 1996), they exhibit fearful behaviour when alone in a novel arena, and thus we conducted each trial with one focal and one nonfocal companion bird, with both birds coming from the same treatment group. To reduce animal use as much as possible while maintaining independent samples, we used each bird in two trials (described below), once as a focal, and once as a nonfocal, individual. At least 2 weeks passed between each bird's two trials and we assigned trials such that no bird was in the arena twice with the same companion. Hence, half of the birds were the focal subject the first time they entered the arena, and the other half were nonfocal during the first trial and focal in their second time in the arena. Both birds in the pair were from the same treatment for practical reasons (since they had to consume the same control or dosed food while in the arena) and because one would expect that, in the wild, all birds (within an age class) in the same location would have similar levels of mercury exposure.

Experimental Arena

We created two identical arenas in two $4.3 \times 4.3 \times 2.7$ m rooms (Fig. 1a). We constructed an observation blind ($1.2 \times 1.5 \times 2.7$ m) around the entrance door and delineated two experimental patches (84×84 cm), each 1.5 m from the blind and 3 m apart. These patches contained the dense cover (provided by artificial evergreen trees), water dishes and food dishes where the birds foraged. The food dishes were pie pans situated within larger, high-rimmed $35 \times 25 \times 6$ cm aluminium trays that reduced the birds' ability to be vigilant while their heads were down during foraging. Food dishes contained ad libitum food, control or dosed, mixed with inedible dried black beans to increase difficulty of foraging. We placed a 1.5 m high exposed perch constructed from PVC pipe and wooden dowels approximately 2.5 m from either patch to give birds another perching option outside of cover. Two video cameras

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