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Dietary exposure to methylmercury affects flight endurance in a migratory songbird☆

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ABSTRACT

Although there has been much speculation in the literature that methylmercury (MeHg) exposure can reduce songbird fitness, little is known about its effects on migration. Migrating songbirds typically make multiple flights, stopping to refuel for short periods between flights. How refueling at MeHg-contaminated stopover sites would contribute to MeHg bioaccumulation, and how such exposure could affect subsequent flight performance during migration has not been determined. In a dosing experiment we show that migratory yellow-rumped warblers (*Setophaga coronata*) rapidly accumulate dietary MeHg in blood, brain and muscle, liver and kidneys in just 1–2 weeks. We found that exposure to a 0.5 ppm diet did not affect vertical takeoff performance, but in 2-h wind tunnel flights, MeHg-treated warblers had a greater median number of strikes (landing or losing control) in the first 30 min, longer strike duration, and shorter flight duration. The number of strikes in the first 30 min of 0.5 ppm MeHg-exposed warblers was related to mercury concentration in blood in a sigmoid, dose-dependent fashion. Hyperphagic migratory songbirds may potentially bioaccumulate MeHg rapidly, which can lead to decreased migratory endurance flight performance.

1. Introduction

Mercury (Hg), a well-known and potent neurotoxin, is one of the most widespread pollutants threatening human and wildlife health (Driscoll et al., 2013). The most bioavailable and bioaccumulative form, methylmercury (MeHg) is of great concern in aquatic (Boening, 2000; Jackson, 1998; Wolfe et al., 1998) as well as terrestrial ecosystems (Cristol et al., 2008). The negative effects of MeHg on avian species of relatively higher trophic positions have been well documented (Evers et al., 2008; Fimreite, 1974; Frederick and Jayasena, 2011), and MeHg exposure has been linked to impaired motor skills and cognitive behaviors in piscivorous birds (Bennett et al., 2009; Kenow et al., 2010; Wolfe et al., 1998). Recent studies suggest that songbirds, particularly insectivores, may experience lower reproductive success (Brasso and Cristol, 2008; Jackson et al., 2011; Varian-Ramos et al., 2014) and disrupted immune function when exposed to MeHg (Hawley et al., 2009; Lewis et al., 2013). Flight performance could also be affected. For example, chronically MeHg-treated zebra finches (*Taeniopygia guttata*) hesitated to forage under high predation risk, suggesting impaired escape flight ability (Kobiela et al., 2015). European starlings (*Sturnus vulgaris*) exposed to chronic sub-lethal MeHg over 36 weeks molted wing primary feathers more quickly than controls, which may lead to poor feather quality, and these birds also had weaker take-off flight performance (Carlson et al., 2014). Homing pigeons (*Columba livia*) that were exposed to MeHg prenatally and continually after hatch exhibited flight impairment manifested by less efficient homing, reluctance to fly, slower flight speed on initial flights (Moye et al., 2016). These findings suggest that MeHg exposure could negatively affect the migration ability of songbirds.

Every year, billions of birds migrate on regional and continental scales between their breeding and wintering grounds, and migration is part of the life cycle of over half of the avian biodiversity in North America (Berthold, 2001). Migration is challenging for birds not only because it requires a large expenditure of energy and is dangerous (unpredictable weather, habitats, disease and predation

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risk), but also because it requires dramatic changes in behaviors (e.g. nocturnality, diet preference, orientation and navigation) and physiology (body composition, muscle metabolism, digestive morphology and function) (Alerstam and Lindström, 1990; Berthold, 2001). Prior to and during migration, birds are hyperphagic, leading to rapid body mass gain through the deposition of fat and lean mass (Lindström and Piersma, 1993). Hyperphagic migrants could be especially vulnerable to MeHg in sites or regions where forage contains elevated concentrations of MeHg, such as wet and acidic habitats in the boreal forests (St. Louis et al., 1994), industrialized sites (Ebinghaus et al., 2013; Li et al., 2009; Turner and Southworth, 1999), gold mining areas (Telmer and Veiga, 2009) and agricultural regions (Abeysinghe et al., 2017).

Migration is an energetically demanding component of a bird's life history (Wikelski et al., 2003). The flight phase requires songbirds to exercise continuously at an intensity of about 12 times the basal metabolic rate (Alexander, 1998) for several hours to a few days (Berthold, 2001). Between flights, small passerines generally rest and refuel at stopover sites, and approximately 90% of the migratory period (Newton, 2008) and almost 70% of the total energy required for migration are spent at stopovers (Wikelski et al., 2003). Any factor that inhibits the ability to take off at a steep angle to escape predators (Williams and Swaddle, 2003) at stopover, or to complete long endurance flights will increase the risk of migration failure. Here, we sought to understand how MeHg bioaccumulation in the hyperphagic state may affect flight performance of small songbirds, a question of vital importance to bird conservation (Seewagen, 2010).

We performed two studies to investigate the effects of MeHg on the yellow-rumped warbler (*Setophaga coronata*). In Study 1, we fed diets containing MeHg at concentrations that may be found at contaminated sites to songbirds in a photo-stimulated migratory state, and measured changes in body weight, body composition, and total Hg concentrations (hereafter [THg]) in key tissues. In Study 2, we tested the hypothesis that as a neurotoxin MeHg would negatively affect burst and endurance flight performance. We predicted that MeHg-treated birds would have reduced vertical takeoff speed, and would fly poorly and expend more energy in 2-h wind tunnel tests.

2. Materials and methods

2.1. Animal care

The yellow-rumped warbler is one of the most abundant and widespread songbird species in North America (Hunt and Flaspohler, 1998). It breeds in the boreal and western montane forests of Canada and the United States, and winters in mangroves, scrub, forests, and coffee plantations across a wide geographical range extending from the southern United States to Neotropics. The diet includes small invertebrates and fruits. Yellow-rumped warblers will readily eat formulated diets in captivity and can be flown for many hours in wind tunnels (Guglielmo et al., 2017). Birds ($N = 51$) were caught by mist nets at Long Point, Ontario, Canada (42°34′ 58″ N, 80°23′53″ W) from 19 September to 10 October 2014, and transported by vehicle to the Advanced Facility for Avian Research (AFAR), University of Western Ontario (UWO), London, Canada. They were housed in four large indoor aviaries (2.3W × 2.4H × 3.5L m) until experiments began. All birds were kept healthy under constant environmental conditions at approximately 20 °C, 47% of relative humidity (RH), with *ad libitum* access to MeHg-free synthetic diet and water until trials started. The synthetic agar-based mash diet contained 60.2% carbohydrate, 13.4% protein, and 10.7% lipid (dry mass basis, hereafter dw) and was prepared as described in Table S2. Birds were collected under a scientific collection permit from the Canadian Wildlife Service (SA-0208), and under Animal Ethics Protocol 2010-216 from the University of Western Ontario Animal Care Committee.

We manipulated the light cycles to simulate seasonal overwintering and migration conditions. In first two months of captivity, birds were kept under a 12 h light: 12 h dark (12L:12D) fall migration photoperiod. Then, the photoperiod was switched to a winter photoperiod (9L:15D) in November to break photo refractoriness (Nicholls et al., 1988). By increasing the day length, we stimulated the spring migration phase. Specifically, before each experiment started, birds were changed to a long-day photo cycle (16L:8D) to initiate migratory condition (fattening and restlessness, see below).

2.2. Wind tunnel

The hypobaric climatic wind tunnel with adjustable air pressure, temperature and humidity can simulate environmental conditions that birds would experience in flight. It is a specialized tool designed for flying animals in which warblers and other birds will fly individually for many hours (Gerson and Guglielmo, 2011; Guglielmo et al., 2017; Maggini et al., 2017). The wind tunnel has a recirculating design with the test section enclosed in a plenum (about 4W × 2.5H × 5L m). The closed octagonal test section is 1.5W × 1H × 2L m and an open section allows birds and investigators easy access to the closed test section without disturbing the flow (Gerson and Guglielmo, 2011). Birds in this study were flown in dim light conditions and a net was installed at the rear of the open test section to catch any birds that lost control. In the first month of captivity, birds were habituated to the wind tunnel at 15 °C, 70% RH, air speed range between 7 and 10 m s^{-1} for two 15 min-flights to screen their baseline flight performance. Birds ($N = 24$) that flew without encouragement with higher flight scores (see Table S1) were assigned to Study 2, the remaining ($N = 27$) with lower flight scores were assigned to Study 1.

2.3. Study 1 dietary methylmercury dosing

Two dosing concentrations were chosen to simulate relevant environmental MeHg (MeHgCl) diets that migrants may encounter at contaminated stopover sites. A 0.5 ppm (unit: μg/g, hereafter ppm) MeHg wet weight (ww) (validated as 1.56 ppm dw as [THg]) dose was close to the concentrations found in invertebrates (like spiders) at contaminated sites in the United States (Cocking et al., 1991; Cristol et al., 2008; Ortiz et al., 2015), while a 1 ppm wet weight (2.73 ppm dw) dose was related to the most heavily contaminated mining site in China (Abeysinghe et al., 2017) and industrial terrestrial sites in United States (Talmage and Walton, 1993; Zhang et al., 2012; Zhou et al., 2016). Diet preparation is described in Table S2.

In February 2015, 27 birds were randomly assigned to Control, 0.5 and 1 ppm groups (9 per group). Birds were housed separately or in pairs from the same diet treatment in cages (70 W × 50 L × 50 H cm). The light cycle was switched from the short-day winter photoperiod (9L:15D) to long-day photoperiod (16L:8D) to initiate migratory conditions 1 week before dosing. Control birds were fed a MeHg free diet with validated background [THg] of 0.005 ppm (ww), while the other two groups were fed nominal dietary concentrations of 0.5 and 1 ppm MeHg diet, respectively.

We measured body mass and body composition as well as blood [THg], at the start of the experiment (day 0) and then weekly (day 7 and day 14). Body mass was measured with a balance (±0.001 g) while body composition (fat and lean mass) was measured with a quantitative magnetic resonance body composition analyzer (QMR;