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ORIGINAL ARTICLE

Stopover departure behavior and flight orientation of spring-migrant Yellow-rumped Warblers (*Setophaga coronata*) experimentally exposed to methylmercury

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Abstract

Mercury (Hg) is a global pollutant that has wide-ranging impacts on the physiological systems of birds, but almost nothing is known about how this affects migration. We manipulated methylmercury (MeHg) burdens of 24 wild-caught Yellow-rumped Warblers (*Setophaga coronata*) before releasing them and tracking their spring migration with automated radiotelemetry to study the effect of MeHg on stopover departure behavior and flight orientation. Dosing half the birds for 14 days prior to release resulted in environmentally relevant mean blood total Hg (THg) concentrations of 6.61 ($\pm$ 0.16) p.p.m., while a group of 12 controls had nearly undetectable blood THg. We observed starkly different departure behavior between groups, with dosed birds leaving the release site significantly sooner than controls. Among birds that were detected beyond the release site, seven (three dosed, four control) initially made a landscape-scale relocation before a longer-distance migratory flight, while two (controls) migrated directly from the release site. All flights were in the seasonally appropriate direction regardless of group. Rapid departures by dosed birds could have been the result of hyperactivity that can be induced by MeHg, or due to decreased social dominance that caused them to seek areas with less resource competition. We found no evidence that MeHg impaired orientation, although sample sizes were small and we had less ability to detect birds flying in "incorrect" than northward directions. The dramatic difference in departure decisions between groups indicates a potential effect of MeHg on the neurological and/or physiological mechanisms that control migratory behaviors of birds.

Keywords Migration · Toxicant · Radiotelemetry · Hyperactivity · Social dominance

Zusammenfassung

Fortsetzung des Zuges und Orientierung nach Zwischenstopp beim Frühjahrszug von Kronenwaldsängern (Setophaga coronata), nachdem sie im Experiment Methylquecksilber ausgesetzt waren.

Quecksilber ist ein weltweit verbreitetes Umweltgift mit vielfältigen Auswirkungen auf die Physiologie von Vögeln, wobei jedoch fast nichts über eine mögliche Beeinflussung des Vogelzugs bekannt ist. Wir veränderten im Experiment die Methylquecksilber-Belastung (MeHg) von 24 Wildfängen des Kronenwaldsängers (Setophaga coronata) vor dem Wiederauflassen und verfolgten ihren Frühjahrszug mit automatischer Radio-Telemetrie, um die Effekte von MeHg auf die Wiederaufnahme des Zugs und auf die Orientierung zu untersuchen. Eine Hälfte der Vögel wurde 14 Tage vor Freilassung dem MeHg ausgesetzt, was in ihrem Blut zu einer umweltbiologisch relevanten mittleren Quecksilber-Konzentration (THg) von 6,61 (+/- 0,16) p.p.m. führte, wohingegen die 12 Tiere der Kontrollgruppe kein praktisch nachweisbares Quecksilber im Blut hatten. Das Abflugverhalten der beiden Gruppen war sehr unterschiedlich: die dem MeHg ausgesetzten Vögel verließen den Ort der Freilassung signifikant früher als die der Kontrollgruppe. Von den Vögeln, die in einiger Entfernung zum Ort der Freilassung wiedergefunden wurden, unternahmen sieben (drei mit MeHg, vier Kontrollvögel) zunächst Flüge in die Umgebung, bevor sie ihren Langstreckenzug wieder aufnahmen, während zwei der Kontrollvögel ihren Zug unmittelbar ab dem Freilassungsort fortsetzten. Unabhängig von der Gruppe zogen alle Vögel in die der Jahreszeit entsprechende, korrekte Richtung weiter. Die frühen Abflüge der Vögel mit MeHg könnten an einer von Quecksilber verursachten Hyperaktivität oder

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an einer verringerten sozialen Dominanz liegen, die sie dazu brachte, Gebiete mit geringerer Konkurrenz um vorhandene Ressourcen aufzusuchen. Wir fanden keinen Hinweis darauf, dass MeHg einen Einfluss auf die Orientierung hatte, wobei allerdings die Stichproben sehr klein und wir nicht in der Lage waren, Vögel, die in falsche Richtungen (also nicht nach Norden) zogen, nachzuweisen. Der dramatische Unterschied zwischen den Gruppen in der Entscheidung, den Zug wieder aufzunehmen, weist aber auf einen möglichen Einfluss von MeHg auf diejenigen neurologischen und/oder physiologischen Mechanismen hin, die die Zugbewegungen von Vögeln kontrollieren.

Introduction

Coal combustion, gold mining, and other human activities have dramatically increased environmental mercury (Hg) emissions since the dawn of the industrial revolution more than 200 years ago (United Nations Environment Programme 2013). Hg emitted into the atmosphere can later enter ground and water thousands of kilometers away from its original source, allowing Hg to become a globally pervasive pollutant (Selin 2009; Driscoll et al. 2013). In many ecosystems, Hg is converted by microbial processes into a more toxic and bioavailable form, methylmercury (MeHg), which can then contaminate aquatic and terrestrial food webs and place birds and other wildlife at risk of harmful levels of exposure (Evers 2018). Laboratory and field studies have documented myriad adverse effects of MeHg on birds, mostly relating to reproduction. These studies include a broad taxonomic spectrum of species that spans multiple foraging guilds and habitat associations. Carnivorous raptors, piscivorous waterbirds, and insectivorous songbirds, for example, have all been observed to have reduced reproductive success, impaired endocrine and immune system function, and altered behaviors as a result of environmental or environmentally relevant MeHg exposure (Whitney and Cristol 2017; Evers 2018).

Compared to these other end points and life cycle events, however, almost nothing is known about the effects of Hg on birds during migration (Seewagen 2010, 2018). Migration is a highly energetically and cognitively challenging behavior that is underpinned by several coordinated neurological and physiological processes. Many of these processes are expected to be sensitive to disruption by MeHg, including geomagnetic compass orientation, fuel transport and oxidation, oxidative balance, and stopover refueling (Seewagen 2010, 2018). Any such disruption would be likely to diminish the probability of completing what is already the phase of their annual cycle in which the vast majority of migratory bird mortality occurs (Seewagen 2018). Indeed, autumn migrant Blackpoll Warblers (*Setophaga striata*) and American Redstarts (*Setophaga ruticilla*) were recently found to have higher feather Hg levels than conspecifics passing through the same location the following spring, possibly indicating that the individuals that departed towards their wintering grounds with the greatest Hg burdens were the least likely to survive autumn migration, winter, or their return trip in the spring (Ma et al. 2018a).

Only a few other studies have investigated the effects of Hg on birds during or in the context of migration. Seewagen (2013) found no relationship between blood Hg levels and the stopover refueling rates of autumn migrant Northern Waterthrushes (*Parkesia noveboracensis*) in New York. Similarly, Hg was found to be negatively associated with refueling rate in only one (*Geothlypis trichas*) of four songbird species studied during autumn and in none of the same four species studied during spring at a stopover site in Florida (E. Adams, K.A. Williams, B.J. Olsen, and D.C. Evers, unpublished data). However, environmentally relevant doses of MeHg have been found to impair the coordination and endurance of Yellow-rumped Warblers (*Setophaga coronata*) flying in a wind tunnel (Ma et al. 2018b) and reduce the peak metabolic rates of Zebra Finches (*Taeniopygia guttata*) exercising in a hop-hover wheel (Gerson et al. 2019), raising concern that the biomechanics and flight ranges of migrating birds exposed to MeHg could be compromised. MeHg has been observed to also weaken flight performance in captive European Starlings (*Sturnus vulgaris*) (Carlson et al. 2014) and domestic Rock Pigeons (*Columbia livia*), while also reducing the pigeons' homing abilities (Moye et al. 2016). A study of captive Zebra Finches suggested that during long-distance flight, migrating birds might experience dangerous surges in circulating MeHg levels as the MeHg accumulated within their lean tissues is remobilized by the catabolism of protein (Seewagen et al. 2016).

To our knowledge, no study has yet investigated the influence of MeHg exposure on the migratory movements of birds in the wild. Here, we experimentally manipulated the MeHg body burdens of wild-caught Yellow-rumped (Myrtle) Warblers (*Setophaga coronata coronata*) and radio-tracked their spring migration through Ontario, Canada to study the effect of MeHg on the stopover patterns and flight orientations of free-living migratory birds. Based on the suspected adverse effects of MeHg on magnetic compass orientation, flight endurance, and stopover refueling (Ma et al. 2018b; Seewagen 2018; Gerson et al.

2019), we hypothesized that MeHg-dosed birds would orient improperly, and make shorter flights and have longer stopovers than those that had not been exposed to MeHg.

Methods

Study species and site

Setophaga coronata coronata, the Myrtle subspecies of the Yellow-rumped Warbler, is a migratory songbird with a broad breeding range that covers much of the northern US and most of Canada. The wintering range extends from southern New England in the US, south through Central America, and west to California (Hunt and Flaspohler 1998). Yellow-rumped Warblers are primarily nocturnal migrants, but occasionally move during the day (Ball 1952; Hunt and Flaspohler 1998) and are known to sometimes make landscape-scale stopover movements between longer, migratory flights (Woodworth et al. 2015; Dossman et al. 2016). They are common and abundant migrants at our study site on Long Point, Ontario, Canada, where they stop to refuel (Dunn 2001). Long Point is a narrow spit that extends 35 km east into Lake Erie from the northern shore and represents the first landfall opportunity for many songbirds migrating across the lake. This, combined with limited upland habitat availability, commonly results in high densities of migrant songbirds on Long Point.

Capture and dosing

We captured Yellow-rumped Warblers (n = 24) in mist nets in a small woodlot on Long Point (42°34′58.0″N, 80°23′52.6″W) during October 2016 and brought them to the Advanced Facility for Avian Research at the University of Western Ontario. The birds were maintained there together in an indoor aviary at room temperature (~ 20 °C), with a light cycle of 12 h light and 12 h dark (12L:12D), and fed ad libitum a synthetic agar-based diet (dry mass 60.2% carbohydrate, 13.4% protein, and 10.7% lipid) that was supplemented with approximately five small mealworms (*Tenebrio molitor* larvae) each day following Ma et al. (2018b). On 22 December 2016, the light cycle was changed to 9L:15D to simulate winter conditions. Approximately 75 µL of blood was collected from the brachial vein to measure baseline blood total Hg (THg) concentrations and determine sex molecularly (as described by Morbey et al. 2018). On 27 March 2017, twenty-four birds (12 male, 12 female) were alternately assigned to a MeHg-dosing or control treatment group (six birds per sex per treatment) upon transfer from the aviary to individual cages (34 cm × 18.25 cm × 17 cm). While in individual cages, prior to dosing, the birds were each maintained on 12 g/day of the same diet described above. On 3 April 2017, the birds were weighed to 0.1 g and then their light cycle was switched to match the photoperiod of the projected release date (3 May) at Long Point (15L:9D; on at 0550 hours, off at 2050 hours) and induce a migratory state. After 2 weeks on this light cycle (beginning 17 April), the birds were weighed again and then fed 12 g of either the same diet (control group) or the same diet mixed with MeHg at a concentration of 0.5 p.p.m. wet weight, along with five mealworms (Ma et al. 2018b) every day for 14 days. This dosing concentration was intended to represent the upper range of Hg levels found in the invertebrate prey of songbirds in areas that have atmospheric Hg deposition or point-source contamination (Cristol et al. 2008; Rimmer et al. 2010; Rowse et al. 2014).

Radio-tagging and release

On 1 May 2017, all birds were weighed (to 0.1 g), and fat mass and lean mass were measured (to 0.001 g) using quantitative magnetic resonance body composition analysis (Guglielmo et al. 2011; Kennedy et al. 2017). Approximately 50 µL of blood was taken by brachial venipuncture to again measure blood THg concentration. The birds were then outfitted with 0.29-g digitally coded radio transmitters (model NTQB-1, pulse rate, 12.7 s; Lotek Wireless, Newmarket, ON) attached with a modified leg-loop harness (Rappole and Tipton 1991) and returned to their cages.

Two days later (3 May 2017), the birds were weighed again (minus the mass of their transmitter) and then released at approximately 1100 hours Eastern Daylight Time (EDT) from where they had been originally captured to coincide with the normal spring passage period of Yellow-rumped Warblers through Long Point. We considered the release to simulate arrival at a stopover site during spring migration. All birds flew out of the hand normally and perched in nearby trees. One bird (treatment group unknown) was observed to hawk a flying insect out of the air within approximately 30 s of its release, indicating that birds were immediately returning to normal feeding behaviors after spending the winter in captivity.

We used a network of automated telemetry receivers (Motus Wildlife Tracking System) (Taylor et al. 2017) to determine the date of departure from the release site and to track the birds' movements beyond it. A receiver station at the release site ensured 100% probability of detection upon release, with the number of detections per unit time expected to then either decline slowly as foraging birds gradually moved out of detection range or decline abruptly when birds departed on a nocturnal migratory flight. Based on a previous comparison of manual and automated radiotelemetry of Yellow-rumped Warblers and Black-throated Blue Warblers (*Setophaga caerulescens*), actively foraging Wood Warblers have a 0.5 probability of detection by automated radiotelemetry within ± 30 s if they are known to be within 300–500 m of the receiver station at our release site, depending on the antenna (T.L. Crewe, A.T. Beauchamp, J.E. Deakin, and Y.E. Morbey, unpublished data). We considered a bird to still be present at the release site on a given day if it was detected by the receiver station there > 50 times (between 0448 and 1720 hours EDT). This threshold was chosen to avoid false and ambiguous detections and to ensure high certainty of identifying birds in close proximity to the receiver station. Length of stay (days) at the release site was calculated as the last day present minus the release day plus 1. Nocturnal migratory departure events (Taylor et al. 2017) were too infrequent to be used to determine length of stay. The detection range for birds in flight is expected to be 15 km in ideal conditions (Taylor et al. 2017), but sparse and incomplete data from receiver stations beyond the release site limited our ability to reconstruct flight paths and subsequent stopover locations.

Hg analysis

THg concentration (p.p.m. wet weight) was measured in the blood as a proxy for MeHg (Fournier et al. 2002; Rimmer et al. 2005) with a Direct Mercury Analyzer (DMA 80; Milestone, Shelton, USA) following Ma et al. (2018b). All samples were analyzed in the same batch. A calibration check standard (CCS) was measured at the beginning of the batch, and quality controls in the batch included a certified reference material (Caprine Blood SRM 955c), a method blank, and a duplicate for every ten to 15 blood samples. Mean percent recovery was 97.29 ± 3.55% for SRM 955c ($n = 4$) and 99.97% for the CCS ($n = 1$). The relative difference between duplicates ($n = 3$ pairs) was 3.28 ± 1.57% for all samples with concentrations greater than ten times the instrument's minimum detection limit of 0.005 ng. Seven samples (all from the control group) were below the minimum detection limit and treated as 0.00 p.p.m.

Data analyses

We used two-sample t-tests to compare the following variables between treatment groups: wing length upon capture, fat and lean mass 2 days prior to release, total body mass moments before release, and blood THg concentration upon conclusion of the 14-day dosing period. Length of stay (days) at the simulated stopover site was compared between treatments with an exact Wilcoxon Mann–Whitney rank sum test. This non-parametric comparison of distributions was used because length of stay deviated from normality within dosed birds (Shapiro–Wilk $W = 0.6$, $p = 0.0002$). We also compared length of stay using the non-parametric survival analysis in procedure LIFETEST in SAS version 9.3 (SAS Institute 2011). Using this framework, we tested whether covariates (sex, fat mass) were associated with length of stay in models that also included treatment. We also visualized presence per hour (> 50 times detected) for the first 24 h after release to evaluate the dispersal pattern over a shorter time scale. The proportion of birds detected by receiver stations beyond the release site was compared between treatment groups using a χ^2-test. Significance was accepted for all tests when $p < 0.05$. Flight paths beyond the release site were plotted with ggmap in R version 3.5.1 (R Core Team 2017) and characterized qualitatively because detections at other receiver stations were too few to allow for a statistical comparison of movement attributes between dosed and control birds.

Results

Blood THg concentrations of the dosed birds averaged 6.61 (± 0.16 SE) p.p.m. (range = 5.63–7.63 p.p.m.) and were significantly greater than those of the controls, which averaged 0.00 (± 0.00 SE) p.p.m. (Table 1). Both groups gained an average of 1.7 g (± 0.34 SE dosed group, ± 0.29 SE control group) over the 14 day dosing period on the simulated spring light cycle. Dosed and control birds did not differ in wing length at capture, body mass on the day of release, or fat mass or lean mass 2 days prior to release (Table 1).

The distribution of length of stay at the release site differed between treatment groups ($Z = 2.3$, $p = 0.020$). Survival curves were also significantly different between treatment groups (log-rank test for homogeneity: $\chi^2 = 4.3$, $p = 0.037$), with dosed birds leaving significantly sooner (median = 1.5 days) than controls (median = 6 days; Fig. 1a). Sex was not significantly associated with length of stay when included in the survival model with treatment (rank test for association: $\chi^2_1 = 0.05$, $p > 0.5$). A nearly significant positive association between fat mass

Table 1 Mean (± SE) blood total mercury (THg) concentration, total body mass, fat mass, lean mass, and wing chord of methylmercury (MeHg)-dosed and control Yellow-rumped Warblers released at Long Point, Ontario, Canada

	Dosed	Control	t test
Blood THg (p.p.m. wet weight)	6.61 ± 0.16	0.00 ± 0.00	$t_{22} = 40.4$, $p < 0.0001$
Body mass (g)	13.5 ± 0.2	13.3 ± 0.4	$t_{22} = 0.5$, $p = 0.66$
Fat mass (g)	2.3 ± 0.2	2.6 ± 0.2	$t_{22} = -1.1$, $p = 0.31$
Lean mass (g)	8.6 ± 0.1	8.5 ± 0.2	$t_{22} = 0.3$, $p = 0.74$
Wing chord (mm)	70.0 ± 0.5	70.4 ± 0.7	$t_{22} = -0.5$, $p = 0.61$

Blood THg, fat mass, and lean mass were measured 2 days before release, body mass was measured on the day of release, and wing chord was measured upon initial capture

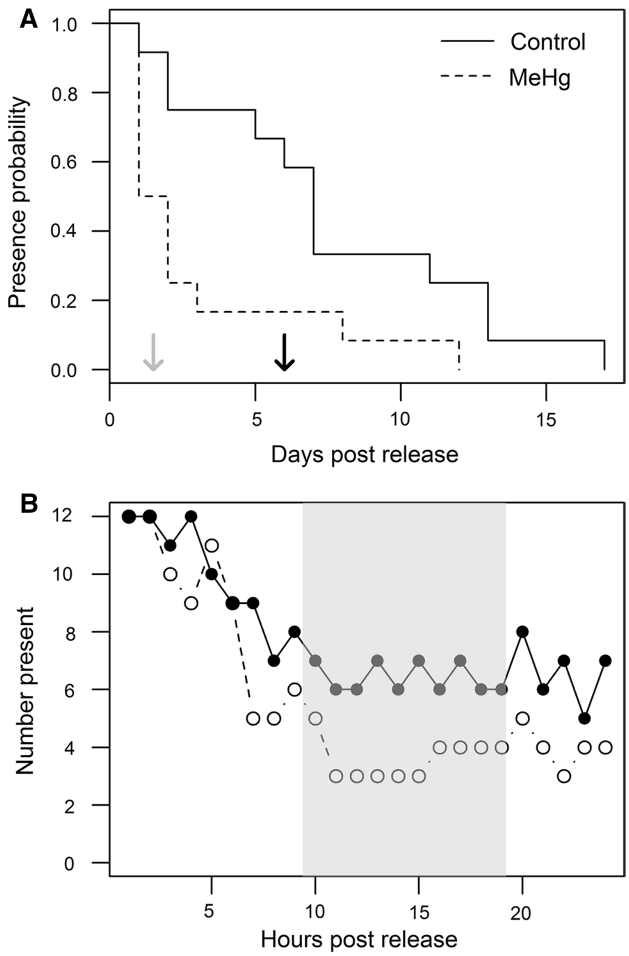

Fig. 1 Movements of radio-tagged Yellow-rumped Warblers away from the release site on Long Point, Ontario, Canada. **a** Probability that birds were present at the release site as a function of days since release. Median length of stay is indicated by gray arrow [methylmercury (MeHg)-dosed (1.5 days) birds] and black arrow [control (6 days) birds]. **b** Number of birds present at the release site as a function of hours since release for the first 24 h following release. Presence was defined as > 50 detections per day (between 0448 and 1720 hours EDT) in **a** and as > 50 detections per hour in **b**. Birds were released at approximately 1100 hours EDT on 3 May 2017, so that hour = 1 corresponds to 1100–1200 hours EDT. Gray shading in **b** indicates the period between local sunset and sunrise

and length of stay ($\chi_1^2 = 3.6$, $p = 0.053$) was due to an influential observation of a control bird with an unusually high fat mass (4.6 g) and long length of stay (17 days). Excluding this outlier, fat mass was not significantly associated with length of stay ($\chi_1^2 = 1.1$, $p = 0.29$) while the distribution of length of stay remained different between treatment groups ($Z = 2.1$, $p = 0.037$). Repeating these analyses with a lower threshold for determining presence at the release site (e.g., ten detections) did not qualitatively affect the results. A difference in hourly presence between dosed and control birds was apparent by 1700–1800 hours

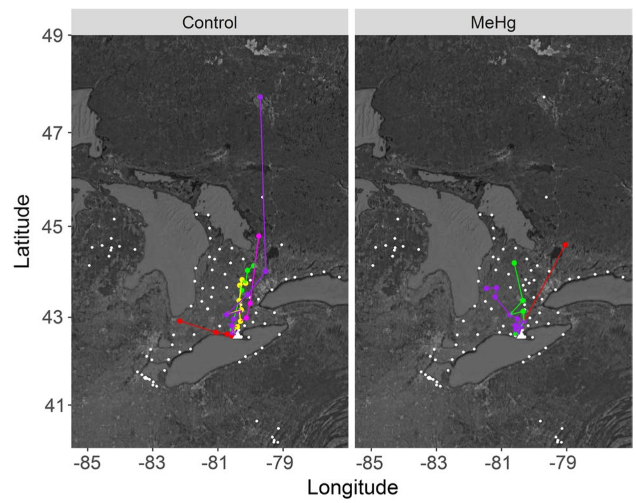

Fig. 2 Movement paths of MeHg-dosed and control Yellow-rumped Warblers after departing the release site on Long Point. Colored circles show receiver stations at which the Yellow-rumped Warblers were detected and black circles show all other active receiver stations in the region at the time of the study. Tracks of individuals birds are represented by uniquely colored circles and correspondingly colored connection lines

EDT (7 h post release; Fig. 1b). Foraging movements of birds through intervening vegetation in combination with other sources of variation in signal detection likely account for the finer scale variation in hourly presence in Fig. 1b. Nighttime inactivity did not appear to strongly reduce the hourly presence of birds.

The proportion of birds detected beyond the release site did not differ between treatments ($\chi_1^2 = 0.13$, $p > 0.5$) even though more than twice as many control birds (seven out of 12) as dosed birds (three out of 12) were detected by receiver stations elsewhere. The timing and directions of movement varied among individuals (Figs. 2, 3). Of the ten birds that were detected beyond the release site, seven (three dosed, four control) first made a landscape-scale movement north to the mainland before eventually making a nocturnal migratory flight from there 5–19 days later in the case of dosed birds and 3–10 days later in the case of controls. During the relocation period on the mainland, there were daytime detections of these seven birds at four receiver stations all within 30 km of the release site. An eighth bird, from the control group, also made a northward landscape-scale relocation from the release site but was never found to make a nocturnal migratory flight away from there. The other two birds detected beyond the release site (both from the control group) made a nocturnal migratory flight directly away from the release site (at 0117 and 0121 hours EDT) without any obvious landscape-scale movement beforehand. All nighttime detections of birds making nocturnal migratory flights away from the release site and the mainland relocation sites

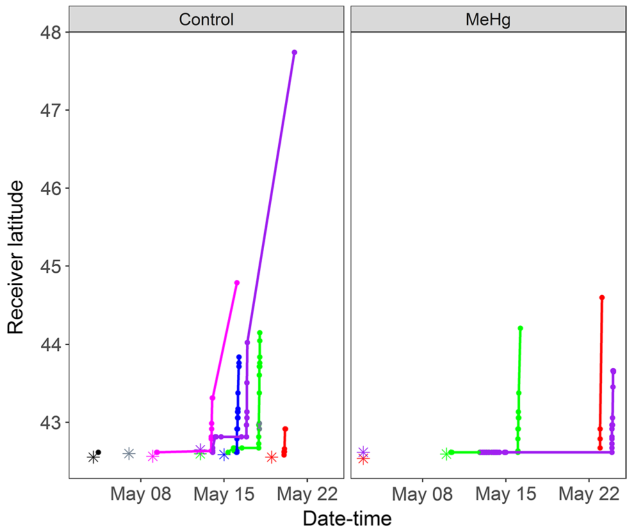

Fig. 3 Movement timing of MeHg-dosed and control Yellow-rumped Warblers (dosed, $n = 3$; control, $n = 7$) detected beyond the release site on Long Point. Asterisks show the day when birds were no longer present at the release site (< 50 daytime detections). Seven birds showed a nocturnal migratory flight after first relocating away from the release site for > 2 days. Two control birds (shown in blue and red) made a nocturnal migratory flight directly away from the release site and one control bird (shown in black) was never detected on a nocturnal migratory flight after initially making a landscape-scale relocation away from the release site

occurred between 2116 and 0609 hours EDT, with peak detections occurring between 2200 and 2300 hours EDT. Two of the control birds with longer movement paths interrupted migration for 2 or 4 days in the final leg, representing one or more bouts of stopover. All birds that were detected beyond the release site flew in seasonally appropriate northwest to northeast trajectories during both landscape-scale relocations and longer distance migratory flights, regardless of treatment group (Fig. 2). The fate of the 14 birds that were never detected beyond the release site could not be determined. These birds left the release site by daytime movements, and none made a characteristic nocturnal migratory departure.

Discussion

There is strong potential for MeHg to disrupt several of the neurological and physiological processes that underlie bird migration, but we are unaware of any previous study of the effects of MeHg exposure on the movement behaviors or flight orientations of migrating birds. Here, we found that environmentally relevant MeHg dosing of Yellow-rumped Warblers significantly affected their length of stay at, but not flight directions away from, a simulated springtime stopover site. Although the sample size was small and the effect of MeHg on length of stay was in the opposite direction than expected, we observed dramatically different post-release departure timing between birds that had and had not been exposed to MeHg while all other factors were held constant. This suggests some yet unknown effect of MeHg on the neurological and/or physiological mechanisms that control the migratory behaviors of birds.

Determining the direct or indirect causes of the behavioral differences that we observed between dosed and control birds will require further and more detailed experimentation, but one potential explanation is the effect that MeHg can have on activity levels and social dominance. MeHg has been found to shift the behavioral phenotype of Zebra Finches towards hyperactivity and subordination, with MeHg-exposed birds exhibiting restlessness and extreme movement patterns, and a low social position that weakens their ability to compete for food (Swaddle et al. 2017). Similar symptoms of restlessness, anxiety, and decreased sociality are common among humans who have been exposed to Hg (e.g., Siblerud et al. 1994; Powell 2000). Any such hyperactivity and restlessness among the Yellow-rumped Warblers that were dosed with MeHg would be expected to influence their migratory behaviors and may explain why most dosed birds left the release site so much sooner than control birds. Social subordination could have further contributed to the dosed birds' propensity to leave the release site so quickly, particularly if competition for resources was high. Social status and competitive exclusion can affect the ability of migrating songbirds to acquire food during stopovers (Moore et al. 2003; Newton 2006) and thereby influence bird distribution, with subordinate individuals shifting into areas with less competition or abandoning a site altogether (Wang et al. 1998; Woodrey 2000; Newton 2006). If the Yellow-rumped Warblers exposed to MeHg had a lesser ability to compete for resources, they may have moved away from the release site in search of alternative habitat that had lower densities of other birds.

Many toxicants, including polychlorinated biphenyls, organophosphates, and neonicotinoids have been shown to impair orientation in migratory songbirds (Vyas et al. 1995; Flahr et al. 2015; Eng et al. 2017). MeHg is thought to have the potential to interfere with orientation by disrupting visual-based magnetoreception (Seewagen 2018), but there have yet to be any tests of the effects of MeHg on the migratory orientations of birds either in captivity or the wild. In our experiment, the three MeHg-dosed Yellow-rumped Warblers that were detected along migratory flights each headed in seasonally appropriate northerly directions that were comparable to those of the control birds. All daytime, landscape-scale relocations in advance of those migratory flights were also to the north. This suggests an unimpaired ability to properly orient following MeHg exposure at the level used in our study.

However, fewer than half as many dosed birds (three out of 12) as controls (seven out of 12) were ever detected by receiver stations beyond the release site. We cannot rule out the possibility that a greater proportion of the dosed birds migrated in an incorrect direction and that the three dosed birds that were known to have flown north did so by chance. This is because at the time of our study, receiver station coverage was much greater to the north of Long Point, throughout southern Ontario, than to the east and south of there (see Fig. 2). Birds were therefore more likely to be detected beyond the release site if they flew north than in those other directions, particularly south. We must also consider the possibility that we detected far fewer dosed than control birds beyond the release site because of reduced survivorship that could have resulted from adverse effects of MeHg on predator avoidance (Carlson et al. 2014; Kobiela et al. 2015), foraging (Evans et al. 1982; Kobiela et al. 2015; Swaddle et al. 2017), energy management (Gerson et al. 2019), and/or other aspects of migration performance (Ma et al. 2018a; Seewagen 2018).

Although the conclusions we can reach are limited and further research is needed, our findings significantly build upon a growing effort to identify the effects that MeHg can have on birds during migration (Seewagen 2013, 2018; Ma et al. 2018a, b; Gerson et al. 2019; E. Adams, K.A. Williams, B.J. Olsen, and D.C. Evers, unpublished data). We found environmentally relevant MeHg exposure to substantially alter the movement decisions of migrating songbirds, but possibly without affecting their compass orientation abilities. We have also presented an effective technique for studying the effects of environmental contaminants on animal migration performance by exposing wild birds to Hg experimentally. Maintaining birds in captivity over the winter allowed us to control their Hg burdens before photo-stimulating them into a migratory state and releasing them back into the wild to be tracked by a coordinated network of automated telemetry receivers. This combined field and laboratory approach has strong potential for investigating the effects of MeHg and other toxicants on migrating birds while avoiding many of the biases and shortcomings of purely captive studies and field studies of free-living animals in sites with differing degrees of contamination (see Whitney and Cristol 2017). We call for others to employ this or other techniques to advance the presently limited understanding of the threats posed to migrating birds by global Hg pollution.

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Compliance with ethical standards

Ethical standards All procedures were approved under a University of Western Ontario animal use protocol (2010–216) and permits from the Canadian Wildlife Service (CA-0256, 10169BU).

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