Use of Chemical Tracer to Detect Floaters in a Tree Swallow (*Tachycineta bicolor*) Population

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In many species of birds, a non-breeding portion of the population spends the breeding season on or near the nesting grounds. This floating subset of the population is often comprised of young or low-quality individuals that can subsequently recruit into the breeding population. However, floaters are difficult to study and most documentation has been the result of nest site manipulation or experimental removal of residents. Here, using a contaminant as a tracer, we show unequivocal recruitment of floater Tree Swallows (Tachycineta bicolor) into a breeding population without experimental manipulation. In 2005, a nest box trail was established along the South River (Virginia, USA) to monitor breeding Tree Swallows exposed to aquatic mercury. Because feather mercury levels reflect exposure during the previous breeding season, we were able to use mercury to detect prior occupancy among new recruits in the population. Through this technique, we estimated that 58% of 79 new breeders had been present in our contaminated study area during the previous breeding season. Future studies could profit from incorporating floater abundance and behavior into evaluations of contaminant impact because floaters at contaminated sites receive more exposure than would be estimated based only on their longevity in the breeding population.

Key Words: chemical tracer, floater, mercury, territoriality, Tree Swallow

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Introduction

A floater is a member of a population that lacks a territory but lives among residents, moving transiently over an area encompassing several territories. Most research concerning floater behavior has been conducted on breeding grounds, but floaters also occur in systems that are territorial during the non-breeding season (Brown and Long 2007). In fact, floaters have been detected in nearly all populations of territorial birds that have been studied appropriately (reviewed in Winker 1998). Previous research has described the behavior of floaters to better understand the specific roles that these individuals hold within populations (e.g. Smith 1978). However, because of the difficulty in identifying and following floaters, many gaps remain in our understanding of the maintenance and evolution of this ubiquitous life history strategy, and floaters have rarely, if ever, been incorporated into ecotoxicological studies.

Floaters are, by definition, reproductively capable individuals, and although they are unable to defend a breeding territory, they are sometimes able to reproduce in other ways. As a consequence, floaters of some species may gain varying degrees of fitness through either brood parasitism (e.g. Sandell and Diemer 1999) or extra-pair copulations with resident females (e.g. Kempenaers et al. 2001). Even in the absence of immediate reproductive benefits, floating may allow individuals to gain familiarity with territories that will become available in the future. Several studies have indicated that floaters achieve an advantage in social dominance during competition for new vacancies (reviewed in Zack and Stutchbury 1992).

Although floaters may play a significant role in many populations, both in terms of direct reproductive output and as a source of new recruits, most aspects of floater behavior remain poorly understood due to the practical difficulties inherent in studying them. In fact, their mobility and cryptic nature have earned floaters a reputation for being an invisible portion of populations. Traditional methods of detecting avian floaters have included 1) supplementing a limiting resource, such as nest sites, in order to lure floaters into view (e.g. Stutchbury and Robertson 1985); or 2) removing one or both members of breeding pairs in order to determine whether there is a pool of floaters available to replace them (e.g. Bruinzeel and van de Pol 2004). These methods have been effective in documenting the existence of floaters in a number of species (reviewed in Winker 1998); however, as a result, there have been few comprehensive accounts of floater abundance or behavior under unmanipulated conditions (but see Smith 1978, Heg et al. 2000).

The use of chemical tracers may offer new insights. Chemical tracers are compounds that are specific to a particular location or sector of a population and that can be used to infer characteristics of individuals. For example, much recent work has demonstrated the efficacy of stable isotope analysis in uncovering information about avian migration and space use (reviewed in Inger and Bearhop 2008). Localized contaminants in the environment may prove of similar value and we demonstrate here that mercury pollution can be used as a tracer to detect prior use of a contaminated area by cryptic floaters. In its organic form, mercury has a high affinity for the disulfide bonds present in keratins, and is deposited in developing feathers during growth (Condon and Cristol 2009). Thus, feather mercury levels reflect exposure during the period prior to the most recent molt. Most species of migratory songbirds undergo a full ("pre-basic") molt at the end of the breeding season before departing for fall migration. If this molt occurs on a breeding ground contaminated with mercury, then mercury levels in the feathers of birds captured during one breeding season will reflect exposure during the previous one. If an adult bird on a contaminated site has high feather mercury levels, but was not breeding on that site in the previous year, then it can be deduced that this bird was a floater that spent substantial time on the breeding site and has subsequently been recruited into the breeding population. Our objectives were to determine whether feather mercury levels could be used as a tracer to detect floaters and whether such a technique could be applied to more closely examine important characteristics associated with this cryptic portion of many bird populations.

Methods

Study Species

The Tree Swallow (*Tachycineta bicolor*) is an insectivorous, migratory songbird that breeds throughout the northern half of North America (Robertson et al. 1992). Tree Swallows are obligate secondary cavity nesters (Robertson et al. 1992) and are thus nest-site limited. At our study site in Virginia (see *Study Area*), their breeding season consists of two discrete periods, an early nesting period from late April through early May and a late nesting period from late May through June. Traditionally, it has been assumed that females nesting in the late period are floaters who were excluded from breeding early (Stutchbury and Robertson 1985, but see Monroe et al. 2008). In an unmanipulated population, 11% of all breeders were reported to be late-nesting floaters (Stutchbury and Robertson 1985). When the number of available nest sites was experimentally increased late in the season in that same population, floaters comprised approximately 25% of all breeders (Stutchbury and Robertson 1985). This estimate of 25% is still widely cited as the best approximation of floater abundance in Tree Swallows (e.g. Rosvall 2008).

In order to make inferences concerning the efficacy of a mercury tracer, it is necessary to establish that feathers collected during one breeding season actually reflect behavior during the previous one. In Tree Swallows, several lines of evidence suggest this to be the case. First, in contrast to many other birds, Tree Swallows undergo a single molt each year that begins in late July and continues well into migration (Robertson et al. 1992). Among the flight feathers, primaries are molted in sequence beginning with the innermost (P1) and continuing outward (Robertson et al. 1992). Thus, the majority of swallows molt their first primaries on the breeding grounds (see Sellick et al. 2009). Brasso and Cristol (2008) tested this assumption by correlating feather mercury levels of returning breeders with blood levels in the previous year. As expected, blood mercury in one breeding season was highly predictive of feather mercury in the subsequent year (see *Statistical Analyses*).

Study Area

The South River in Virginia, USA was contaminated with mercury from an industrial source between 1929 and 1950 (Carter 1977). In 2005, a nest box trail was established at 26 sites along the South River and two nearby uncontaminated tributaries, the North and Middle Rivers (described in Cristol et al. 2008). Nest boxes were placed in cropland or pasture approximately 25 m apart and within 300 m of river shoreline. In 2005, 146 nest boxes were provided. This number was increased, prior to the breeding season, to 296 in 2006, 361 in 2007, and 504 in 2008. Nest boxes were constructed using a popular bluebird nest box design (Eastern/Western Bluebird, North American Bluebird Society 2009) and each was fitted with a “stovepipe” predator guard (Erva Tool, Chicago, Illinois) that almost entirely eliminated snake and mammalian predation (e.g. nest failure due to predation, abandonment, and disruption by House Sparrows (*Passer domesticus*) was < 10% in 2005-2007). There is no natural wetland habitat suitable for Tree Swallow nesting in the study area and prior to the establishment of our nest box trail, few, if any, Tree Swallows were nesting on or near the study sites.

Capture and Sampling

Adult female Tree Swallows were captured in their nest boxes during incubation or the nestling period using one of two trapping methods (Stutchbury and Robertson 1986, Friedman et al. 2008) or by hand. Tree Swallows are a rarity among birds in that age can be determined by plumage in females, but not males. Second year (SY, hatched in the previous breeding season) females have a predominantly brown plumage while after-second-year (ASY) females exhibit an iridescent blue plumage similar to all ages of males (Robertson et al. 1992). Upon capture, each female was uniquely banded with a USGS metal band. In addition, a small blood sample (< 100 ul) was collected and one primary (P1) was removed from each wing for mercury analysis (as described in Brasso and Cristol 2008). During 2005-2006, it was demonstrated that feather mercury level in one breeding season correlated with blood mercury level sampled during the previous breeding season, validating a fundamental assumption of our study - swallows in this population grow their first primary feather (P1) on the breeding grounds (Figure 3 in Brasso and Cristol 2008). Because a substantial proportion of breeding females evaded capture in 2005 (captured 66.7%; 20 of 30 contaminated breeders), we did not attempt to analyze prevalence of returning floaters in 2006. However, from 2006-2008 we captured nearly every breeding female, and thus could be almost certain that an unbanded ASY breeder in 2007 or 2008 had not been breeding on or near one of these study sites in the previous season. In 2006, we captured at least 92% of adult female Tree Swallows (58 of 63) breeding on contaminated sites in the early nesting period. In addition, we captured eight of 12 late-breeding females. All nine of the females that evaded capture had abandoned their nests before the eggs hatched and thus some may have renested and, unbeknownst to us, been caught and banded later in the season. In 2007, we captured at least 93% (100 of 107) of early-breeding females and three of six late-nesters. Of the 10 unbanded females, 9 failed in their nesting attempts and abandoned their eggs before capture, while one nested successfully but evaded capture.

Mercury Analysis

Following collection, blood and feathers were kept on ice for approximately 3-6 hours, after which time they were stored at -25° C. Feathers were washed with deionized water and air dried at low humidity prior to analysis in order to remove particulate surface mercury residues. Samples were analyzed for total mercury at the College of William and Mary on a Milestone® DMA 80 (as in Cristol et al. 2008). All results are presented as wet/fresh weight (ug/g) concentrations.

Statistical Analyses

Unbanded females represented new breeders in our population that were either formerfloaters on the site in the previous breeding season or breeders/floaters at other, presumably uncontaminated sites. Because the levels of mercury in birds at this study site greatly exceed those found at nearby uncontaminated sites, or previously reported contaminated sites elsewhere in North America (Brasso and Cristol 2008), it is unlikely that a female swallow could have obtained comparable levels of mercury without having been present on these contaminated study sites during a substantial portion of the previous breeding season. All SY females were dropped from the analysis since they had been nestlings in the previous year, and therefore could not have been floaters.

Earlier work on this Tree Swallow population had documented a significant and strong correlation between blood mercury level in one year and feather mercury level in the following year (Brasso and Cristol 2008). Using those data, we created discrete criteria for classifying newly-arriving, unbanded ASY females as either former floaters or non-floaters based on the presence of mercury in their feathers. In order to provide a conservative estimate of floater prevalence, we used the highest blood mercury level of all reference birds breeding on the nearby North or Middle Rivers as an upper estimate of mercury exposure possible for birds not present on the contaminated sites. We then applied this diagnostic blood mercury value to the regression equation presented in Brasso and Cristol (2008) to generate the expected corresponding feather mercury level. In order to reduce the possibility of falsely classifying birds as floaters, we created a 95% confidence interval around the diagnostic feather mercury value. All females that could potentially have been former floaters were then assigned to one of three categories: Females with levels below the lower limit of the confidence interval were designated as 'non-floaters,' while those above the upper limit were designated as 'floaters.' Females with feather mercury levels falling within the 95% confidence interval were classified as 'undetermined'. These same criteria were applied separately for each of the two years in which floater prevalence was estimated because of annual variation in mercury exposure. From these classifications, we estimated the minimum proportion of new breeders that had been floaters on our contaminated sites in the previous year. In 2006, the highest blood mercury level of all Tree Swallows breeding on uncontaminated reference sites (n = 51) was 0.227 ug/g. In 2007, this level was 0.310 ug/g (n = 68). The corresponding confidence intervals yielded the following criteria for assignment of floaters to three categories: In 2007, unbanded ASY breeding females with feather mercury levels below1.34 ug/g were designated as non-floaters and those above 5.32 ug/g were classified as floaters. Females with feather mercury levels between these levels were classified as undetermined (Fig. 1). In 2008, the relevant levels were 1.73 and 5.61 ug/g. Finally, we analyzed feather mercury levels for a subset of unbanded ASY females breeding on reference sites several kilometers away from contaminated sites (n = 11 sites, mean nearest distance to contaminated site 16.7 km, range 3.6-30.8 km). All analyses were performed using MINITAB Statistical Software Version 15 (Minitab Inc., State College, Pennsylvania). All means are presented ± SD.

Results

In 2007, 34 unbanded ASY females nested in boxes on mercury-contaminated sites and thus could have been detected as potential floaters from the year before. Of these, 70.6% (n = 24) had feather mercury levels above 5.32 ug/g and were classified as floaters (Fig. 2). The remaining 10 females were classified as undetermined. In 2008, 48.9% of the 45 unbanded ASY breeding females (n = 22) were classified as floaters, while 42.2% (n = 19) fell within the undetermined interval and 8.9% (n = 4) were non-floaters (Fig. 2). There was a marginally significant difference in floater prevalence between years (chi-square test: $\chi^2 = 3.75$, $P = 0.05$, df = 1). The average feather mercury level of females designated as floaters was 23.4 ± 16.6 ug/g in 2007 (n = 24) and 16.1 ± 9.8 ug/g in 2008 (n = 22). Between-year comparison of average feather mercury level of floaters yielded a non-significant trend toward higher feather mercury levels in 2007 than in 2008 (2-sample t-test: $t = 1.84$, $P = 0.07$, df = 37), consistent with the difference in blood mercury levels found in breeders in the previous two years (2006: 3.88 ± 2.40 ug/g; 2007: 2.42 ± 1.12 ug/g; 2-sample t-test: $t = 3.90$, $P < 0.001$, df = 52).

Of the 50 females sampled from nests on reference sites in 2007-2008, only 4% (n = 2) were classified as having previously floated on a contaminated site. Of the remaining 48 females, 20 were classified as non-floaters and 28 as undetermined.

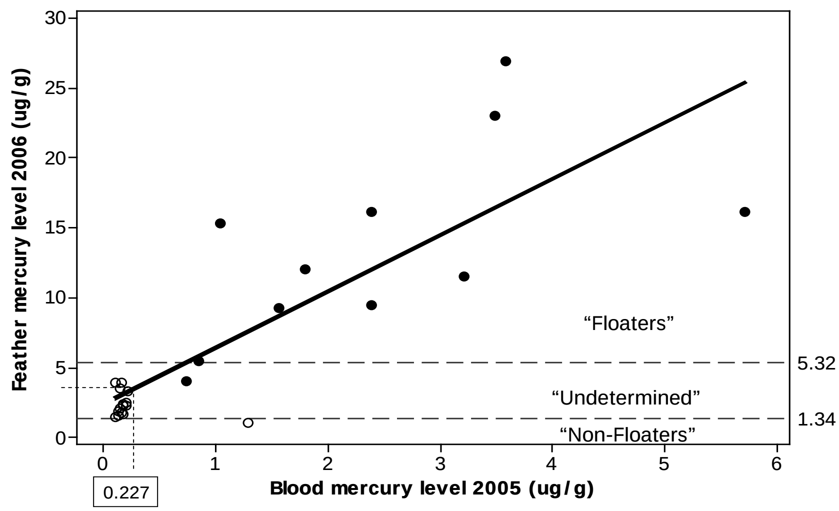

Figure 1: Criteria for classification of female Tree Swallows in 2007 as either "non-floaters," "undetermined," or "floaters," based on feather mercury level. Categories were created using the data presented in Figure 3 of Brasso and Cristol (2008). These same criteria were applied separately to both years; however, for clarity, only the categories for 2007 feather mercury levels are shown. See text for details.

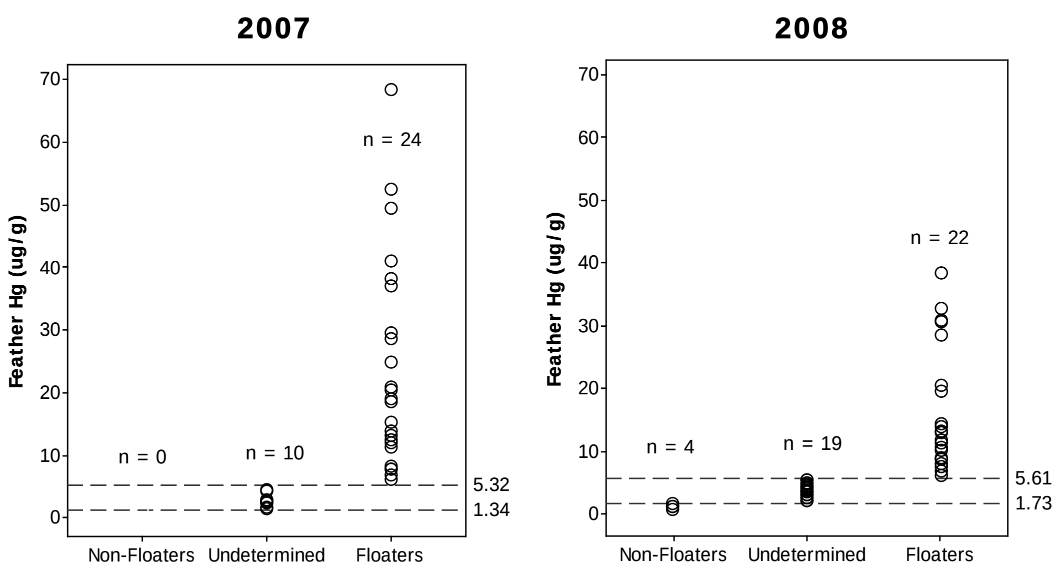

Figure 2: Interval plots of feather mercury levels of new ASY breeders present on contaminated sites in 2007 and 2008 with floater criteria for each year indicated.

Discussion

We were successfully able to employ mercury in feathers as a tracer to detect former floaters that had subsequently recruited into our breeding population of Tree Swallows. Of all new breeders on contaminated sites (excluding those hatched the previous year), we estimate that 58% (46 of 79 for 2007-2008 combined) had been floaters on one of the contaminated sites in the prior year. This is a minimum value because most other new breeders fell in the range classified as undetermined. Because our criteria were conservative, many of these undetermined birds may have been former floaters as well. None had been identified in the prior breeding season as a late-nesting bird, the method employed previously to detect floaters in this species (Stutchbury and Robertson 1985). Thus, the 46 floaters that we detected using a mercury tracer were in addition to the late-nesting floaters identified by traditional methods. On our study sites, late-nesting floaters made up approximately 10% (18 of 188 in 2006-2007) of all females present, concurring with the 11% value for an unmanipulated site reported by Stutchbury and Robertson (1985). In that study, nest box supplementation increased the estimate of floater abundance to 25% of all reproductively mature females present in the breeding population (Stutchbury and Robertson 1985).

Using the tracer described here we detected more former floaters than would have been expected if 25% of the previous year's population had been floaters. In 2006 there were 63 breeding females in the early round. Assuming, as has been done previously, that floaters comprised 25% of all females provides a total population estimate of 84 females, of which 21 would have been floaters. Of these, approximately 50% (~10 females) would have been expected to survive and return to the study site in 2007, based on typical survival rates for small songbirds, and for swallows at this site (K. K. Hallinger, unpublished data). We identified 24 former floaters in 2007 based on feather mercury levels, and an additional two recruits were identified as former floaters because they had entered the population as late breeders in 2006. These 26 former floaters represent approximately 150% more than would have been expected if floaters indeed comprised 25% of the overall population. A similar analysis for 2008 revealed 25 former floaters, approximately 40% more than expected. These results suggest either that the actual proportion of floaters within our breeding population is significantly greater than the previously reported 25%, or that floating conveys exceptionally large benefits to future cavity acquisition.

In either case, care must be taken in interpreting these data, as high rates of floater recruitment could be a direct or indirect consequence of mercury poisoning in the wider population. For example, if survival of adult breeders on contaminated sites was impaired relative to floaters, this could have led to an unusually high rate of breeder turnover and floater recruitment. Mercury has been documented to have a number of deleterious effects on wildlife (Wolfe et al. 1998), and both reproductive and immune system consequences have been reported in this population (Brasso and Cristol 2008, Hawley et al. 2009). Further investigations are currently underway to determine survivorship of contaminated and reference populations (K. K. Hallinger, unpublished data).

One possibility that we did not investigate is that Tree Swallows identified as former floaters were actually transient birds that bred or floated elsewhere before moving into our study area at the end of the breeding season to molt. It is theoretically possible that Tree Swallows from other areas were attracted to the large numbers of breeding adults at our sites and spent the period of time between reproduction and migration molting on contaminated South River sites. If this occurred, and transients acquired enough mercury to mimic true floaters, then we would have misclassified such individuals as former floaters. However, this is unlikely as there is very little suitable breeding habitat in the region other than our nest box trail. Even on nearby reference sites, only 4% of new ASY recruits bore evidence of exposure to mercury-contaminated sites, suggesting that space use by floaters is fairly localized around sites of eventual breeding. Additionally, there is a lag of several weeks between the onset of mercury exposure and high levels in feathers (Bearhop et al. 2000), further decreasing the possibility that we misclassified many transients as floaters.

Documenting degree of contaminant exposure is one of the primary goals of ecotoxicological research. An additional season of mercury exposure in a short-lived bird such as a swallow could significantly affect fitness in former floaters relative to birds arriving on a contaminated site for the first time. Additionally, floating represents a unique life history stage, and one that, at least among Tree Swallows, is not employed by all members of a population. For researchers interested in the effects of contaminants on fundamental life history and demographic parameters such as reproductive success or survival, it is critical to understand the individual histories of the birds being studied.

It is important to note that our estimates of floater abundance exceed those reported in other studies (Stutchbury and Robertson 1985). If our findings are robust, then the population of Tree Swallows living along the contaminated South River and thus, the number of individuals at risk of mercury exposure, is greater than would have been estimated by simply counting the number of breeding adults and sampling their exposure. If the population size is indeed significantly larger than previous estimates of floater abundance have implied, then traditionally performed ecological risk assessments may have underestimated the number of impacted individuals.

We successfully employed a mercury tracer to document the recruitment of many floaters into a breeding population of Tree Swallows. Little is known about the local recruitment of floaters, and the use of chemical tracers could open new avenues for their study. It is important to understand recruitment mechanisms, as these have the potential to significantly impact demographic trends and life history characteristics. In fact, there are some cases in which floaters have proven to be a "missing link" in demographic models (Penteriani et al. 2006, 2008). It has not escaped our attention that mercury is a toxic metal with potentially harmful effects on wildlife (Wolfe et al. 1998); mercury could confound results by reducing survival, making caution necessary in interpretation. However, applied conservatively, such a tracer has great potential to illuminate little known aspects of floater behavior, including the localization of movements around eventual sites of recruitment. Many regions across the world have endemic and localized compounds (either natural isotopes or contaminants); thus, a number of tracers could theoretically be applied in a similar manner to more effectively study this significant, but often invisible portion of bird populations.

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