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The Effects of Experimental Reservoir Creation on the Bioaccumulation of Methylmercury and Reproductive Success of Tree Swallows (*Tachycineta bicolor*)[†]

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Reservoir creation results in decomposition of flooded organic matter and increased rates of mercury methylation. Methylmercury (MeHg), the most toxic form of mercury, bioaccumulates through aquatic food webs. Our objective was to quantify the transfer of MeHg from aquatic food webs into terrestrial organisms. We examined rates of MeHg bioaccumulation in an insectivorous songbird, the tree swallow, breeding near an experimentally created reservoir. We also determined the impact of flooding and MeHg bioaccumulation on the reproductive success of these birds. Mean MeHg burdens in nestling swallows from near the experimental reservoir increased from 1210 $\pm$ 150 ng before flooding to 2200 $\pm$ 102 ng after flooding. Postflood MeHg concentrations in both the body and feathers of the birds were significantly greater than preflood MeHg concentrations. Although MeHg burdens in swallows were elevated in postflood years, we found no overt toxicological affects. An increase in dipteran productivity (the primary food source of tree swallows) after reservoir creation resulted in earlier nest initiation, larger eggs, and faster growth rates of wing and bill length in nestlings raised during postflood years.

Introduction

Predatory fish in reservoirs created for the production of hydroelectricity, recreation, flood control, or other purposes almost always contain methylmercury (MeHg) concentrations that far exceed consumption guidelines (*1*). Methylation of inorganic Hg appears to be enhanced by the decomposition of organic carbon in flooded soils and vegetation (*2*). MeHg is a strong neurotoxin that readily bioaccumulates through aquatic food webs (*3*−*5*).

The Experimental Lakes Area Reservoir Project (ELARP) was a multidisciplinary experiment designed to increase knowledge of the environmental impacts of reservoir creation. The two primary objectives of the study were to improve our understanding of the biogeochemical cycling of Hg in reservoirs and to quantify greenhouse gas production as a result of flooding (*6*). The ELARP was a whole-ecosystem manipulation experiment carried out at the Experimental Lakes Area (ELA) in northwestern Ontario, beginning in 1991 (*6*).

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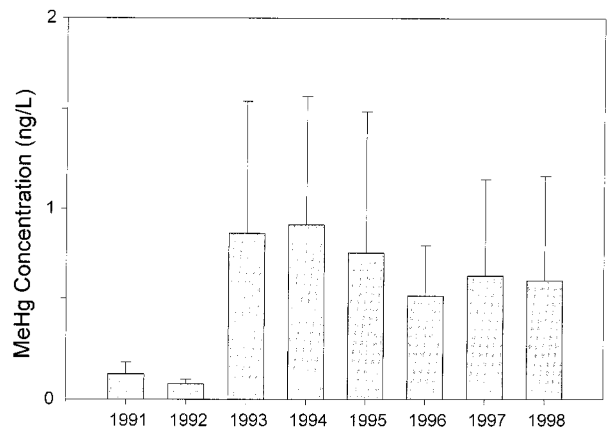

FIGURE 1. Mean annual MeHg concentration in the surface water of the central pond of the experimental reservoir. The reservoir was flooded in June of 1993.

Initial findings of the ELARP included a profound postflood increase in MeHg production in the experimental reservoir with a subsequent increase in MeHg concentrations in water and aquatic biota. Preflood MeHg concentration in the water of the central pond averaged 0.1 ng/L. This increased to 0.9 ng/L during the first two postflood years but reached concentrations as high as 2.4 ng/L (Figure 1). In surface waters, the average percentage of total Hg (THg; all forms of Hg) comprised of MeHg increased from 4% before flooding to 32% after flooding (*6*). In 1998, 6 years after initial flooding, water column MeHg concentrations were still significantly higher than those measured preflood (Figure 1).

Our objective as part of the ELARP was to quantify the transfer of MeHg between aquatic and terrestrial food webs by examining long-term rates of MeHg bioaccumulation in insectivorous songbirds (tree swallows; *Tachycineta bicolor*) breeding near the experimentally flooded reservoir. We also determined the impact of flooding and MeHg bioaccumulation on the reproductive success of these birds.

Methods

Site Description and the ELARP Experiment. A 16.7 ha riverine wetland with a 14.3 ha peatland surrounding a 2.4 ha pond (Lake 979; L979) was experimentally flooded, providing the worst-case scenario for organic carbon decomposition and Hg methylation (*6*). After 2 years of studying the natural biogeochemical cycling of MeHg and inorganic Hg in the wetland, the outflow was dammed and the water level raised 1.3 m with water flowing in from an upstream lake (Lake 240). The flooding of the peatland increased the pond's surface area by 300% and the water volume by 600%. The effects of flooding on whole-ecosystem and process-level Hg cycling were quantified by comparing preflood and postflood results (*6*). Two oligotrophic lakes (Lakes 224 and 239) were used as reference sites for this study to determine natural levels and interannual variation in Hg bioaccumulation in birds.

Dipteran Emergence. Tree swallows are aerial insectivorous birds that feed primarily on emergent dipterans from their nest site lakes (*7*). Modified LaSage Harrison emergence traps (*8*) were used to quantify the biomass of dipteran emergence from the experimental site and to collect emergence for MeHg analyses. Ten traps with sampling jars containing 70% ethylene glycol antifreeze were deployed in a transect over the pond and peatland and sampled weekly

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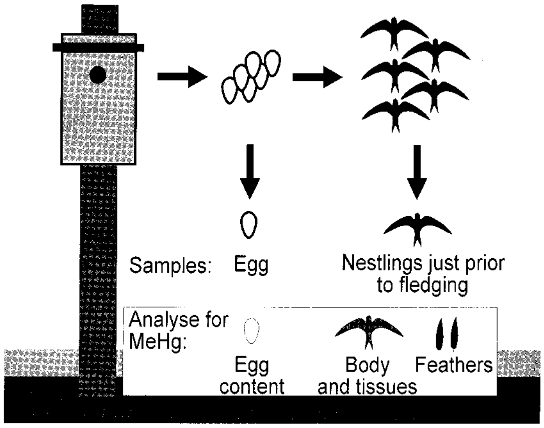

FIGURE 2. Sampling protocol to quantify MeHg bioaccumulation in embryo and nestling tree swallows.

during the ice-free season. Three additional traps without ethylene glycol sampling jars were deployed over both the pond and peatland and emergence was collected three times each week for MeHg analyses using a modified Dust-Buster vacuum system (*9*). Emergence sampled for MeHg analyses was stored in sterile Whirl-paks and frozen immediately after collection. Dipteran specimens were separated from other orders and freeze-dried prior to analyses. Dipteran tissues from 1992 to 1995 were analyzed for organic Hg (primarily MeHg) using a 3:2 methylene chloride:hexane extraction and cold-vapor atomic absorption spectrophotometry as described by Armstrong and Uthe (*10*) and Malley et al. (*11*). A number of subsamples were also analyzed by Flett Research Ltd. (Winnipeg, Manitoba) for MeHg using distillation, ethylation, and atomic fluorescence (*12*) to confirm that the organic Hg extracted using methylene chloride:hexane was MeHg. Flett Research Ltd. analyzed all dipteran tissues from 1998. One or two replicate analyses, blanks, and spikes (32 ng) were done with every distillation set of eight samples. Duplicate samples were repeated if they deviated more than 15% from the mean. Spike recovery for emergence samples was 96%. Emergence on L979 was collected initially during the first 4 years of the experiment (1992−1995) and then again in 1998 as part of an alternate year monitoring program. No emergence was collected or monitored for biomass flux on reference lakes used to monitor tree swallows. The full study of emergence biomass and MeHg flux from the entire catchment and reference wetland during the 1991−95 portion of the ELARP was completed by A. P. Weins and D. M. Rosenberg (Freshwater Institute, unpublished data).

MeHg Bioaccumulation. We began monitoring tree swallows nesting at the experimental reservoir and reference lakes in 1992 (Figure 2). All birds were handled in accordance with recommendations of the Canadian Council on Animal Care (Protocol #240804, University of Alberta). Each spring, prior to lake ice-out and swallow arrival, nestboxes were installed and mounted on either wooden posts about 1 m from shore or snags or live trees along the shoreline.

Because tree swallows feed primarily on insects emerging from near their nestsite (*7*), MeHg accumulation in nestlings is a reflection of bioavailable MeHg in the waterbody on which they were raised. Conversely, MeHg concentrations in adult tree swallows may reflect environmental levels of Hg in the wintering grounds and along migration routes. Although we did not actively sample adult tree swallows, we did occasionally find dead adults in nestboxes during the early spring and analyzed them for MeHg concentrations and burdens. These adults were collected soon after death and treated in the same manner as nestlings collected later in the season.

We used the following protocol to quantify MeHg bioaccumulation in swallows nesting near the various sites (Figure 2). To quantify the transfer of MeHg from the mother to her young, one egg was collected from each nestbox prior to hatching (Environment Canada migratory bird scientific/capture permit #CA-0016). To determine the amount of MeHg accumulated through ingestion of emergent insects during nestling growth, two or three nestlings were collected prior to fledging (approximately 17 days old). Both eggs and fledglings were frozen, usually within 1 h of collection. All tissues were stored in Ziploc bags or sterile Whirl-paks and freeze-dried prior to analysis. Other studies in our lab have shown that freeze-drying tissues resulted in no loss of MeHg (*13*). Eggshells were removed from frozen embryos, and whole embryos were analyzed. Feathers were removed from nestlings and analyzed separately because contaminants are often shunted into feathers, where they can be bound and excreted annually during molt. Feathers were first washed using warm deionized water and then homogenized using cleaned stainless steel scissors. Stomachs and intestines were removed from nestlings using acid-washed (dilute 10% HCl) stainless steel scalpels, and contents were rinsed out with deionized water prior to tissue analyses. Whole nestlings were ground using a stainless steel coffee grinder that was rinsed between uses with dilute HCl (*14*). Beginning in 1996, we analyzed three target tissues (brain, liver, and breast muscle) for MeHg bioaccumulation. These tissues were dissected out of each nestling using dilute acid-washed stainless steel scalpels and tweezers. All target tissues and embryos were homogenized using an acid-washed glass mortar and pestle. Brain tissues from birds in the same nestbox were pooled due to small brain biomass. Tissues were handled exclusively in Hg clean rooms at the Freshwater Institute, Winnipeg, and the Experimental Lakes Area field station.

A random sample of feathers, whole birds, and isolated target tissues were analyzed for both THg and MeHg. MeHg was analyzed by Flett Research Ltd. as previously described for dipteran analyses. Results from these analyses confirmed that almost all Hg in tree swallow tissues is MeHg (see results). Therefore, we used the cheaper THg analytical technique to quantify MeHg accumulation in bird tissue.

THg was analyzed at the Freshwater Institute using cold-vapor atomic absorption spectrophotometry (CVAAS) (*10, 15*). Certified Mercury Reference Solution for atomic absorption was used for standardization (0.5, 1, 5, 10, 25, 50, 100, 200 ng of THg; $r^2 = 0.99-1.0$). Two method blanks and one to three NCR Certified Reference materials (NRCC dogfish muscle, Dorm-1; dogfish liver, Dolt 2; lobster hepatopancreas, Tort-2) were analyzed using the same procedures as the samples. Recovery for all reference material was 92.3%. Spikes of 500 and 1000 ng were added to some feather tissues, with a mean (±std) spike recovery of 97.2 ± 10.5%. Mean (±std) coefficient of variation (CV) between replicates was 8.73 ± 7.85%. Interyear calibrations were conducted between periods of analyses and showed variability similar to that between replicates (CV = 11.73%).

We calculated Hg burdens for individual tissues from the dry weight of the tissue and its concentration of MeHg. Total burden for a given nestling was simply the sum of all tissue burdens (feather, body, muscle, liver, brain). Similarly, whole nestling concentrations were calculated by dividing total nestling Hg burden by total dry weight of all combined tissues.

Because parents tend to feed similar food items to all nestlings within a clutch, we calculated mean Hg concentrations and burdens for all birds within the same clutch prior to calculating mean site values. We also pooled data from both reference lakes prior to calculating mean Hg concentrations and burdens to increase sample sizes. Any late nesting attempts (e.g., due to failed first clutches) were excluded from all analyses because as lake temperatures increase, so do Hg methylation and MeHg bioaccumulation in dipteran emergence.

We predicted that there would be elevated MeHg concentrations in all organisms throughout the food chain following the large increase in the MeHg concentration in the water of the experimental reservoir after flooding (*6*). To determine if flooding had an impact on MeHg accumulation in tree swallows, we used a one-way analysis of variance (ANOVA-SigmaStat 4) to compare nestling tissue concentrations and MeHg burdens between years. A pairwise multiple comparisons Tukey test was used to determine which years were significantly different from the others. To identify natural interannual variation, we compared MeHg concentrations and burdens in tree swallows at reference lakes using the same procedure as that for the experimental reservoir (ANOVA and pairwise multiple comparison Tukey test). We compared individual tissue concentrations from the experimental reservoir with those from reference lakes using nonparametric Mann−Whitney tests to compensate for nonnormal distributions. To examine the relationship between feather and body tissues we used linear regression to correlate feather with muscle, liver, and brain concentrations. Conversion ratios of feather:liver:muscle were then calculated for all birds by dividing feather and liver concentrations by muscle concentrations.

This experimental design is an impact analysis (*16, 17*) and does not replicate experimental units, due to the difficulty of replicating whole-ecosystem experiments. We were further limited statistically on the reference lakes by the small number of clutches laid and the lack of successful clutches during the first year of the experiment (1992), leaving us with only one comparable preimpact year for reference lakes. However, the data are strong enough to show clear trends and we use inferential statistics to emphasize our results, acknowledging the implication of pseudoreplication as described by Hurlbert (*18*).

Reproductive Success. In conjunction with monitoring MeHg bioaccumulation in tree swallows, a number of reproductive parameters were measured to determine whether flooding and increased levels of MeHg had an effect on reproductive success. Clutch initiation date, number of eggs per clutch, egg size, incubation length, hatching success, growth rates of nestlings, and fledging success were quantified for all clutches, as outlined by St. Louis and Barlow (*19*). Growth rates were quantified by measuring wing, tail, tarsus, and bill lengths, bill width, and body weight every 2−3 days between hatching and fledging. Due to funding constraints, no reproductive parameters were measured during 1996 and growth rates of nestlings were not quantified in 1997 and 1999. We also omitted all reproductive parameters measured for females less than 2-years old, identified by noniridescent brown feathers on their back. Young females tend to be inexperienced breeders, and their reproductive success may be lower than older birds (*19, 20*).

To examine the impact of flooding on reproductive success, we used t-tests to compare the different reproductive parameters between preflood and postflood. We accepted p-values < 0.01 as indicating significant differences, due to the large number of parameters tested (*21*). We pooled all reproductive parameters measured at the two reference lakes prior to conducting t-tests between the preflood (1993) and postflood (1994−98) years. We tested for differences in the growth rates between preflood and postflood years by comparing linear slopes of temporal changes of wing, tail, and bill lengths ($r^2 = 0.92-1.0$ for wing length; $r^2 = 0.91-1.0$ for tail length; $r^2 = 0.80-1.0$ for bill length). Sigmoidal changes in bill width, tarsus length, and weight were fitted to a logistic model ($r^2 = 0.87-1.0$ for bill width; $r^2 = 0.90-1.0$ for tarsus length; $r^2 = 0.91-1.0$ for weight) and used to compare the growth rate constant (K) and the asymptote (a) or upper limit of growth (*22, 23*). For bill width we included days 1−13 and for weight days 1−15, thus avoiding the recession period in both measurements. After removing the females less than 2-years old from our reference lake data set, there were only two clutches for the preflood period. Thus, we only compared growth rates and constants from postflood reference lakes with those from the postflood experimental reservoir. We used nonparametric Mann−Whitney tests for all comparisons to account for nonnormal distributions or inequalities in variance of some growth rates or constants.

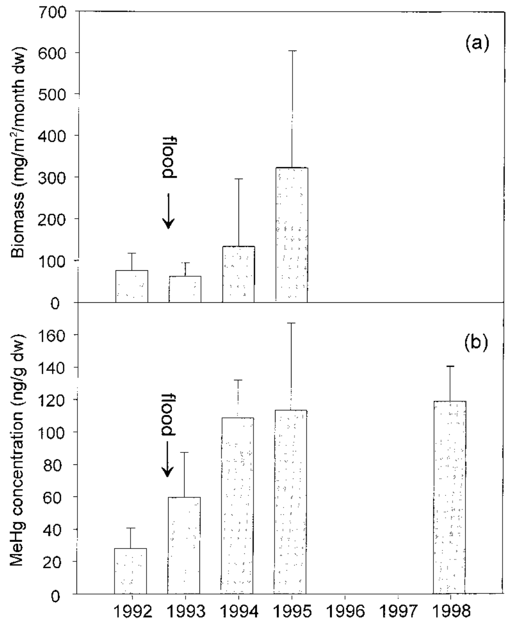

FIGURE 3. Mean monthly biomass of Dipteran emergence from the pond of the experimental reservoir before and after flooding (a), mean monthly MeHg concentration in the emergence (b) (A. P. Weins and D. M. Rosenberg, unpublished data).

Results

Dipteran Emergence. The mean (±std) monthly (May−October) biomass of dipteran emergence (primarily Chironomidae) from the pond of the experimental reservoir was greater in postflood years (197 ± 238 ng/m^2/month) than in preflood years (73.9 ± 40 ng/m^2/month; Figure 3a), although this difference is not significant due to seasonal variation (A. P. Weins and D. M. Rosenberg, unpublished data). Similarly, mean (±std) postflood MeHg concentrations in emergent dipterans were greater (111 ± 2.4 ng/g dry weight) than preflood (43.8 ± 15.8 ng/g dry weight) (A. P. Weins and D. M. Rosenberg, unpublished data). Six years after the initial flooding of the reservoir, dipteran MeHg concentrations were still elevated (119 ± 21.6 ng/g dry weight; Figure 3b). Because postflood biomass of emergence and MeHg concentrations in diptera were greater than preflood, postflood flux of MeHg out of the reservoir via dipteran emergence was also greater. These results only include dipteran emergence directly over the pond of the reservoir and not over the flooded peatland.

Chemical Form of Hg in Tree Swallows. We found a near 1:1 relationship between concentrations of THg and concentrations of MeHg in all tissues analyzed from tree swallows ($r^2 = 0.88$, slope = 0.91, $p < 0.001$; Figure 4), excluding two liver samples with much lower concentrations of MeHg than concentrations of THg. From the 20 liver samples that we analyzed for both MeHg and THg, all but those two fit a 1:1 relationship ($r^2 = 0.83$, slope = 1.06, $p < 0.001$). Although these two liver samples suggest that there might be MeHg demethylation occurring in some proportion of livers, due to funding constraints we could not directly analyze more liver samples for MeHg.

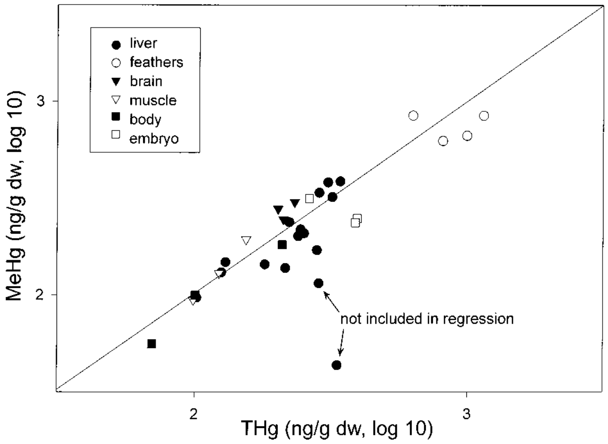

FIGURE 4. log−log relationship between MeHg and THg concentrations (ng/g dry weight) in nestling tree swallow tissues. Indicated liver samples were not included in the regression because Hg demethylation may have occurred in these livers (see discussion).

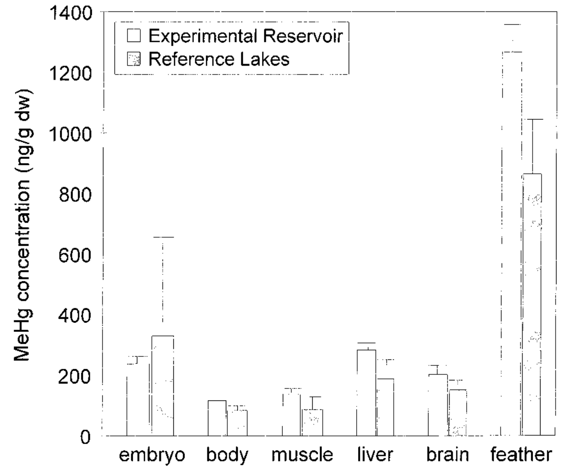

FIGURE 5. MeHg concentrations in nestling tree swallow tissues near the experimental reservoir and reference lakes.

Hg in Adult Tree Swallows. We found nine adult tree swallows dead in nestboxes over the course of the study. Hg concentrations and burdens in adults were highly variable. Body concentrations ranged from 214 to 1110 ng/g dry weight (mean = 517 ng/g dry weight; coefficient of variation = 57%). Feather concentrations ranged from 843 to 2740 ng/g dry weight (mean = 1690 ng/g dry weight; coefficient of variation = 41%). Total body burden of Hg in adult tree swallows ranged from 2760 to 8540 ng (mean = 4760 ng). Although we did not include adult bird tissue in our analyses of MeHg:THg, we assume that the majority of the Hg in adult birds is methylated.

Hg Bioaccumulation in Tree Swallow Embryos and Nestlings. *Concentrations.* MeHg concentrations in embryos were variable between years at all sites (Table 1). Mean (±std) MeHg concentrations at the experimental reservoir and references lakes were 365 ± 35 and 270 ± 18 ng/g, respectively (Table 1). Concentrations of MeHg in embryos collected in 1992, a preflood year, were higher than other years ($p < 0.01$) on the experimental reservoir, whereas there were no differences between years in concentrations of MeHg in embryos at reference lakes ($p = 0.31$) (Table 1).

Mean concentrations of MeHg in nestling bodies were 81.6 ± 5.1 ng/g at the reference lakes and 82.8 ± 2.2 ng/g at the experimental reservoir in the 2 years prior to flooding (Table 1). Mean concentrations of MeHg in nestlings bodies were 130 ± 11 ng/g after flooding (Table 1). Although mean concentrations of MeHg in postflood nestling bodies were 36.3% higher than concentrations measured preflood, only concentrations in nestlings collected in 1994 were significantly higher than all other years ($p < 0.001$).

Postflood feather MeHg concentrations were also higher than preflood (Table 1). Preflood mean concentration of MeHg in feathers was 747 ± 43 ng/g at reference lakes and 872 ± 75 ng/g at the experimental reservoir. Postflood mean feather MeHg concentration was 1210 ± 53 ng/g in nestlings collected at the experimental reservoir and was higher ($p = 0.01$) than during the preflood period, with the exception of 1992 versus 1994 and 1995. There were no differences in feather MeHg concentrations between years at reference lakes ($p = 0.06$).

Concentrations of MeHg in tissues dissected from nestlings from 1996 to 1999 were higher in those collected from the experimental reservoir than in those collected from the reference lakes (Figure 5). For all nestlings combined, concentrations of MeHg were highest in feathers, 78% lower in liver, 84% lower in brain, and 90% lower in muscle tissue. Liver, muscle, and brain concentrations correlated with

TABLE 1. MeHg Concentrations (dry weight) in Tree Swallow Embryos, and Nestling Bodies and Feathers, from the Experimental Reservoir and Reference Lakes

		embryo			body			feather		
		concentration (ng/g)	SE	*N*	concentration (ng/g)	SE	*N*	concentration (ng/g)	SE	*N*
		experimental reservoir								
preflood	1992	518	25.9	4	80.7	3.2	4	947	34.2	4
	1993	476	50.0	5	86.0	7.0	6	796	26.6	6
postflood	1994	364	47.1	6	110	4.7	6	1070	68.6	6
	1995	314	38.8	8	188	15.1	8	1090	63.8	8
	1996	285	17.4	9	124	10.6	9	1290	43.9	9
	1997	318	21.8	9	120	4.2	9	1330	61.5	9
	1998	413	41.8	6	117	4.9	7	1110	55.3	7
	1999	230	28.4	6	123	5.3	6	1340	75.4	6
		reference lakes								
	1992	267	31.6	3						
	1993	366	59.2	4	70.4	7.5	4	604	75.0	4
	1994	276	42.1	3	95.6	9.9	4	924	81.8	4
	1995	288	8.2	3	70.2	5.1	3	648	46.7	3
	1996	307	7.1	2	75.0	12.8	2	735	46.0	2
	1997	220	7.1	2	102	32.2	2	851	174	2
	1998	214	70.5	3	81.7	6.3	3	677	43.3	3
	1999	221	12.0	2	67.5	5.0	3	788	21.8	3

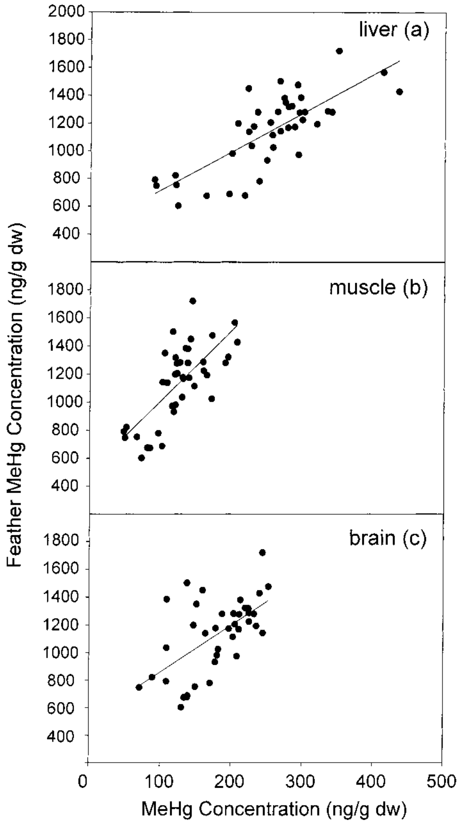

FIGURE 6. Plot of relationship between MeHg concentration in feathers and liver ($r^2 = 0.59$, $p < 0.001$) (a), muscle ($r^2 = 0.52$, $p < 0.001$) (b), and brain ($r^2 = 0.35$, $p < 0.001$) (c) in nestling tree swallows.

TABLE 2. MeHg Burdens in Tree Swallow Embryos and Nestlings from the Experimental Reservoir and Reference Lakes

		embryo burden (ng)	embryo SE	embryo N	whole bird burden (ng)	whole bird SE	whole bird N	% burden from embryo
		experimental reservoir						
preflood	1992	108	5.5	4	1370	83.1	4	7.99
	1993	111	6.9	6	1060	121	6	10.7
postflood	1994	110	31.6	6	1930	109	6	5.94
	1995	81.4	9.5	8	1950	150	8	4.16
	1996	82.4	4.6	9	2410	105	9	3.46
	1997	86.7	12.8	4	2430	131	9	3.37
	1998	96.4	8.3	6	2080	88.6	7	4.69
	1999	61.5	5.7	5	2460	118	6	2.43
		reference lakes						
	1992	67.62	10.1	3				
	1993	82.18	9.4	4	1050	168	4	8.21
	1994	55.61	24.1	3	1640	105	4	3.64
	1995	69.70	5.2	3	1150	60.3	3	6.12
	1996	77.98	20	2	1280	207	2	5.99
	1997	66.09	9.3	2	1460	383	2	4.66
	1998	43.96	15.8	3	1320	70.2	3	3.22
	1999	59.03	4.4	2	1400	83.5	3	4.03

feather concentrations ($r^2 = 0.59$, $p < 0.001$ for liver; $r^2 = 0.52$, $p < 0.001$ for muscle; $r^2 = 0.35$, $p < 0.001$ for brain; Figure 6). We calculated a conversion ratio for feather:liver: muscle of 10:2:1 for birds from all sites. There was some variation in this ratio between individuals, ranging from 6.8 to 16.3 for feather:muscle and from 1.5 to 2.6 for liver:muscle.

Body Burdens. As with concentrations, embryo Hg burdens at all sites were variable between years (Table 2). Mean embryo burdens ranged from 44 to 111 ng MeHg. We found

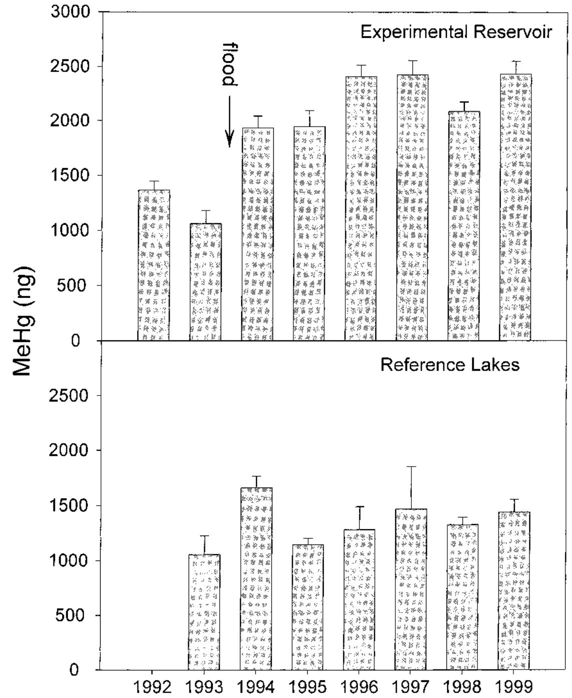

FIGURE 7. MeHg burdens in nestling tree swallows near the experimental reservoir and reference lakes.

no difference between preflood and postflood years on the experimental reservoir ($p = 0.17$) or on reference lakes ($p = 0.58$). Embryo burdens, representing the transfer of Hg from mother to young, ranged from 1.2% to 10.7% of the eventual total Hg burden in prefledging nestlings (Table 2).

Mean postflood MeHg burdens in nestlings at the experimental reservoir were higher (2200 ± 102 ng; $p < 0.001$) than before flooding (1210 ± 150 ng; Figure 7). Conversely, there was no difference in mean Hg burdens at the reference lakes between years ($p = 0.317$), although there was some year-to-year variation (Figure 7).

Reproductive Success. Tree swallows on the experimental reservoir began nesting earlier in the postflood years than preflood. Mean clutch initiation date changed from day 151 ± 1.2 preflood to day 145 ± 0.8 postflood in clutches on the experimental reservoir ($p = 0.006$; Table 3). Tree swallows on the reference lakes establish nests on day 150 ± 1.0 in all years ($p = 0.07$ for 1992/93 versus 1994−99 on the reference lakes; Table 3). Postflood egg width and volume were higher than preflood at the experimental reservoir. Egg width was 13.4 ± 0.07 mm^3 preflood and 13.8 ± 0.06 mm^3 postflood ($p = 0.004$). Egg volume was 1670 ± 19 mm^3 preflood and 1820 ± 18 mm^3 postflood ($p < 0.001$). There were no between-year differences in egg width or egg volume at the reference lakes ($p = 0.07$ for egg width and $p = 0.08$ for volume). There were also no differences between preflood and postflood clutches in egg weight or length, eggs per clutch, total volume in the clutch, incubation length, hatchability, growth period, or fledging success at the experimental reservoir. Similarly, there were no differences between years in any of these same tree swallow reproductive parameters from reference sites (Table 3).

Both wing and bill length growth rates were higher in tree swallows nesting at the experimental reservoir after flooding than prior to flooding (Figure 8). Wing length growth rates changed from 4.2 ± 0.1 to 5.0 ± 0.1 mm/day ($p = 0.001$), and bill length growth rates changed from 0.17 ± 0.01 to 0.22 ± 0.01 mm/day ($p = 0.005$; Table 4). There were no differences in preflood and postflood tail length growth rates or growth

TABLE 3. Mean Values ($\pm$SE) for Egg Size and Reproductive Parameters Examined in Tree Swallows Nesting near the Experimental Reservoir and Reference Lakes

	preflood experimental reservoir			postflood experimental reservoir			t-test[a]	92/93 reference lakes			94−99 reference lakes			t-test[b]
	mean	SE	*N*	mean	SE	*N*	*p*	mean	SE	*N*	mean	SE	*N*	*p*
reproduction														
initiation date (day of year)	151	1.2	8	145.2	0.8	41	0.006	153.8	1.2	5	150	1.0	18	0.07
no. of eggs/clutch	6.3	0.3	8	6.3	0.1	41	0.81	6.0	0.3	5	5.7	0.3	20	0.3
incubation length (days)	19.3	0.5	8	19.9	0.3	34	0.36	19.5	0.5	2	19.6	0.5	14	0.95
hatchability (%)	87.8	6.1	8	86.2	4.4	41	0.88	53.3	22.6	5	73.0	7.9	19	0.3
growth period (days)	17.0	0.7	6	15.4	0.2	27	0.012	17.5	0.5	2	15.8	0.4	13	0.1
fledging success (%)	75.0	16.4	8	89.3	5.1	29	0.27	66.7	33.3	3	98.6	1.4	14	0.04
egg size														
weight (g)	1.7	0.03	8	2.0	0.04	41	0.039	1.7	0.06	5	1.6	0.06	19	0.6
length (mm)	18.5	0.19	8	19.0	0.1	41	0.059	18.7	0.5	5	19.0	0.2	19	0.6
width (mm)	13.4	0.07	8	13.8	0.06	41	0.004	13.2	0.1	5	13.6	0.09	19	0.07
volume (mm^3)	1670	19.3	8	1820	17.5	41	<0.001	1660	41.7	5	1770	30.4	19	0.08
total volume in clutch (mm^3)	10480	505	8	11520	245	41	0.084	9900	362	5	10020	536	19	0.9

[a] Preflood vs postflood on the experimental reservoir. [b] Preflood period vs postflood period on the reference lakes.

constants for bill width, tarsus length, and weight (Table 4). Similarly, preflood and postflood asymptotes for bill width, tarsus length, and weight were not different.

We found no significant difference between any of the growth characters measured (growth rate, growth constant, and asymptote) in postflood nestlings from the experimental reservoir and nestlings from reference lakes during the same period (1994−1998), including wing and bill length. Unfortunately, mature females (>2 years old) on reference lakes raised only two successful clutches during the preflood period (both in 1993). Given these low numbers, we could not statistically compare preflood and postflood periods on reference lakes.

Discussion

We found that tree swallow nestlings from around the experimentally created reservoir had higher MeHg tissue concentrations and body burdens after flooding than prior to flooding. MeHg burdens were elevated in nestling tree swallows during the first year of flooding and remained high during six consecutive breeding seasons. Conversely, MeHg concentrations and burdens in nestling tree swallows on reference lakes in the area did not increase during the course of the study. Changes in MeHg concentrations and body burdens in nestlings on the experimental reservoir mirrored changes in concentrations observed in both the water of the experimental reservoir and in dipteran insects emerging from the reservoir.

Dipteran Emergence. Preflood mean MeHg concentrations in emergent dipterans were lower than those of the first three postflood years, and concentrations were still elevated in 1998, 6 years after initial flooding. Hg methylation primarily occurred in the sediments and flooded vegetation and peat of the experimental reservoir (*6*) where larval diptera live prior to emergence. Parkman and Markus (*24*) found that Hg uptake by sediment-dwelling organisms was likely the result of elevated Hg concentrations in both their diet and physical surroundings. Postflood mean monthly flux of MeHg in dipteran emergence from the central pond was higher because of both elevated MeHg concentrations in postflood insects and elevated biomass of emergents from the reservoir. Given that tree swallows at the ELA are known to feed on emergents from their nestsite lake (*7*), we conclude that the experimental reservoir provided a large source of MeHg to tree swallows nesting near it, especially when emergence biomass is high (*25*). Similarly, an examination of bioaccumulation of heavy metals (not including Hg) in nestling tree swallows revealed that metal body burdens in adult midges were accumulated from contaminated sediments and that ingestion of these insects resulted in accumulation of metals in nestling tree swallows (*26*). Bishop et al. (*27*) also showed that Hg concentrations in tissues of tree swallows and red-winged blackbirds (*Agelaius phoenicues*) correlated with Hg levels found in sediment from the lakes near their breeding sites.

Postflood MeHg concentrations in diptera (63−202 ng/g dry weight) were below those known to cause toxicological effects in birds but near those that may cause reproductive or behavioral impairment. In a controlled feeding experiment of three generations of mallard ducks, females laid fewer eggs and produced fewer ducklings, and ducklings were less responsive to warning calls and hypersensitive to fright stimuli after being fed 500 ng/g dry weight MeHg (*28*). Similarly Barr (*29*) found reductions in egg laying and territorial fidelity in common loons (*Gavia immer*) consuming prey with 300−400 ng/g wet weight MeHg.

Chemical Form of Hg in Nestling Tree Swallows. We found a strong 1:1 relationship between MeHg and THg in all tree swallow tissues, confirming that most Hg in nestling tree swallows is MeHg. Studies have demonstrated that all mercury in feathers is MeHg, and it has a high affinity for sulf-hydryl groups found in the amino acids of feather keratin (*30, 31)*. Thompson and Furness (*30*) also found that all Hg found in muscle of a number of species of seabirds was MeHg, although others have found less than 100% MeHg in muscle tissue (*32*). The relationship between MeHg and THg found in livers is less clearly understood. It appears that as Hg accumulation increases, the proportion of the hepatic Hg that is MeHg decreases. Scheuhammer et al. (*33*) showed that as THg concentrations increased in liver tissues of common loons, the fraction that was MeHg decreased. Furthermore, some long-lived, slow-molting species (most commonly from the order Procellariiformes) have more than 90% inorganic mercury in their livers despite high MeHg concentrations in other tissues, while other seabirds with low Hg burdens have close to 100% hepatic MeHg (*30, 32, 34, 35*). We found 100% hepatic MeHg in most of the tree swallows we analyzed. However, there were two individuals with considerably lower hepatic MeHg:THg. It is possible that Hg demethylation may occur in tree swallow livers; however, additional examinations of both the demethylation process and proportion of MeHg:THg in specific species of birds are required.

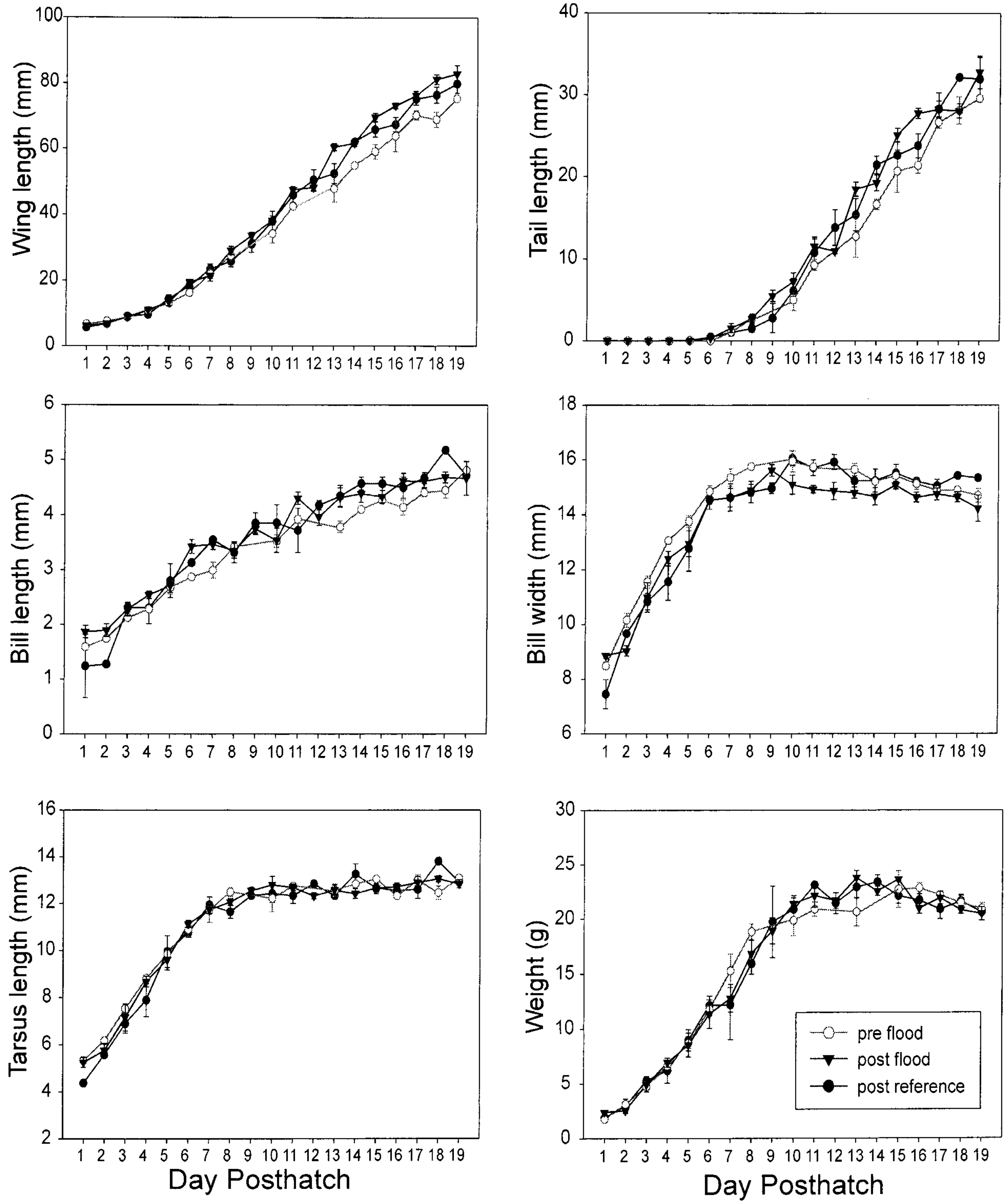

FIGURE 8. Growth plots (mm/day) for nestling tree swallows near the experimental reservoir (preflood and postflood) and reference lakes.

Hg in Adult Tree Swallows. Hg burdens in birds should depend on levels of Hg in the food they consume, their length of exposure to Hg (i.e., their age), and/or stage of molt because birds shed Hg in their feathers (*36*). Tree swallows breeding at our study site winter in the southern United States, Central America, and northern South America (*37*) and undergo one complete molt annually between mid-July and early November (*38*). All adult tree swallows collected were found in early spring, following migration and exposure on their wintering grounds, and most likely varied in age. In the limited number of adult tree swallows analyzed, Hg concentrations were highly variable. This is to be expected in birds of the same species that are possibly from different wintering areas and of different age and is common in all birds. Hg concentrations ranged from 80 to 330 ng/g THg in muscle of adult mallard (*Anas platyrhnchos*) and black ducks (*Anas rubripes*) surveyed nationwide in the United States (*39*). Similarly THg concentrations in adult common loon blood from five regions across North America ranged from 600 to 3600 ng/g (*40*).

Hg in Tree Swallow Embryos. Embryonic MeHg burdens represent the transfer of MeHg from mother to young. As

TABLE 4. Growth Rates and Growth Rate Constants (*K*, the logistic equation; mm/day) for Growth Measurements on Nestling Tree Swallows from the Experimental Reservoir and Reference Lakes

	preflood experimental reservoir			postflood experimental reservoir			Mann−Whitney[a]	1994−1998 reference lakes			Mann−Whitney[b]
	mean	SE	*N*	mean	SE	*N*	*p*	mean	SE	*N*	*p*
						growth rate					
wing length	4.20	0.095	6	4.96	0.06	20	0.001	4.82	0.14	13	0.95
tail length	2.65	0.084	6	2.89	0.07	20	0.055	3.01	0.08	13	0.17
bill length	0.17	0.007	6	0.22	0.01	20	0.005	0.203	0.01	12	0.69
						growth constant					
bill width	3.68	0.20	6	4.92	0.19	19	0.12	5.34	0.45	10	0.08
tarsus length	4.53	0.34	6	4.44	0.16	21	0.98	4.71	0.29	12	0.83
weight	6.16	0.43	8	6.86	0.30	19	0.58	6.92	0.28	12	0.91

[a] Preflood vs postflood on the experimental reservoir. [b] Postflood on the experimental reservoir vs postflood period on the reference lakes.

with adults arriving at our breeding sites, we found highly variable MeHg concentrations in tree swallow embryos. There were no between-year differences between preflood and postflood embryonic MeHg concentrations or burdens, although embryonic MeHg concentrations and burdens from the experimental reservoir were higher than those from the reference lakes (Tables 1 and 2).

According to Becker (*41*), who examined Hg levels in clutch sequence of Charadriiformes (Plovers, Sandpipers, Gulls, Terns, and Jaegers), the first egg laid contained up to 39% more Hg than the second or third eggs laid. Because we do not know the order in which eggs were laid or which egg was sampled within a clutch, variation in Hg loading between eggs may explain some of the variability in embryonic MeHg concentrations and burdens.

We chose to analyze freeze-dried tissues to eliminate variability associated with partial desiccation of wet samples during freezing and storage. By drying samples we reduced the total nestling weight by between 60% and 75% (but considerably less for feathers) and as a result concentrated the Hg in tissues. Many of the studies we have used for comparison purposes used wet weight Hg concentrations that would be much higher if given on a dry weight basis. Unfortunately tissues were not weighed before they were freeze-dried and mean moisture content is not available.

In a controlled feeding experiment with ring-necked pheasants (*Pheucticus ludovicianus*), eggs containing 500−1500 ng/g wet weight showed lower hatchability (*42*). Heinz (*28*) also found declines in reproductive success in mallard ducks with egg Hg concentrations of 860 ng/g wet weight. Our mean embryo concentrations ranged from 213 to 518 ng/g dry weight, and, with the exception of one that was 710 ng/g dry weight, all individual embryo concentrations were below 600 ng Hg/g dry weight. All our embryo were well below the suggested threshold for overt toxic effects.

Hg in Nestling Body and Tissues. Postflood MeHg burdens were higher than preflood MeHg burdens in tree swallow nestlings from around the experimental reservoir. Six years after the initial flooding of the reservoir, there was no evidence of decline. Because embryonic MeHg burdens from around the experimental reservoir were extremely variable and showed no difference between pre- and post-flooding, higher postflood MeHg burdens in nestling tree swallows were most likely the direct result of changes in MeHg concentrations in their dipteran insect food source.

Although not statistically significant, nestlings raised on the experimental reservoir after flooding had higher MeHg body concentrations than those raised before flooding. These postflood whole body concentrations (110−188 ng/g dry weight) were lower than most levels (110−690 ng/g Hg wet weight) found in four other species of first-year birds (grackles, *Quiscalus quiscula;* starlings, *Sturnus vulgaris;* red-winged blackbirds; and cowbirds, *Molothrus aterwhat*) in Maryland (*43*). Feather MeHg concentrations were higher in postflood nestlings and were within the range of concentrations (median, 1400 ng/g; range, undefined−1.4 ng/g wet weight) summarized by Burger (*44*) from eight studies based on passerines. It is generally accepted that 5000 ng/g MeHg wet weight in bird feathers is the critical level for toxic effects (*31*). All tree swallows that we examined had feather MeHg concentrations well below that level.

MeHg concentrations in liver, muscle, and brain were higher in birds from the experimental reservoir than from the reference lakes. However, all tissue concentrations remained below critical levels known to cause toxic effects. For example, concentrations of MeHg in tree swallow nestlings were similar to those seen in immature insectivorous ducks (common goldeneyes, *Bucephala clangula*) from uncontaminated areas (*45*). Fimreite (*45*) found livers in immature common goldeneyes in northwestern Ontario to have between 220 and 530 ng/g THg wet weight, similar to the mean liver MeHg concentrations of 282 ± 9.6 ng/g dry weight in nestlings from the experimental reservoir after flooding. As in feathers, liver Hg concentrations of 5000 ng/g wet weight are generally associated with major toxic effects (*46*). Although there is no established critical level for MeHg concentrations in muscle, Heinz (*28*) associated a decline in reproductive success with concentrations between 670 and 830 ng/g wet weight in muscle of mallard ducks, much higher than postflood concentrations in tree swallow nestlings in our study (137 ± 5.7 ng/g dry weight). Elbert and Anderson (*47*) found that the critical brain concentration of MeHg in birds is 500 ng/g wet weight, although other studies have cited slightly higher levels (*46*). In passerines, Scheuhammer (*48*) reported 25% fatality in zebra finches with brain Hg residues of 20 000 ng/g wet weight, much higher than the 202 ± 7.8 ng/g dry weight brain concentrations in tree swallows nesting on the experimental reservoir after flooding.

Although Hg concentrations in tree swallow tissues were below those known to be fatal, relatively little is known about long-term, low-level Hg uptake and associated behavioral and physical changes. Heinz (*28*) found that females of three generations of mallard ducks fed 500 ng/g MeHg dry weight laid a greater percentage of their eggs outside their nestboxes and laid fewer eggs then control birds. Ducklings from parents fed MeHg were less responsive to maternal calls and were hyper-responsive to fright stimuli relative to ducklings from control broods. Long-term, low-level exposure may also increase susceptibility to infection (*49*). Spalding et al. (*50*) examined great white herons (*Ardea herodians*) that were dying of chronic multiple diseases and found elevated Hg body burdens as compared with those birds that were only acutely sick.

Once their plumage has completed development (at about 30 days old), tree swallows must rely on other physiological mechanisms of Hg excretion. If they continue to feed in areas with food containing relatively high MeHg levels, such as those found around our experimental reservoir, concentrations in their body and tissues will likely continue to increase relatively quickly. The impact of elevated MeHg in young birds and the associated postfledging risks may also be important and should therefore be examined.

Tissue Hg Relationships. Bird feathers are commonly used as a noninvasive method of monitoring MeHg bioaccumulation in bird populations and archived museum specimens (*51*−*53*). Hg that is bound to feathers is stable and resistant to weathering even over long periods of time (*54*). In an effort to improve understanding of the relevance of using feather Hg concentrations in assessing levels of Hg toxicity in birds, many studies have examined the relationship between concentrations of Hg in feathers and concentrations of Hg in target tissues such as muscle, liver, and brain. Our study is one of only a few, however, that have focused on passerines or immature birds.

The relationship between Hg burdens in embryos and nestlings has also been left relatively unexamined. We found that embryo burdens formed a small percentage of the total nestling MeHg burden after approximately 18 days of growth and that there was no relationship between concentrations of MeHg in embryos and in tissue of nestlings subsequently collected from the same nestbox. This lack of relationship is most likely due to nestlings receiving the majority of their MeHg burdens from the food they consume and not from their mother. This conclusion is supported by observations of increased rates of Hg methylation and concentrations of MeHg in dipterans in the reservoir throughout the summer.

The relationship between concentrations of MeHg in feathers and body tissues was much stronger than those found between nestlings and embryos. The relationship between feather:liver:muscle Hg concentrations was found to be approximately 7:3:1 ratio wet weight in a variety of other studies (*55, 56*), although Thompson et al. (*34*) explained in his review that molting pattern and the relative proportion of MeHg to inorganic Hg can complicate this generalization. We found a ratio of 10:2:1 for feather:liver:muscle dry weight MeHg concentrations with some variation between birds. During feather growth, MeHg in the blood readily binds with sulf-hydryl groups in feathers and feathers can act as MeHg sinks that are lost during molt. After feather growth ceases, the blood supply to them atrophies and MeHg can no longer be bound. MeHg then begins to accumulate in body tissues. This phenomenon may explain the proportionately higher concentration of MeHg in nestling bird feathers when compared with feathers in adult birds from other studies. According to Thompson (*34*), the generalized relationship is best used in species with low Hg burdens where the majority of Hg is MeHg and when demethylation of MeHg to inorganic Hg in the liver is not important. Here the use of feathers from nestlings of a relatively constant age standardizes for recent dietary intake and molt stage.

In our study, brain concentrations were only weakly correlated with feather concentrations. Elbert and Anderson (*47*) found brain concentrations in grebes (*Aechmophorus occidentalis*) to plateau at 335 ng/g. If brain concentrations of MeHg plateau early during nestling growth, we would not expect to find a relationship between brain concentrations and those in feathers still growing and accumulating MeHg. However, we have no evidence of a plateau of MeHg concentration in the brains of tree swallow nestlings.

Reproductive Success. All tree swallow embryos and nestlings collected at the experimental reservoir and reference lakes had MeHg concentrations below documented critical concentrations for extreme toxicological effects. We also found no obvious negative impacts of elevated MeHg bioaccumulation on the reproductive success and survivorship of the birds at the experimental reservoir. Instead, we found that the fitness of birds nesting on the experimental reservoir positively responded to the increase in dipteran food supply after flooding. In particular, postflood clutches were started earlier and had eggs with a slightly larger volume than preflood clutches. Growth rates of wing and bill length were also greater in postflood nestlings compared to those raised at the site prior to flooding. In contrast, there was no change in any reproductive parameters in clutches from the reference lakes over the course of the study, although there was also no difference between growth rates in nestlings at the experimental reservoir and those at reference lakes.

It appears that the increase in dipteran insect emergence after creation of the experimental reservoir had a positive effect on female fitness as reflected in certain aspects of egg size. We found that individual egg width and volume were greater in postflood clutches than in preflood. However, the increase in food abundance at our experimental site did not affect total egg volume per clutch, hatchability, or fledging success. Total investment in a clutch most likely reflects the ability of females to overcome the energetic demands of egg production (*19*). Quinney et al. (*57*) examined tree swallow populations on three lakes in Ontario with varying degrees of insect abundance and suggested that food availability had a large impact on the quality of parental care during the nesting period. Both DeSteven (*20*) and Quinney et al. (*57*) found that female condition had significant effects on egg mass, and many studies have linked food abundance with reproductive success (*20, 58*).

It has also been suggested that food supply is a cue for the timing of breeding in birds and that laying date is determined by the timing and availability of enough food for females to form eggs (*59*). Dipteran insect emergence was much greater on the experimental reservoir in the years after flooding and thus probably affected the clutch initiation date of breeding tree swallows there. In small birds, Davies and Lundberg (*60*) suggested that overall reproductive success might be limited more by the ability to feed young rather than to form eggs. As a result, clutch initiation date and fledging success may be more affected by food supply than clutch size.

Food supply and parental care also play a large role in nestling growth. Quinney et al. (*57*) found that tree swallow nestlings raised in regions with abundant food supplies grew more quickly and survived better than those from regions where food was less abundant. In an experimental setting, Boag (*61*) found that the quality of food available to nestling zebra finches affected growth rates as well as adult size. This suggests that the increase in food abundance as a result of flooding had a positive affect on the fitness of nestling tree swallows in the area. Our findings of elevated growth rates in wing length and bill length in postflood nestlings as compared with preflood nestlings suggests that the increase in food abundance as a result of flooding had a positive affect on the fitness of nestling tree swallows in the area. However, the lack of preflood growth data from reference systems limits our interpretation of these results.

This study showed that higher rates of Hg methylation in sediments and flooded vegetation in an experimental reservoir increased MeHg levels in insectivorous songbirds nesting nearby. MeHg concentrations in tree swallows nesting around the experimental reservoir did not reach critical levels, and the reproductive success was positively impacted by the increase in food supply. In a similar study on reservoirs in Quebec ranging from 9 to 11 years old, DesGranges et al. (*62*) found osprey (*Pandion haliaetus*) nesting around reservoirs had much higher Hg concentrations than those nesting in natural habitats, although their overall reproductive success was not impacted. As in our experimental reservoir, reservoirs on the La Grand River stimulated biological productivity and fish populations increased in size. Hg concentrations in osprey blood were strongly correlated with Hg concentrations in the fish they were eating (*62*). Reservoir creation and the subsequent increase in Hg methylation within reservoirs resulted in a transfer of MeHg from the aquatic ecosystem into terrestrial species. Although reservoir creation may result in an increase in food supply for piscivorous and insectivorous species, the impact of moderately elevated MeHg concentrations is still not fully understood.

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