Bioenergetics-Based Modeling of Individual PCB Congeners in Nestling Tree Swallows from Two Contaminated Sites on the Upper Hudson River, New York

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A bioenergetics-based model was used to simulate the accumulation of total PCBs and 20 PCB congeners by nestling tree swallows at two contaminated sites on the Upper Hudson River, New York. PCB concentrations in birds were calculated as the sum of inherited residues and those acquired through consumption of contaminated insects. Close agreement between simulations and measured residues in 5-, 10-, and 15-day-old nestlings was obtained when PCB concentrations in the diet were set equal to those in food boli taken from adult birds. These simulations were further optimized by fitting the value of a dietary assimilation efficiency constant. Fitted constants for both sites were similar and averaged about 0.7. An evaluation of model performance for individual congeners provided no evidence of metabolic biotransformation. The results of this study are consistent with a companion effort in which principal components analysis was used to compare PCB congener patterns in insects and in tree swallow eggs, nestlings, and adults. Together, these studies establish a quantitative linkage between nestling tree swallows and the insects that they consume and provide strong support for the use of nestling swallows as a biomonitoring species for exposure assessment.

Introduction

Tree swallows have been used as a biomonitoring species to identify areas of local sediment contamination and to evaluate the potential for sediment-associated contaminants to adversely impact other avian species (*1*−*7*). The tree swallow is a widely distributed passerine bird that feeds extensively on emergent insects. Aquatic insect larvae accumulate sediment-associated contaminants and are consumed by swallows following metamorphosis to flying adult forms (*8*−*14*). Tree swallows readily accept nest boxes placed in open areas adjacent to wetlands, and breeding colonies can be established in suitable locations throughout the northern tier of states (*15*). For biomonitoring purposes, nestling swallows are preferred to adults or eggs because they are thought to more closely represent sediments in the vicinity of the nest box. Presently, nestling swallows are used as qualitative indicators of sediment contamination. Efforts to quantitatively relate chemical residues in nestlings to those in sediments have been complicated by considerations such as prey selection, the relationship between inherited and acquired residues, and the bioavailability of sediment-associated contaminants to sediment-dwelling organisms.

A bioenergetics-based model was developed previously to describe the accumulation of PCBs by nestling swallows in the Saginaw River watershed of Lower Michigan (*16*). This model explicitly accounted for changes in weight-normalized food consumption rate as well as changes in food conversion efficiency. PCB concentrations (total PCBs and congeners 077, 101, 118, and 180 in 15-day-old nestlings) predicted by the model were in good agreement with those measured in nestlings from a relatively uncontaminated site but over-estimated concentrations in birds from an area of known sediment contamination. Several possible explanations were given for this result, including overestimation of the insect consumption rate and a lack of correspondence between insects sampled for PCB analysis and those consumed by birds. On the basis of this modeling effort, it was suggested that growth dilution of contaminant residues was likely to occur but should vary in extent and duration depending on the amount of chemical inherited from maternal sources and degree of site contamination. This finding was advanced as a possible explanation for inconsistent reports of growth dilution in juveniles of other bird species. Unfortunately, data collected from nestling swallows on the Saginaw River were insufficient to test this prediction.

In this study, the bioenergetics-based model developed for the Saginaw River project was used to simulate the accumulation of PCBs by nestling swallows from two contaminated sites on the Upper Hudson River, NY. The sampling effort conducted on the Hudson River differed from that conducted on the Saginaw River in two important respects: (i) chicks were collected at 5, 10, and 15 d post-hatching, thereby providing a kinetic data set, and (ii) insects were collected from adult birds as they returned to the nest boxes to feed their young. The model was used to simulate concentrations of total PCBs and 20 PCB congeners representing a range of log K_{OW} values and expected metabolic potential. Measured and predicted concentrations were then examined for evidence of metabolic biotransformation and log K_{OW}-dependent differences in dietary assimilation efficiency. In a companion paper, principal components analysis (PCA) was used to compare PCB congener patterns in insects and tree swallow eggs, nestlings, and adults from several sites in the Hudson River watershed (*17*).

Materials and Methods

PCB Congener-Specific Data Set. The PCB data used in this study were obtained from samples collected during the spring of 1995. A companion paper (*17*) describes analytical methods

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TABLE 1. Parameters Used in a Bioenergetics-Based Model for PCB Accumulation by Nestling Tree Swallows

A	activity coefficient	1.0 from days 0 to 5, 1.0 + 0.05 T from days 5 to 15
ASSIM	percent chemical assimilation efficiency	90[a]
BW	body weight (g)	calculated from *G*
C	food consumption rate (kcal g^{-1} d^{-1})	0.49 $BW^{0.23}$
CD_B	caloric density of nestling (kcal g^{-1})	0.037 BW + 0.477
CD_I	caloric density of insects (kcal g^{-1})	1.24
FU	elimination rate (kcal g^{-1} d^{-1})	0.30 C
G	growth rate (g g^{-1} d^{-1})	P/CD_B
HWT	hatching weight (g)	1.65
P	tissue growth and fat storage rate (kcal g^{-1} d^{-1})	calculated from *C*, *R*, FU
PCB_I	PCB concentration in insects (μg g^{-1})	measured
R	respiration rate (kcal g^{-1} d^{-1})	RMR·*A*
RMR	resting metabolic rate (kcal g^{-1} d^{-1})	0.15 $BW^{0.38}$

[a] Later adjusted as described in the text to optimize model performance.

and QA/QC procedures and presents concentrations of total PCBs and individual PCB congeners in emergent insects and tree swallow eggs, nestlings, and adults from several sites in the Hudson River watershed. Details pertaining to study sites and sampling procedures are reported elsewhere (*3*, *5*). The modeling effort was focused on two contaminated sites, Special Area 13 (SA13) and Remnant Deposit 4 (REMN). At both of these sites, insects were obtained as food boli from adult birds as they returned to nest boxes to feed their young (*18*). These samples consisted mostly of chironomid midges (*Diptera* sp.).

Bioenergetics-Based Model. A detailed description of the bioenergetics-based model developed in the Saginaw River study has been provided (*16*). The following description is limited to an overview of the model, except where parameter values differ from those used previously. A list of model parameters is given in Table 1.

The growth of nestling swallows was modeled using a balanced energy equation, arranged to solve for the production term:

$$P = C - (R + \mathrm{FU}) \tag{1}$$

The terms in this equation are expressed in units of energy and time, normalized for the mass of the animal (kcal g^{-1} d^{-1}). Production (*P*) is the energy invested in tissue growth and fat storage, and consumption (*C*) is defined as the rate of gross energy intake. The respiration rate (*R*) includes energy expended for resting metabolism (RMR) and physical activity. RMR includes basal metabolism, specific dynamic action, and thermoregulation. The elimination term (FU) refers to energy that is lost due to egestion of feces and excretion of nitrogenous waste. Growth rate (*G*, in g g^{-1} d^{-1}) is calculated by dividing *P* by the caloric density of the chick (CD_B). Integrating *G* gives the body weight (BW, in g) at each time interval. Changes in *C* and *R* that occur as nestlings grow and develop are accomplished by calculating both terms as allometric functions of the form: $Y = \alpha BW^{\beta}$, where α and β are constants. FU was calculated as a constant fraction of *C*.

The PCB body burden of nestling swallows (μg $bird^{-1}$) was calculated as:

$$\text{mass PCB} = \text{inherited egg residue} + \int C \cdot BW \cdot PCB_I \cdot ASSIM / CD_I \tag{2}$$

where PCB_I and CD_I refer to the average PCB concentration and caloric density of insect prey, and ASSIM is the percentage assimilation of PCBs from the diet. Dividing the PCB mass by BW gives the concentration of PCBs in the chick at each time interval.

Allometric constants used to calculate *R* were set equal to those used earlier (*16*). A linear equation given by the same authors was used to calculate changes in CD_B as a function of BW. In the Saginaw River study, an effort to fit the allometric constants for *C* was complicated by the lack of a clear pattern in published data for passerine birds. Allometric constants were therefore determined by modeling to the observed growth of nestling swallows. A similar approach was employed in the present study (Figure 1). The points in Figure 1 are mean values for nestling swallows in the Hudson River watershed during the spring of 1995 (unpublished data for all sampling sites), and the solid line is the optimized model simulation. An advantage of this approach is that the energetic demand on birds in a given region depends on factors such as food availability and local weather patterns. Fitting allometric constants for *C* using observed growth data thereby "calibrates" the model to a specific situation. The optimized equation for *C* is similar to that developed in the Saginaw River study (*16*) and appears to be reasonable given reported consumption values for passerine birds (Figure 2). The complete bioenergetics model predicts the total energy budget of nestling swallows. Figure 3 shows predicted values for metabolizable energy ($C -$ FU), resting metabolism (RMR), and total respiration (R). These simulations closely resemble patterns of energy allocation reported for other passerine species (*20*, *21*).

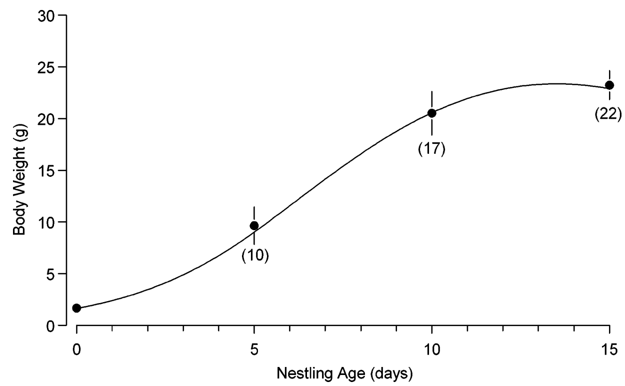

FIGURE 1. Growth of nestling tree swallows from the Hudson River watershed, New York, 1995. Measured nestling weights (mean ± SD) are shown as individual points with sample sizes in parentheses. The model simulation is shown as a solid line and was fitted to untransformed data by adjusting allometric constants for prey consumption rate to minimize the sum of squared differences between observed and predicted values.

As eq 2 suggests, the total PCB body burden at any time point equals the sum of the inherited residue and that accumulated over time. Two key assumptions were made when performing these calculations. First, absorbed PCBs were assumed to be unavailable for elimination as untransformed compounds. This assumption implies that dietary assimilation efficiency remains constant as birds accumulate chemical. Second, metabolic biotransformation was assumed

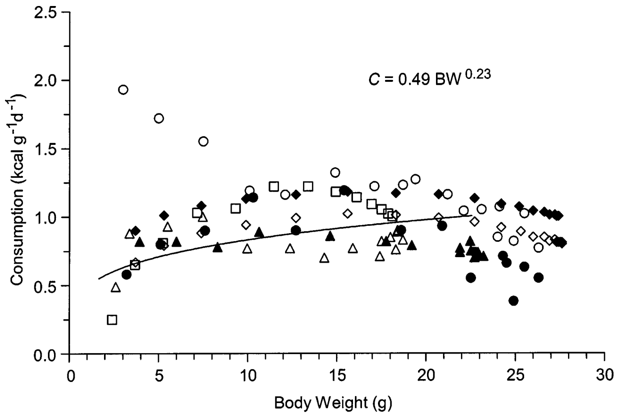

FIGURE 2. Allometric equation for gross energy consumption by nestling tree swallows. Consumption values are shown as individual points and were obtained from the following species: solid circles, red-backed shrike (*19*); open circles, house sparrow (*20*); open squares, yellow-eyed junco (*21*); solid triangles, house sparrow (*22*); open triangles, tree sparrow (*22*); solid diamonds, ash-throated flycatcher (*23*); open diamonds, western bluebird (*23*). The equation was obtained by fitting model simulations to growth data shown in Figure 1.

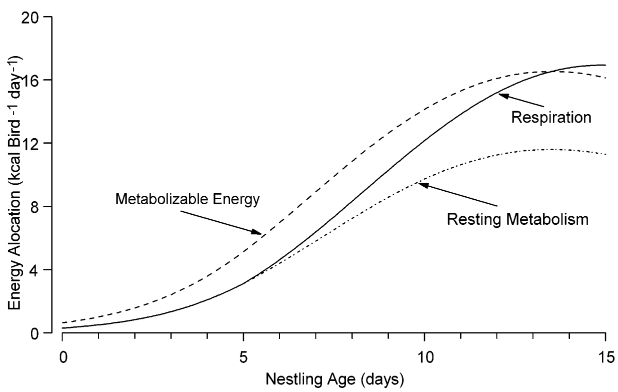

FIGURE 3. Tree swallow energy budget predicted by the bioenergetics model. Simulations are given for metabolizable energy (dashed line), total respiration (solid line), and resting metabolism (dotted line). Energy available for production is equal to the difference between metabolizable energy and total respiration. The difference between total respiration and resting metabolism is due to the energy cost of activity.

to be negligible. In the Saginaw study, support for the second assumption was provided by the observation that model performance was consistent among congeners within each sampling site (*16*). In the present study, the possible contribution of metabolism was evaluated further by comparing observed and predicted residues for 20 PCB congeners representing a range of metabolic potential.

The hatching weight of nestling swallows was set equal to an average measured value of 1.65 g (mean value for the SA13 and REMN sites), and the birds were assumed to assimilate 90% of the PCBs presented to them. This latter figure is higher than that (70%) used in the Saginaw modeling effort and is based on PCB assimilation efficiencies reported in feeding studies with adult ring doves (*24*).

Modeling Approach. Model simulations were generated by setting the PCB concentration in the diet (total PCBs or an individual congener) equal to that in food boli collected from adult birds at each site. Congener selection was based on the need to model compounds with different degrees of chlorine substitution and presumed metabolic potential (*25*, *26*). In most cases, the selected congeners were among the most abundant PCBs at each level of chlorine substitution.

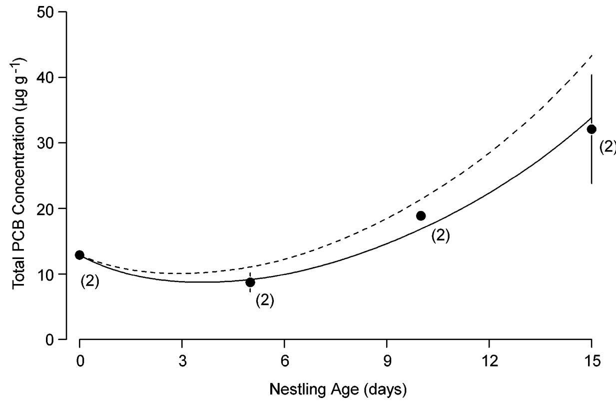

FIGURE 4. Simulated and observed total PCB concentrations in nestlings from the SA13 study site. Simulations were generated by setting the PCB concentration in the diet equal to that in food boli taken from adult birds. Dashed and solid lines represent simulations obtained by setting dietary assimilation efficiency equal to 0.9 and 0.7, respectively. Measured PCB concentrations (mean ± SD) are shown as individual points with sample sizes in parentheses. The value given for nestling age 0 represents the mean of measured concentrations in eggs.

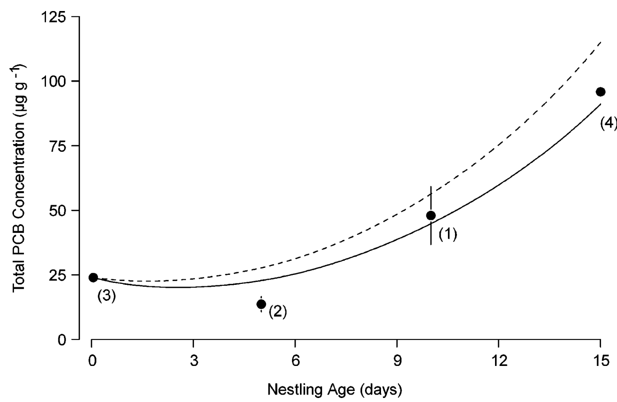

FIGURE 5. Simulated and observed total PCB concentrations in nestlings from the REMN study site. Simulations were generated by setting the PCB concentration in the diet equal to that in food boli taken from adult birds. Dashed and solid lines represent simulations obtained by setting dietary assimilation efficiency equal to 0.9 and 0.72, respectively. Measured PCB concentrations (mean ± SD) are shown as individual points with sample sizes in parentheses. The value given for nestling age 0 represents the mean of measured concentrations in eggs.

Several nonortho (nos. 077 and 126) and mono-ortho (nos. 105, 118, and 156) substituted congeners were also included because of their toxicological activity as A_h-receptor agonists. The selected congeners represent a range of estimated log K_{ow} values from 5.02 (no. 019) to 7.36 (no. 180) (*27*).

Results

At both study sites, total PCB concentrations in nestling swallows declined between day 0 and day 5 and then increased rapidly between day 5 and day 15. This pattern of accumulation is consistent with that predicted for nestlings in an earlier modeling effort (*16*). When total PCB concentrations in the diet were set equal to those in food boli taken from adult birds, model simulations reproduced the general pattern of accumulation at both sites but tended to overestimate measured values (Figures 4 and 5). Dietary assimilation efficiency constants were therefore reduced to optimize model performance. This optimization effort was accomplished by minimizing the sum of squared differences between observed and predicted concentrations at 5, 10, and 15 d. Fitted assimilation efficiencies for the SA13 and REMN sites were 0.70 and 0.72, respectively.

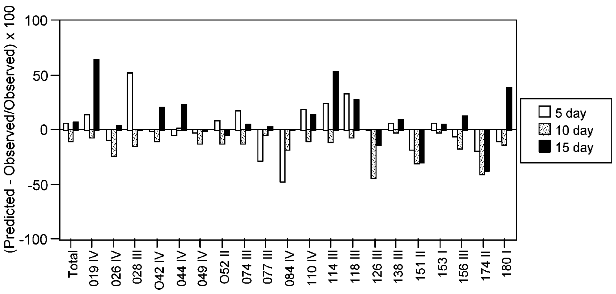

FIGURE 6. Model performance for total PCBs and individual PCB congeners at the SA13 study site obtained by setting PCB concentrations in the diet equal to those measured in food boli. In this figure and in Figure 7, model performance at each sampling time was characterized as the percentage deviation of the predicted value from the measured concentration. Congeners are identified by their IUPAC numbers. Roman numerals refer to the four structure−activity-based congener group designations given by Kannan et al. (*26*).

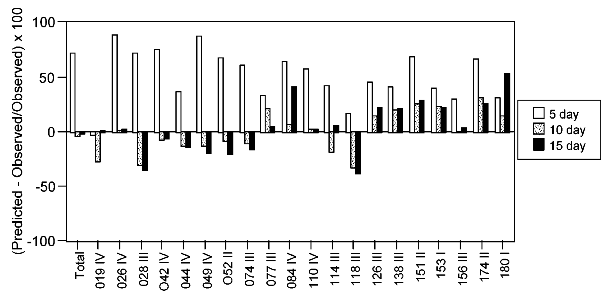

FIGURE 7. Model performance for total PCBs and individual PCB congeners at the REMN study site obtained by setting PCB concentrations in the diet equal to those measured in food boli.

Models optimized for each site (by adjusting ASSIM) were then used to simulate the kinetics of individual PCB congeners. Model performance was characterized at each sampling time as the percentage deviation from the measured residue [(measured − observed/observed) × 100] (Figures 6 and 7). Of particular interest during this evaluation was the possibility that individual congeners differed with respect to metabolic biotransformation or dietary assimilation efficiency. A slight decline in PCB assimilation efficiency with increasing log K_{OW} was reported in feeding studies with ring doves (*24*). In the present study, a similar relationship between log K_{OW} and dietary assimilation efficiency would have been expected to result in underestimation of measured residues for low log K_{OW} congeners and overestimation of high log K_{OW} congeners.

The metabolism of PCBs has been demonstrated in a broad array of vertebrate and invertebrate organisms and is primarily accomplished by microsomal cytochrome P-450-dependent mixed-function oxidases. In an effort to broadly characterize their potential for metabolism, researchers have grouped PCB congeners according to common structural elements (*25*, *26*). Here we use the group distinctions given by Kannan et al. (*26*). Briefly, group I congeners lack vicinal hydrogen atoms in the ortho−meta (*o,m*) or meta−para (*m,p*) configurations and undergo little if any metabolism. Among congeners examined in the present study, this group includes congeners 153 and 180. Group II congeners possess *m,p* vicinal hydrogens but do not contain *o,m* vicinal hydrogens. This group is metabolized by isozymes of the Cyp 2B subfamily and includes congeners 052, 151, and 174. Congeners in group III possess *o,m* vicinal hydrogens but do not contain *m,p* vicinal hydrogens. This group is metabolized by isozymes of the Cyp 1A subfamily and includes congeners 028, 074, 077, 114, 118, 126, 138, and 156. Group IV congeners possess vicinal hydrogen atoms in both the *m,p* and *o,m* configurations and are metabolized by Cyp 2B and Cyp 1A isozymes. Included in this group are congeners 019, 026, 042, 044, 049, 084, and 110.

Model simulations generated using congener levels in food boli from the SA13 site did not exhibit any patterns with respect to increasing congener number (roughly corresponding to an increase in chemical log K_{OW}), and all but two of the model predictions for individual sampling times were within 50% of measured values (Figure 6). Model performance also appeared to be unrelated to congener group designation (I−IV). Simulations obtained using congener levels in food boli from the REMN site consistently overestimated observed residues in 5-day-old nestlings (Figure 7). The extent of this overestimation for individual congeners tended to be about same as that observed for total PCBs. Simulated residues for 10- and 15-day-old nestlings were generally within 50% of measured values and did not exhibit any patterns with respect to congener group designation. An examination of model residuals suggested a trend, however, toward underestimation of measured concentrations for congeners containing 3 or 4 chlorines (nos. 019, 028, 042, 044, 049, 052, and 074), and overestimation of congeners with 6 or more chlorines (nos. 138, 151, 153, 156, 174, and 180). Congeners in the former category (3 or 4 chlorines) were distributed among groups II, III, and IV, while those in the latter category (≥6 chlorines) were distributed among groups I, II and III.

Discussion

A 320 km reach of the Upper Hudson River has been designated a U.S. EPA Superfund site due to PCB contamination originating from two capacitor manufacturing plants (*28*). Research on the Hudson River has been conducted by U.S. EPA and other State and Federal agencies to evaluate risks posed by PCBs to human health and the environment. As part of this effort, the U.S. Fish and Wildlife Service created several study populations of tree swallows by placing nest boxes at both contaminated and reference sites (*3*, *5*). Nestling swallows have been used at several locations in the United States and Canada to assess sediment contamination by PCBs, TCDD, chlorinated pesticides, and mercury (*1*−*3*). Additional field work has been conducted to evaluate reproductive and developmental effects on highly exposed birds (*4*−*6*).

The use of nestling swallows as exposure biomonitors is based on a presumed relationship between contaminants in birds and those in aquatic sediments (*7*). In a companion paper, principal components analysis was used to compare PCB congener patterns in insects and tree swallow eggs, nestlings, and adults from several study sites in the Hudson River watershed (*17*). PCB congener patterns in nestlings more closely resembled those of emergent insects than those of adults or eggs and were characterized by relatively higher proportions of less chlorinated congeners. These observations suggest a linkage between nestling swallows and emergent insects but do not indicate whether the PCB mass accumulated by nestlings quantitatively reflects the extent of dietary contamination.

In this study, a bioenergetics-based model was used to simulate the accumulation of PCBs by nestling swallows from two highly contaminated sites (REMN and SA13) on the Hudson River. Chemical concentrations in insects were set equal to those in emergent dipterans, collected as food boli from adult birds. Initial simulations were obtained by setting the dietary assimilation efficiency constant equal to 0.9. Good agreement between measured values and model simulations was obtained when concentrations in the diet were set equal to those in food boli. An additional improvement in model performance was obtained by adjusting the assimilation efficiency constant to optimize model performance. Optimized models for each site were then used to simulate data for individual PCB congeners.

Previous studies have documented the preference of tree swallows for dipterans and other relatively small emergent insects (*18*). Larval dipterans generally live in aquatic sediments and feed on sediment-associated organic matter. The results of the present study suggest that insects collected from a particular site will provide a linkage between nestling swallows and contaminated sediments if they develop within the sediments and are representative of species being consumed by the birds. These observations underscore the need for field data on animal diets to predict patterns of contaminant transfer.

The feeding study from which the initial assimilation efficiency estimate was obtained was performed by feeding adult ring doves a single meal of food pellets spiked with an Arochlor mixture (*24*). To date, very few studies have been conducted to determine dietary uptake of chemicals in adult birds, and no data are available for young birds of any species (*29*). On the basis of studies with mammals, however, we can identity several factors that are likely to impact dietary assimilation of organic chemicals by birds including feeding rate, food type and method of chemical incorporation (spiked or naturally incorporated), and differences in anatomy and physiology appropriate to the utilization of different food sources. Given these sources of uncertainty, fitted assimilation efficiency values obtained using PCB concentrations in dipterans from both the SA13 and REMN sites (0.70 and 0.72, respectively) appear to be reasonable.

Of equal importance to the fitted value of this constant is the fact that a single value could be used to simulate chemical concentrations in 5-, 10-, and 15-day-old nestlings. Factors that control dietary uptake of PCBs in birds (*24*), mammals (*30*), and fish (*31*, *32*) remain incompletely understood and may differ among taxa. There is general agreement, however, that assimilation efficiency should decline as an animal accumulates PCBs due to a reduction in activity gradients that promote diffusive flux. The use of a single fitted assimilation efficiency constant might be expected, therefore, to result in underestimation of chemical residues in 5-day-old nestlings and overestimation of residues in 15-day-old birds. One explanation for the performance of the model is that nestlings were far from steady state at all sampling times, with the result that dietary assimilation efficiencies were maintained at near maximal values. The rapid increase in PCB concentrations between 5 and 15 d provides support for this suggestion.

In the present study, the rate of PCB metabolism by nestling swallows was set equal to zero. Modeling results for individual congeners were then examined for evidence to the contrary. The metabolic capabilities of birds are poorly known; however, several generalizations can be attempted based on studies of domestic fowl and several species of seabirds (*29*). PCB metabolism in birds appears to be limited to congeners that contain *m,p* vicinal hydrogen atoms (groups II and IV). The activities of enzymes responsible for this metabolism are lower than in mammals, but levels expressed in ovo and in very young birds may be equal to or greater than those in adult birds. In contrast, the activities of xenobiotic metabolizing enzymes in mammalian neonates are often lower than those in adults.

The metabolism of congeners in groups II and IV might have been expected to cause model simulations to overestimate observed PCB concentrations in nestlings. Among the congeners examined in this study, this would include nos. 019, 026, 042, 044, 049, 052, 084, 110, 151, and 174. However, because the congeners in these two groups comprise a large fraction of the total PCB mass in swallows, their metabolism could also impact model predictions for total PCBs. This creates a problem of interpretation since optimization of the model based on total PCB concentrations would tend to reduce the overestimation of individual metabolized congeners by setting a "baseline" that represents both metabolized and unmetabolized compounds. Because of this possibility, the results of the congener-specific modeling effort were examined for systematic differences within and among all four congener groups.

A comparison of PCB congener concentrations in nestlings to the levels predicted from congener concentrations in food boli did not suggest any patterns related to congener group designation at either of the two study sites (Figures 6 and 7). All congener concentrations in 5-day-old nestlings from the REMN site were overestimated by the model. In contrast, model simulations for days 10 and 15 tended to underestimate concentrations of congeners containing 3 or 4 chlorines, while overestimating concentrations of congeners with 6 or more chlorines. This pattern was unrelated to congener group designation but may have been due to a decrease in dietary assimilation efficiency with increasing chemical log K_{OW}. Modeling results for the SA13 site did not provide support for a dependence of dietary assimilation efficiency on log K_{OW}, as there were no patterns with respect to increasing congener number.

Using a bioenergetics-based model we have shown that PCB concentrations in nestling swallows can be quantitatively related to levels present in the insects that they consume. The remaining uncertainty in the chain of events that results in contaminant transfer from sediments to nestlings is the relationship between sediments and emergent insects. Equilibrium partitioning theory for hydrophobic compounds suggests that the biota−sediment accumulation factor (BSAF) in benthic invertebrates should not change with chemical log K_{OW} and that it should be possible to estimate the value of this BSAF based on an organism's lipid content and the organic carbon content of the sediment. BSAFs calculated for mayflies from Lake St. Clair were close to theoretical values (lipid/TOC normalized); however, the data suggested a trend of increasing BSAF with increasing chemical log K_{OW} (*9*). In laboratory studies with mayfly larvae, BSAFs were independent of K_{OW} for compounds with log $K_{OW} > 5.8$, but decreased at lower log K_{OW} values (*33*). Perhaps more importantly, BSAFs determined for high log K_{OW} compounds were higher by about a factor of 10 than values predicted on the basis of equilibrium partitioning, and it was suggested that bioaccumulation had occurred due to the ingestion of contaminants sorbed to sediment organic carbon. The chemical concentration in emergent insects may also change as they undergo metamorphosis to adults. For example, expressed on a fresh weight basis, the PCB content of adult midges was more than twice that of the larvae from which they derived (*8*).

The results of this study, together with those of a companion effort (*17*), provide strong support for the use of nestling swallows as a biomonitoring species for exposure assessment. Progress on understanding the relationship between contaminant levels in sediments and those in emergent insects will strengthen the linkage between nestlings and sediments even further. The model described in this study can be used to predict the kinetics of PCB accumulation in nestling swallows from measured concentrations in the insects that they consume. The only parameters that were adjusted in this effort were allometric constants for food consumption and dietary assimilation efficiency. Tree swallow nestling survival and growth are known to depend on local factors (*15*), and consumption rates can be expected to vary with year and location. Nevertheless, allometric constants from this and an earlier modeling effort (*16*) yielded very similar consumption relationships. The factors that control dietary absorption of PCBs by nestling swallows are poorly know. The close agreement between optimized assimilation efficiencies for both study sites suggests, however, that a value of 0.7 should be used in future applications of the model to PCB data sets. Additional research is required to determine assimilation efficiency values appropriate to other chemical classes.

Acknowledgments

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