

Environmental Toxicology

REPRODUCTIVE SUCCESS OF BELTED KINGFISHERS ON THE UPPER HUDSON RIVER

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Abstract: Belted kingfishers (*Megaceryle alcyon*) are predators in many North American aquatic ecosystems; as such, they are prone to bioaccumulation of certain environmental contaminants. In 2002 and 2004, kingfisher eggs collected near the upper Hudson River in New York had elevated concentrations of polychlorinated biphenyls (PCBs), and the kingfisher population in this area was reported to be at risk because of PCB exposure. From 2007 to 2009, the authors monitored 69 kingfisher nests on the Hudson River to track both nest success and survival of individual nestlings. The study site consisted of 2 adjacent sections of the Hudson River, 1 upstream and 1 downstream of a historic PCB source. The authors compared models of nest success that differentially incorporated the following 4 variables that they deemed most likely to affect reproductive output: 1) river section (upstream vs downstream of PCB source), 2) year, 3) hatch date, and 4) abandonment by 1 parent. After ranking models according to Akaike's information criterion for small sample sizes, it was clear that parental abandonment was the most important of the factors examined. River section was not an important parameter, and overall nesting success was slightly higher in the PCB-contaminated section than in the upstream area. These findings support the conclusion that kingfisher productivity is not adversely impacted by PCB contamination in the upper Hudson River. *Environ Toxicol Chem* 2013;32: xx–xx. © 2013 SETAC

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INTRODUCTION

The Hudson River is an important ecological resource that supports a wide array of wildlife. The river also contains large amounts of polychlorinated biphenyls (PCBs) that have been deposited in sediment as a result of industrial activity during the mid-1900s [1]. The scientific literature pertaining to the effects of PCBs on wildlife contains both documentation of negative effects as well as studies that find no effects. For example, detrimental effects of environmental PCBs on wildlife have been documented in fish, where they are associated with reproductive failure and impaired development [1–7], as well as mink (*Neovison vison*; [8]), tree swallows (*Tachycineta bicolor*; [9]), and snapping turtles (*Chelydra serpentina*; [10]). However, other studies, often focused on the same organisms listed above, have reported no apparent effects of PCB exposure, including work on tree swallows [11], bald eagles [12,13], and fish [14,15].

Polychlorinated biphenyls are highly stable compounds with a propensity to persist long-term in river ecosystems and to bioaccumulate among top predators [16]. Among the top predators making use of the Hudson River, the belted kingfisher (*Megaceryle alcyon*) would seem to be particularly vulnerable to PCB contamination. Kingfishers feed almost exclusively on fish and aquatic invertebrates (mostly crayfish), which according to the New York State Department of Environmental Conservation [17] have high PCB-exposure levels in the upper Hudson River (defined here as the Hudson River to the north of Troy, New York, USA). Furthermore, as relatively small piscivores, kingfishers have a disproportionately higher metabolism than larger fish-eating vertebrates (e.g., herons, otters, and eagles), which means that kingfishers process more food per unit of body weight and have a greater potential to bioaccumulate toxins from their prey.

In 2002, the US Environmental Protection Agency signed a Record of Decision to remove sediments contaminated with PCBs from the upper Hudson River [18], and this restoration effort began in the summer of 2009. These actions stemmed in part from an environmental risk assessment, which declared that birds and mammals that eat PCB-contaminated fish from the Hudson River, such as the belted kingfisher, are at risk at the population level, because PCBs may adversely affect the survival, growth, and reproduction of these species" [18]. To determine whether belted kingfishers and other birds nesting on the upper Hudson River were exposed to PCBs, the Hudson River Natural Resource Trustees [19] conducted a survey of PCB concentrations in bird eggs. Samples were taken from a section of river ranging from the primary sources of PCBs, 2 manufacturing facilities operated by the General Electric Company in the adjacent townships of Hudson Falls and Fort Edward, NY, USA, to the city of Troy, NY, USA, approximately 50 river miles downstream. This survey documented concentrations of PCBs in the eggs of belted kingfishers averaging 13 900 parts per billion (ppb; $\mu\text{g}/\text{kg}$; $n = 10$); these values were high relative to other birds that were sampled. Except for spotted sandpipers (*Actitis macularius*), averages for other bird species examined were less than 13 000 ppb and usually well under 5000 ppb. In 2004, kingfisher eggs were collected a 2nd time, and PCB concentrations were similar to those in 2002, with a geometric mean of 10 600 ppb and a range of 2410 ppb to 80 300 ppb ($n = 14$; [20]). Polychlorinated biphenyl concentrations in eggs from off-river kingfishers had a geometric mean of 2660 ppb in 2004.

Although there was clear evidence of PCB exposure, the report issued by the Hudson River Natural Resource Trustees [19] did not address the critical question of population-level effects on belted kingfishers breeding along the upper Hudson River. Kingfishers have, in fact, remained abundant on the upper Hudson River throughout the contaminated area for the past decade or more (P. Bernstein, Spencertown, New York, USA, personal communication). Moreover, nest monitoring that was

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part of the 2004 study by Custer et al. [20] revealed a high rate of apparent nest success on the upper Hudson River (7 of 8 nests fledged young) and showed no obvious effects of PCBs on nest success or nestling survival. Although Custer et al. [20] lacked an adequate sample size to detect subtle effects, their study suggests that PCBs have not had a population-level effect on belted kingfishers nesting on the upper Hudson River.

To better evaluate potential population-level effects of environmental PCBs on the reproductive success of belted kingfishers on the upper Hudson River, we monitored kingfisher nests upstream and downstream of historical PCB release sites in Hudson Falls and Fort Edward (Figure 1) during the summers of 2007, 2008, and 2009. Based on the documented patterns of PCB concentrations in eggs collected in 2002 and 2004, we predicted that if belted kingfishers were negatively affected by PCB exposure, then birds downstream of the PCB source would have lower reproductive success than birds upstream of the source and

that downstream birds would fledge fewer young per nest. We also examined the potential effects of hatch date and abandonment of nests by 1 member of a breeding pair on nest success. We expected nests provisioned by only 1 parent to be less likely to fledge young, and we expected earlier nests would have increased reproductive success as suggested by the general relationship between early breeding and reproductive success in a wide range of birds (see Prince et al. [21]).

METHODS

Study system and nest monitoring

The goal of the present study was a rigorous description of the variation in belted kingfisher nest success in relation to a section of the upper Hudson River contaminated with PCBs and a relatively uncontaminated upstream section of the same river. The study area consisted of approximately 75 river miles (120 km), ranging from the Route 418 bridge (43°28'48" N, 73°49'05" W) near Warrensburg, New York, USA, to the convergence of the Hudson River and the Hoosic River (42°55'38" N, 73°49'50" W) near Stillwater, New York, USA (Figure 1). The historic PCB sources in the adjacent townships of Hudson Falls and Fort Edward divide the study site into 2 stretches of river: an upstream section of approximately 40 river miles (64 km), and a downstream section of approximately 35 river miles (56 km). Previous studies of PCB contamination in the upper Hudson River below Fort Edward have established 4 zones that characterize PCB concentrations in relation to water flow and geography (see Hudson River Natural Resource Trustees [19] and Custer et al. [20]). The downstream portion of the study site comprised zones 1 and 2, which are separated by the Fort Miller Dam (Lock 6) at river mile 186.2 (see Figure 1). Because kingfisher territories comprised 2 km to 4 km of river length (E.S. Bridge, personal observation, 2007–2009) only a few pairs would be expected in each of these zones. Therefore, we have combined data from these sections and refer to the entirety of the PCB contaminated section of the study site as the downstream section, and the northwestern portion of the study site is the upstream section (see Figure 1).

Belted kingfishers are common throughout North America, nesting in densities of about 1 pair every 2 km to 4 km along the shorelines of lakes and streams [22]. They nest in burrows approximately 12 cm in diameter and extending horizontally up to 2 m in riverbanks or piles of soil, sediment, or gravel. During the reproductive season, they are highly territorial and closely tied to the aquatic environment within their breeding territory [22]. Hence, in the present study, it was unlikely that any birds foraged routinely both upstream and downstream of the source of the PCBs. Moreover, we visually confirmed that birds assigned to upstream and downstream river sections consistently foraged in water bodies that corresponded with our comparison of PCB contaminated and uncontaminated areas. In other words, behavioral observations indicated that downstream birds foraged only in the downstream portion of the study area and vice versa. All burrows used in the present study were located within 100 m of the river, with the exception of 2 burrows in the upstream portion of the study site that were approximately 800 m and 900 m from the river. At these 2 off-river nests, we regularly observed both members of the breeding pair flying to the Hudson River and back to provision nestlings with fish.

Weather conditions during the study period, while variable, did not reach extreme intensities, and there was no reproductive failure that could be attributed to events such as flooding, high winds, or other adverse circumstances. Similarly, water levels

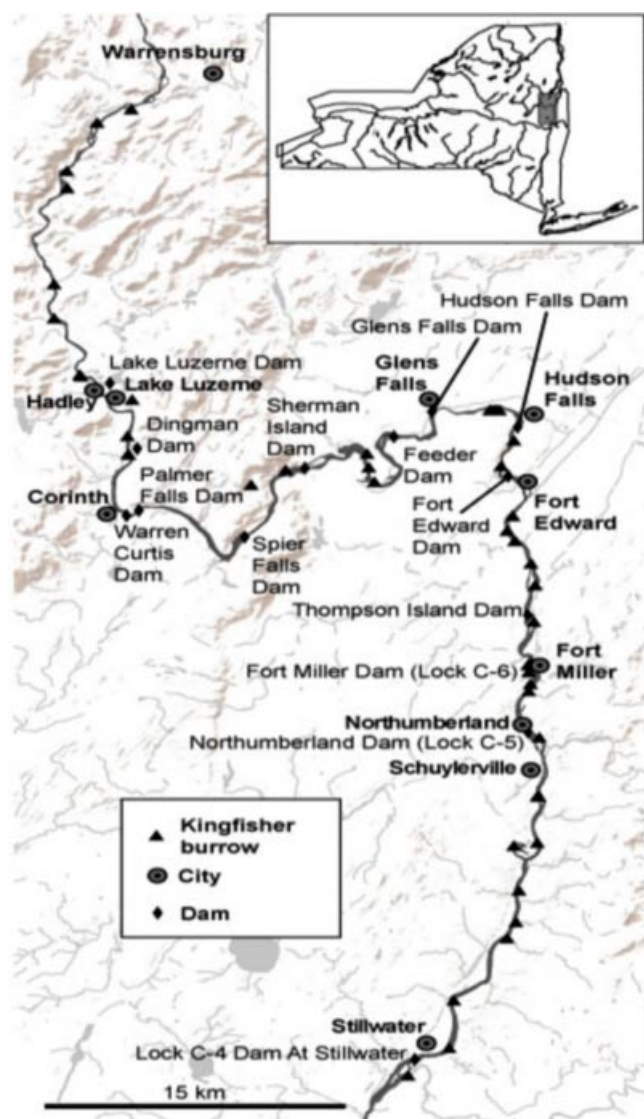


Figure 1. Map of the study area on the upper Hudson River. The general location of the study area is indicated by the shaded region within the state of New York (inset upper right). The relatively uncontaminated reference area or upstream section stretched roughly from Warrensburg to Hudson Falls, and the polychlorinated biphenyl (PCB)-contaminated downstream section ran from Hudson Falls to the convergence of the Hudson and Hoosic Rivers, just south of Stillwater.

and flow rates on the upper Hudson River remained within normal bounds.

Beginning in early May of 2007, 2008, and 2009, we searched for kingfisher nests by floating the river in a kayak or motorboat and carefully inspecting any near-vertical, non-vegetated banks that might serve as burrow sites. We also carefully observed any kingfishers sighted to note behaviors that could lead to finding a nest (i.e., flying to a burrow with a fish). Kingfishers may abandon nests in response to disturbances during incubation, but are much less likely to do so after hatching ([23]; J.F. Kelly, personal observation, ~1995, Cache la Poudre River, CO, USA). Hence, we did not check the contents of a burrow until we observed provisioning behavior, heard nestlings in the burrow, or otherwise had reason to suspect that the eggs had hatched. If nest activity appeared to cease, we probed the burrow on several occasions to confirm whether eggs had been laid and that the nest failed. During the prehatching period, we determined that burrows were active by observing the breeding pair flying in and out of the burrow (presumably to trade incubation shifts). We inferred hatch date based on the apparent incubation time, observations of parents bringing fish to the burrow, developmental stage of the nestlings as determined using a video-camera probe (see next paragraph), and fledging date.

When we observed evidence that hatching had occurred, we probed each burrow with a small infrared video camera attached to a pole approximately 1.5 m in length. The camera was equipped with infrared light-emitting diodes that allowed it to record clear images of the interior of the burrow, while minimizing disturbance to the nestlings. The camera was connected to a personal media player (Coby PMP4320), which allowed us to view the footage in real time while recording it for later analysis. Nests were probed for 20s to 3 min as needed to obtain footage that would allow us to count the nestlings and ascribe an approximate age to the brood based on developmental milestones described in Kelly et al. [22]. To minimize disturbance, we generally probed nests only 2 to 5 times during critical stages (i.e., just after hatching and just prior to fledging) of the 27-d to 30-d provisioning period. We also monitored nests on a more frequent basis (once or twice per week) by simply watching burrows to note provisioning behavior and listening for begging nestlings. When there was any indication that a nest had failed, we investigated it with the video probe.

In 2008, at the beginning of the provisioning period, we equipped most active nests with a customized data-logging device that could record provisioning visits by the parents via a small photoresistor in the burrow entrance. During some parts of the provisioning period, these data-loggers were attached to specialized cameras that could capture video footage of the parents as they flew to the burrow (the cameras continuously stored a 5-s video buffer that allowed them to record the approach to the burrow entrance even though they were triggered as the bird entered). The full record of provisioning data provided by the data loggers and cameras is beyond the scope of the present study, but we occasionally used this resource for determining nest failure dates, fledging dates, and when provisioning by 1 or both members of the breeding pair ended.

We synthesized various sources of information to generate well-resolved phenologies for almost all of the burrows and to account for the fate of each egg/nestling observed. In generating these nest records, we relied on several assumptions about the nesting behavior of belted kingfishers, which we believe to be reasonable based on our experience and published literature.

First, we assumed that maximum clutch size was 7 eggs, and that if at any point we observed 7 nestlings, then the clutch size was necessarily 7. No systematic study of kingfishers has reported a clutch of more than 7 [24–28]. There is a historical record of an 8-egg clutch [29], but we believe that this report is based on an erroneous observation or an extremely unusual event. Second, we assumed that unhatched eggs remained visible within a burrow for at least 7 d after the other eggs hatched. On occasion, the video probe revealed a number of recently hatched chicks as well as 1 or 2 unhatched (i.e., added or infertile) eggs. Repeated probing indicated that these unhatched eggs remained visible in the burrow for up to 2 wk posthatching. Given the darkness of the burrow and space limitations, it would seem difficult for provisioning parents to detect unhatched eggs and remove them. It is likely that they are not removed at all, but are trampled and buried by the nestlings as they approach adult size. Hence, video probe footage depicting a combination of eggs and nestlings provided an accurate count of the clutch size, and when the earliest video footage did not reveal unhatched eggs, it was safe to assume that there were none.

We observed only one likely instance of nest depredation during the incubation stage, and all eggs (presuming they had not hatched prior to depredation) were taken. Hence, we assume that there were no instances in which a predator removed only part of a clutch.

Finally, we confirmed successful fledging at each nest by observing fledglings in the vicinity of each burrow, but we were unable to get accurate counts of the offspring postfledging because free-flying fledglings are often elusive, making it difficult to determine whether fledglings were missing or simply undetected, and the breeding adults may divide the fledglings into 2 groups, and we often observed only 1 group. Hence, for the purpose of determining how many fledglings a nest produced, we used the number of nestlings observed alive and in good condition at the nest visit that preceded fledging, which was generally when we banded the brood. The prefledging nest check usually occurred within 3 d of the fledge date. However, there were 10 nests checked 4 d before fledging and 1 nest checked 5 d before fledging. Lastly, 1 nest was last checked 6 d before the estimated fledging date, but we observed the full clutch of offspring (6 birds) outside the burrow on the subsequent visit.

We use the term *nest success* to describe the fate of an entire nest (nests that fledged at least 1 offspring were considered successful), and *nestling survival* to describe the fates of individual offspring prior to fledging. We use nest survival to describe the probability of at least 1 nestling or egg in an active nest remaining alive over a given time interval (e.g., daily nest survival).

Over the 3-yr study period, we monitored 69 nests. Burrows were frequently reused year after year, although both members of a breeding pair rarely returned to the same site in consecutive years. Use of the same site by the same breeders in consecutive years happened at least 4 and at most 7 times. The exact number of occurrences is unknown because although we banded all adults captured in all years, we were unable to capture all the breeding adults in 2007. Due to the rarity of these occurrences and the fact that each breeding attempt by a returning bird occurred with a different mate and/or during a different breeding season, we regarded each nesting attempt as an independent sample.

Because the focus of the present study was measures of reproductive success in relation to environmental PCBs, predation was not of primary interest as a cause of nest failure.

For this reason and because nest predation was very rare (only 3 occurrences), nests that were depredated were not used in our primary analyses; however, we did incorporate these nests into follow-up analyses. All 3 predation events occurred in the upstream section of the study area. In 2 cases, the burrow entrance had been excavated, so there was little doubt about the cause of nest failure. In the 3rd case, we observed a domestic cat (*Felis catus*) attempting to ambush adult birds at the burrow entrance. When the burrow was checked several days later, it contained 5 dead and emaciated nestlings. We do not know if the cat captured the adults or induced them to abandon their brood; in either case, the failure is attributed to a predator.

In association with our nest monitoring, we banded 402 kingfishers (adults and nestlings). Adults were captured during provisioning using mist nests mounted directly in front of an active burrow or by placing a landing net over the burrow entrance immediately after a parent flew in with a fish. By consulting video footage of food deliveries or by direct observation, we confirmed that recently banded adults continued to provision offspring. During the last few days of the nesting period, we extracted nestlings from the burrow using a noose pole and the video probe. All birds captured were given a band combination specific to each nest with a US Fish and Wildlife Service band on 1 leg and 1 or 2 color bands on the other leg.

Statistical analyses

Because this was a study of wild population of belted kingfishers and thus not subject to randomized sampling or PCB releases in replicates of the upper Hudson River, the data we collected do not meet the assumptions of frequentist statistical methods. Thus, our analyses seek the best model to describe the patterns of variation between our a priori defined study sites. Burnham and Anderson [30] formalized this approach, and because true replication is usually impossible in large-scale field studies, it has come to dominate the natural sciences.

Nests were found throughout the breeding season with offspring at various developmental stages. Thus, despite comprehensive and extensive nest searching, it is possible that nests that failed early were not detected and not included in our data set. Evaluation of nest success as the percentage of observed nests that fledged young (i.e., apparent nest success) can lead to inflated survival estimates because nests that fail early are ignored. For this reason, we evaluated nest success based on the daily survival rate of the nests we found as prescribed by the Mayfield method (see Mayfield [31]). Since the proposal of the Mayfield method, there have been significant advancements in techniques for modeling nest survival based on periodic monitoring [32,33]. We modeled daily nest survival rates using methodology established by Rotella et al. [34,35], which employs numerically fitting nonlinear mixed models in SAS [36]. This modeling approach requires data in the form of time intervals bounded by nest checks (or fledging events), the age of the nest at the beginning of each interval, and the condition of the nest (active or failed) at the end of each interval. The model assumes that the interval lengths are known, but does not assume that the exact days of nest failures are known. Nest age was determined by studying video-probe footage and consulting established developmental stages (e.g., emergence of feather tracts) of nestlings noted in Kelly et al. [22], while taking into consideration fledge date and initial feeding observations. Because we did not directly observe eggs in the majority of the monitored nests, we assumed an incubation period of 22 d [22]. For calculation of survival probabilities, we defined the

nesting period as beginning on the date the nest was found and ending on the day of fledging. If a nest was found before egg-laying was complete, we used our estimated clutch completion date (which corresponds to the onset of incubation) as the beginning of the nesting period. Monitoring was intensified as estimated fledging dates approached, such that our observational data along with occasional use of video and data-logging equipment, enabled estimates of nest age and fledging date that we believe are accurate to ± 1 d, with the exception of 4 burrows that failed before or possibly just after hatching.

Our analyses mirrored the example in Rotella [37]. We used the NLMIXED procedure in SAS to fit parameters to a range of models (described below), and we used the SAS macro from Rotella [37] to calculate Akaike's information criterion (AIC) for each model. Akaike's information criterion is a measure of the relative goodness of fit that is used to rank a set of proposed models. It takes into account the maximized value of the likelihood function of a model as well as the number of parameters, such that models with the lowest AIC scores are the models that fit the data well, while using the fewest number of parameters. In comparing our models, we used AIC_c , a derivation of AIC that applies a larger penalty for extra model parameters and is more appropriate for finite sample sizes [30].

Effective sample sizes for calculating AIC_c were generated as in the program MARK [34,38], wherein each day of known survival for each nest contributed 1 to the effective sample size and each observation interval that ended in a nest failure (which could be several days) contributed 1 to the effective sample size. We interpret models that had AIC values 2 units greater than that of the best model as well supported, those models with AIC scores 2 units to 4 units greater than the best model as having some support, and those with AIC scores more than 4 units greater than the best model to have substantially less support [30]. We evaluated the importance of individual variables in the well-supported models by examining the effect sizes or β estimates for each parameter and the AIC weights of the models that included a particular variable. Beta estimates indicate how much influence a parameter has in a model, and by examining the magnitude and 95% confidence intervals (CIs) for β estimates one can get a sense of the likelihood that the true value of the parameter differs from zero. When the 95% CI of the β estimate for a parameter overlaps zero, it is unlikely that the parameter has much influence on the response variable. Lastly, we followed Arnold's [39] recommendations for discerning noninformative parameters within high-ranking models.

Our modeling was based on a suite of 4 variables we regarded as most likely to affect reproductive success in belted kingfishers on the upper Hudson River. The primary variable of interest was river section (henceforth RIVER), which was coded as a simple binary variable (upstream = 0 and downstream = 1). Other potentially important factors were year (henceforth YEAR), the abandonment of a nest by 1 parent (henceforth PARENTS), and hatch date (henceforth HATCH). YEAR was included among the variables to account for climatic or biotic differences among years, and was coded as 2 binary variables (07 and 08) to allow the models to independently assess each year (see Rotella [37]). Abandonment was determined by direct observation or using video data when 1 parent ceased provisioning nestlings. We coded PARENTS as a binary variable (1 = both parents present) and we matched this variable to the appropriate observation intervals based on the time abandonment occurred. In other words, all nests were initially scored as having 2 parents, but when a parent abandoned, the corresponding time intervals were

scored as having 1 parent present. Finally, because early breeding is broadly associated with increased nest success in many bird species [40,41], HATCH was used in some models as a continuous covariate. Hatch dates were expressed as days since the earliest hatch date noted in each year.

We had no a priori reasons to favor specific combinations of the 4 variables, and our goal was to evaluate the relative importance of the 4 variables rather than to establish the best statistical model. Hence, we proposed a balanced series of models to systematically sample the possible combinations of these variables (see Table 1). The series of models we analyzed included 1) an intercept-only model as well as an “all main effects” model wherein all 4 variables were incorporated; 2) all 6 possible 2-variable models; 3) all 4 possible 3-variable combinations; and 4) all 4 possible single-parameter models. For selected models, we translated model output into daily survival rates using the delta method described in Bolker [42]. We assessed goodness of fit for the all-main-effects model and the best-supported model using the smoothed-residual based method prescribed by Sturdivant et al. [43].

To simplify interpretation and limit the set of models considered, we did not incorporate interactions into the initial set of models. We did, however, carry out post hoc analyses to determine whether interactions among informative variables aided the interpretation of the data. In addition, we conducted several follow-up analyses to address the potential for error in our estimates of nest phenology and for the use of depredated nests to affect our conclusions. These follow-up analyses repeated the initial analyses using an augmented data set. Specifically, we tested whether inclusion of depredated nests and whether removal of all data for which there was some uncertainty about the dates of nest-cycle events affected the resulting model rankings.

Nest success was relatively high in the study population, but partial fledging (i.e., instances in which some, but not all of the offspring failed to fledge) was common (see *Results*). To address the possibility of lower fledging rates in the downstream portion of the study site, we calculated means and 95% CIs for the number of fledglings produced in both river sections. In light of the fact that nest abandonment by 1 parent had a strong effect on nest survival (see *Results*), we also calculated means and CIs for

nests that had 2 parents present at fledging and for nests that were abandoned by 1 parent.

RESULTS

Our primary analysis of nest survival included 66 nests (with 3 depredated burrows excluded; see Table 2 and Supplemental Data, Table S1) and 2517 nest-observation days, which provided an effective sample size of 2481. Of these 66 nests, 88% fledged at least 1 offspring, and of these successful nests, 57% fledged their entire brood. The length of estimated nest cycles (incubation plus nestling periods) ranged from 48 d to 51 d, which corresponded closely with published values [22]. Nests appeared to be more densely spaced and more numerous in the downstream section of the study area, where we had a total of 40 nests over the 3-yr study period in a stretch of river approximately 56 km long. In the upstream section, we found 29 nests (including the 3 depredated nests) within a 64 km stretch of river. Hatch dates ranged from 11 May to 8 July and had a bimodal distribution indicative of 2 waves of reproductive effort (Figure 2).

Based on AIC_c rankings and β -parameter estimates, the number of parents provisioning was clearly the most influential variable. The best model included only PARENTS (AIC_c wt = 0.40), and the remaining models with appreciable AIC_c weights all included PARENTS (Table 1). Moreover, PARENTS had a strong effect size (i.e., β estimate) for all models in which it was included (β ranged from 1.99 to 2.19, with CIs ranging from 1.43 to 1.59 (see Supplemental Data, Table S2).

The 2nd-best model was comprised of PARENTS and HATCH DATE. The ΔAIC_c for this model (1.76) was less than 2, but we view HATCH DATE as noninformative because the addition of this factor did not reduce model deviance enough to overcome the +2 penalty for an additional parameter (see Arnold [39]). Hence, the influence of adding HATCH DATE to the PARENTS only model was arguably negligible with regard to model fit. In other words, HATCH DATE appeared in a high-ranking model because the model also included PARENTS (the only variable with a strong effect on nest survival).

The 3rd-best model ($\Delta AIC_c = 1.99$) is the RIVER + PARENTS model. Because this model is about 2 ΔAIC_c units

Table 1. Comparison of models for predicting belted kingfisher nest survival based on observations of 66 nests over 3 breeding seasons (effective sample size = 2481)^a

Model	k ^b	AIC	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood
PARENTS	2	83.16	83.16	0.00	0.40	1.00
PARENTS+HATCH	3	84.92	84.92	1.76	0.17	0.41
RIVER+PARENTS	3	85.14	85.15	1.99	0.15	0.37
RIVER+HATCH+PARENTS	4	86.91	86.92	3.76	0.06	0.15
YEAR+PARENTS	4	87.08	87.10	3.94	0.06	0.14
INTERCEPT	1	87.75	87.75	4.59	0.04	0.10
HATCH	2	88.18	88.19	5.03	0.03	0.08
YEAR+PARENTS+ HATCH	5	88.78	88.80	5.64	0.02	0.06
YEAR+RIVER+PARENTS	5	89.07	89.09	5.93	0.02	0.05
RIVER	2	89.43	89.43	6.27	0.02	0.04
RIVER+HATCH	3	90.07	90.08	6.92	0.01	0.03
ALL MAIN EFFECTS	6	90.77	90.81	7.65	0.01	0.02
YEAR	3	91.64	91.65	8.49	0.01	0.01
YEAR+HATCH	4	91.82	91.84	8.68	0.01	0.01
YEAR+RIVER	4	93.32	93.33	10.17	0.002	0.006
YEAR+RIVER+HATCH	5	93.74	93.76	10.60	0.002	0.005

^a The models are ordered according to how much their Akaike's information criterion (AIC) for small samples differs from that of the best model (i.e., ΔAIC_c score). The model set consists of all possible main effects models that can be attained by combining our 4 parameters of interest (RIVER, YEAR, PARENTS, and HATCH; see the *Methods* section).

^b The “k” column indicates the number of structural parameters in each model, which was used to calculate AIC scores.

Table 2. Summary of nests used in the primary model comparison analysis^a

River section	Year	Parents at fledging ^b	Nests	Successful nests	Eggs	Nestlings	Fledglings
Up	2007	1	2	1	7	7	4
Up	2008	1	2	1	11	11	6
Up	2009	1	2	2	11	11	5
Up	2007	2	5	5	29	28	28
Up	2008	2	6	5	34	34	26
Up	2009	2	9	7	56	56	41
Upstream Total			26	21	148	147	110
Down	2007	1	0	0	0	0	0
Down	2008	1	2	1	11	10	3
Down	2009	1	1	1	7	7	3
Down	2007	2	9	9	54	50	49
Down	2008	2	12	12	79	77	73
Down	2009	2	16	14	100	86	82
Downstream Total			40	37	251	230	210
Cumulative total			66	58	399	377	320

^a Up (upstream) and down (downstream) designations refer to the position of the burrow relative to the Hudson Falls Dam (approximate source of polychlorinated biphenyls).

^b Indicates how many parents were providing parental care at the end of the nesting period (i.e., at fledging or nest failure).

greater than the best model, we contend that it does not explain any more variation than PARENTS alone. In addition, this model drew only approximately 15% of the AIC weight, and the effect sizes for river across all relevant models were low, ranging from 0.06 to 0.40 with CIs exceeding 1.3 in all models (see Supplemental Data, Table S2). Hence, there is little reason to regard RIVER as an important variable.

Because all variables were equally represented in the model set, we can evaluate relative variable importance by summing Akaike model weights across all models that include a particular variable [30]. This approach yielded values of 0.88, 0.31, 0.27, and 0.13, for PARENTS, HATCH, RIVER SECTION, and YEAR, respectively.

Delta approximations of daily nest survival (see Bolker [42]) were 0.998 for nests with 2 parents in attendance and 0.983 with 1 parent, which translates into cumulative nest survival rates of 0.89 and 0.42, assuming a 50-d nest interval. If we assume that

abandonment occurred on day 31 of the nest interval, which is the mean abandonment day in our data set, then nests in which abandonment occurs have a survival probability of 0.67 over a 500-d interval. Daily nest survival was approximately 0.996 and 0.997 for upstream and downstream river sections, respectively, which yielded survival rates of 0.81 and 0.85 over a 50-d nest interval, respectively (see Figure 3). These values correspond with apparent nest success rates (i.e., the percentage of observed nests that fledged at least 1 offspring), which were 81% in the upstream section and 93% in the downstream section.

To determine whether interaction terms led to improved models, we performed post hoc analyses of the RIVER + PARENTS model and the PARENTS + HATCH model with their respective interaction terms included. Addition of the RIVER × PARENTS interaction led to an increase in AIC_c of 1.83, and addition of the PARENTS × HATCH interaction increased AIC_c by 1.99. Therefore, we conclude that these interaction terms are not informative.

The goodness of fit of the all-main-effects model revealed no evidence against model fit ($p = 0.45$). However, the first assessment of the best model (PARENTS only) did not meet the goodness of fit criteria ($p = 0.02$). Close examination of the data revealed that the goodness of fit test was likely influenced by 1 extremely long observation interval (20 d) during which a nest failure occurred (we were prevented from accessing this burrow because of logistical constraints). When data from this nest were removed, there was no evidence that the model failed to fit the data (PARENTS only: $p = 0.41$, all main effects: $p = 0.48$).

The results from the follow-up analyses differed little from our initial results. Removal of all data for which there was some uncertainty about the dates of nest-cycle events had no substantial effect on relative AIC_c scores or model parameter estimates. In a separate modeling effort in which we added depredated burrows (all of which were located in the upstream section of the study area) to the data set, we observed an increase in the importance of RIVER. The best model was still the 1-variable model with PARENTS (AIC weight = 0.38), but the second-best model included PARENTS and RIVER and had

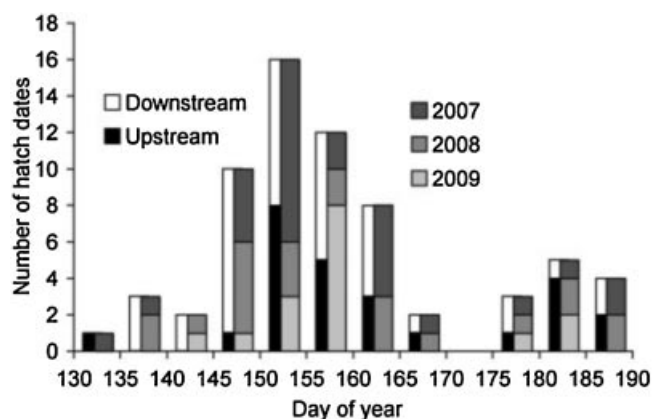


Figure 2. Distribution of hatching dates (expressed as day of year along the x axis) for belted kingfishers on the Upper Hudson River from 2007 to 2009. Broad columns have up to 3 divisions corresponding to each of the 3 yr of the study. Narrow columns with 2 divisions indicate contributions from upstream and downstream burrows.

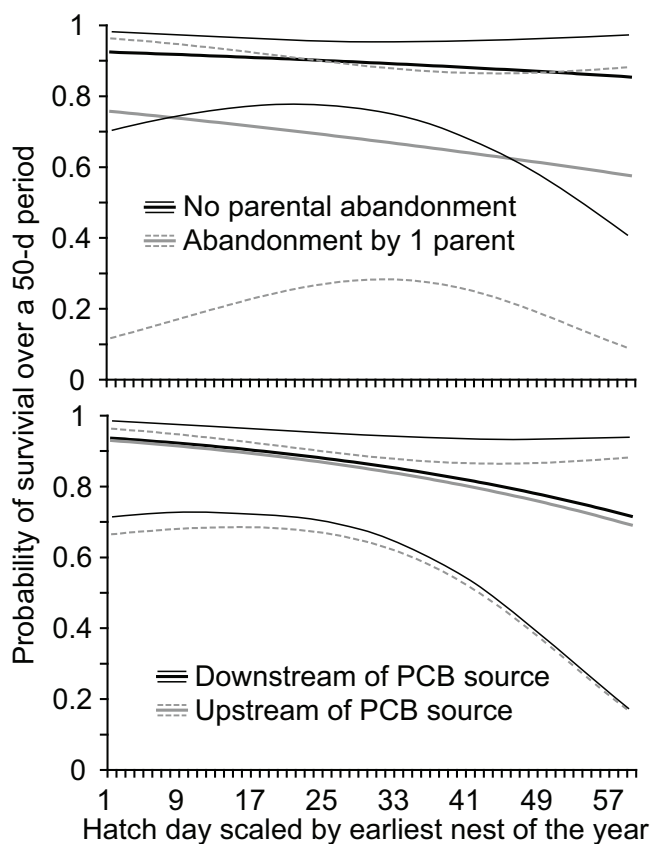


Figure 3. Estimated survival for a 50-d nest period over the observed range of hatch dates (scaled within each year) calculated from the output of the PARENT and HATCH model (top) and the RIVER and HATCH model (bottom) using the delta method (see Perrins [42]). The top panel shows survival curves for nests in which both parents are in attendance for the entire nesting cycle and for nests in which 2 parents are present for the first 31 d and 1 parent is present for the remaining 19 d (a typical scenario in our study population). The bottom panel shows survival curves for burrows upstream and downstream of the primary polychlorinated biphenyl (PCB) contaminant source. This and dashed lines show 95% confidence intervals.

an ΔAIC_c of 1.01 with an AIC weight of 0.23. The β estimate for RIVER in this model was positive (0.63 ± 1.25 ; mean and CI), indicating that downstream burrows (in which RIVER is coded as a 1) were generally associated with increased nest survival. Given that the initial results also predicted slightly higher survival probability in the downstream river section, we interpret these subsequent analyses as evidence that the initial analysis was robust against error associated with our observational protocol and against effects associated with nest depredation.

Forty-three percent of the successful nests we monitored had at least 1 egg that failed to hatch or at least 1 nestling that died prior to fledging. In assessing the number of fledglings produced per successful nest, we found no significant difference between the upstream and downstream river sections (based on overlap of 95% CIs). Successful nests in the downstream river section produced 5.68 ± 0.49 (mean \pm 95% CI) offspring per nest, and successful nests in the upstream section produced 5.24 ± 0.80 offspring per nest. In contrast, the effect of the number of parents attending a nest on the number of fledglings was quite clear. Successful nests in which 1 parent left prior to fledging produced 3.60 ± 1.88 fledglings on average, whereas successful nests with no abandonment produced 5.70 ± 0.41 fledglings.

Return rates of kingfishers banded as adults were similar for upstream (6 of 21) and downstream (9 of 35) portions of the river (Fisher's exact test: $P \approx 1$; Table 3), with 15 of 56 birds banded

Table 3. Banding and return rate summary from kingfisher monitoring on the upper Hudson River^a

	Banded upstream	Banded downstream	Banded total	Returned upstream	Returned downstream	Returned total
Adults	21	35	56	6	9	15
Nestlings	58	120	178	1	2	3
Total	79	155	234	10	11	18

^a Banding counts refer to birds banded in 2007 and 2008 only, and returns are from 2008 and 2009. Banding data from 2009 are excluded as we do not have corresponding return data.

in 2007 and 2008 observed in at least 2 consecutive years, and 4 observed in all 3 yr. Only 3 of 178 nestlings banded in 2007 and 2008 returned to the study area to breed in 2008 or 2009, 2 of which were from the downstream section.

DISCUSSION

Our most striking finding was that kingfisher reproductive success was not diminished in the downstream section of the upper Hudson River relative to the upstream section. In fact, daily nest survival and apparent nest success were higher in the area downstream of the PCB source. Hence, we found no evidence that PCB exposure has a population-level effect on the survival of kingfisher nests and nestlings.

We did not attempt to remeasure PCB concentrations in the blood, tissues, or eggs of belted kingfishers. However, clear evidence of exposure is apparent in surveys conducted in 2002 and 2004 [19,20]. Moreover, ongoing monitoring indicates that PCB loads in small forage fish (primary prey items for kingfishers) downstream of the PCB source remained elevated from 2004 to 2009 relative to areas upstream of the source. Specifically, total PCB concentrations from 3 downstream sites averaged 4.72 mg/kg wet weight in 2004 ($n = 30$), and identical sampling during 2007 to 2009 produced a 3-yr average of 3.31 mg/kg ($n = 90$, General Electric Company, Corporate Environmental Programs, Albany, New York, USA, unpublished data). Although PCBs were slightly reduced during the study period, they remained an order of magnitude higher than PCBs in fish sampled at upstream reference sites, which never exceeded 0.1 mg/kg ($n = 61$; General Electric Company, Corporate Environmental Programs, Albany, New York, USA, unpublished data). Remediation in the form of removing contaminated sediment in the downstream portion of the study site began on 15 May 2009, during our final field season [44]. However, an associated decrease in PCBs that would be relevant to our findings in 2009 is implausible given the size of the river, the timing and scale of the dredging operation, and the time lag between any decline in the PCBs in the river and those in kingfishers.

In light of the evidence of PCB exposure in the downstream nesting sites, the similarity between belted kingfisher reproductive success in upstream and downstream river sections suggests that kingfisher reproduction remains robust in areas of PCB contamination. Given the generally high degree of nesting success observed in many studies of this species [20,25,26], it seems reasonable to assume that most mortality in the study population occurs during the postfledging period when yearling birds must learn to forage and avoid predation. Kingfishers that we banded as nestlings rarely returned to the study area to breed. The 2% nestling return rate we observed (see Table 3) is similar to that reported by Albano [25] in which 2 of 188 nestlings returned to the study site. These findings suggest that postfledging dispersal in belted kingfishers occurs at too great

a spatial extent to adequately study using a simple band/recapture approach. A more sophisticated tracking system may be necessary to evaluate fledgling survival in belted kingfishers. Adult return rates were notably higher (27%), but it is unclear how dispersal and mortality contribute to this figure.

Of the variables we examined, abandonment by 1 parent was most strongly associated with nest success and survival of individual nestlings. We do not know the cause of any of the observed cases of parental abandonment. It could be due to mortality, as we never resighted or recaptured a parent that abandoned a nest. The causal nature of the relationship between abandonment and nestling deaths was also unclear. We observed 3 cases in which nestlings died before abandonment, 2 cases in which nestlings died after abandonment, and 3 instances in which we could not tell whether nestling deaths or abandonment came first. There was also 1 instance in which no nestlings died despite abandonment by 1 parent. Males and females appeared to abandon nests with about the same frequency—of 9 events, males abandoned 5 times and females 4 times. Abandonment was more frequent in the upstream portion of the study area, with 6 instances of abandonment among 26 nests in the upstream section as opposed to 3 cases among 40 nests in the downstream section. Although this trend could be due to random chance (Fisher's exact test; $p = 0.16$), we suspect that more rapid flow in the upstream area is associated with fewer and more transient nest sites for kingfishers, which may have resulted in the upstream area being populated by individuals of lower quality than their downstream counterparts.

This difference between river sections may further account for the slightly lower reproductive success observed in the upstream area, and it underscores the difficulty associated with upstream/downstream comparisons. Our comparison of upstream and downstream sections of the study site is limited by the fact that there are notable habitat differences between these 2 areas. Among these differences are increased human habitation and use of the river in the downstream section as well as increased water volume and decreased current downstream. Nevertheless, based on Mažeika's [45] study of habitat quality and belted kingfisher reproductive success, both upstream and downstream sections would qualify as optimal kingfisher habitat. Despite upstream and downstream differences, we think that this comparison has fewer shortcomings than comparisons across multiple watersheds, in which physical differences in aquatic habitats are compounded by disconnected hydrologies and watershed histories.

Although the upstream and downstream comparison is imperfect, it is important to note that nest success was high in both sections of the study site relative to most bird species [46,47], such that we were not comparing birds in the downstream section to a population sink in the upstream section. Apparent nest success rates in our study (81% upstream and 93% downstream) are similar to other studies such as that of Albano [25], who documented an apparent nest success rate of approximately 80% (which includes some depredated nests) on the Connecticut River in Massachusetts, USA, and Hamas [26], who reported no naturally caused nest failures among 29 nests in the Lake Itasca Region of Northern Minnesota, USA.

Because of its status as a top predator in aquatic systems, the belted kingfisher has often been regarded as an indicator species, one whose survival and reproductive output would reflect the quality of the breeding habitat [48–50]. Although there is some indication of poor health in individual birds living in mercury-contaminated areas [51], both in the present study and in the scientific literature, we found little evidence of an effect of PCB

contamination on the demographics of kingfisher populations [20,52]. The high daily nest survival rates and apparent nest success indicate that during 2007 to 2009 kingfishers breeding on the upper Hudson River was a productive part of the larger regional population. Our work is not alone in documenting a lack of population-level effects on animals in contaminated areas (see Bosveld and van den Berg [53]). Several studies of free-living birds species have found limited or no evidence of PCB-induced effects on survival and reproduction despite clear evidence of PCB exposure (e.g., Custer et al. [11] and Henning et al. [54]). These studies highlight the complexity of discerning the effects of environmental contaminants, and suggest that population-level responses to PCBs may be mitigated or exacerbated by numerous factors including the behavior and physiology of the study species and the distribution and availability of resources in the environment.

SUPPLEMENTAL DATA

Tables S1–S2. (155 KB DOC).

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