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NEST-BUILDING BEHAVIOR IN PCB-CONTAMINATED TREE SWALLOWS

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ABSTRACT.—Considerable attention has been directed toward documenting the effects of environmental chemicals on the endocrine systems of vertebrates, especially on development and reproduction. Given the well-documented role of hormones in controlling behavior, one would expect to see abnormal behavior in contaminated wildlife. We describe abnormal nest-building behavior in Tree Swallows (*Tachycineta bicolor*) breeding along the Hudson River of New York in areas highly contaminated with polychlorinated biphenyls (a group of chemicals known to disrupt endocrine systems). Previous studies of Tree Swallows have shown that nest quality is an important component of reproductive success. Swallows breeding in contaminated areas built smaller nests of lower quality compared with those in uncontaminated areas. Our observations are consistent with the possibility that chemical contaminants interfered with behavior. *Received 31 October 1997, accepted 11 May 1998.*

POLYCHLORINATED BIPHENYLS (PCBs) are widespread contaminants that are associated with reproductive dysfunction, growth impairment, and embryonic deformities in birds and other organisms (Eisler and Belisle 1996, Hoffman et al. 1996). One possible mechanism for these effects is through the endocrine system (Bitman and Cecil 1970, Korach et al. 1988, Li et al. 1994), and recent studies have focused on the relationship between hormonal abnormalities and morphological and reproductive problems in contaminated wildlife (Fox 1992, Colburn et al. 1993, Guillette 1995). Given the influence of the endocrine system on reproductive behavior in birds, we expect that PCBs also affect reproductive behavior (Peakall 1996). Here, we report abnormal nest-building behavior in Tree Swallows (*Tachycineta bicolor*) that were exposed to high levels of PCB contamination.

The Hudson River between Hudson Falls and New York City (a distance of more than 300 km) is highly contaminated with PCBs (Clesceri 1980). In 1994, we initiated a project to determine the effects of PCBs on migratory birds in the Hudson River Valley. Tree Swallows migrate in large numbers along the Hudson River and are a common breeding species in the region. Their abundance and willingness to breed in nest boxes make Tree Swallows a good indicator species for monitoring uptake of environmental contaminants (St. Louis et al. 1993, Bishop et al. 1995, Nichols et al. 1995). Moreover, Tree Swallows nesting near water feed primarily on adult insects that have aquatic larvae, thereby providing a pathway for the transfer of contaminants between aquatic and terrestrial systems (Larsson 1984, Robertson et al. 1992).

Prior to egg laying, Tree Swallows spend two or more weeks defending a nest cavity and building a grass nest within the cavity. The nest is lined with a variable number of feathers (Sheppard 1977). Both sexes construct the nest, with females responsible primarily for building the grass cup and males gathering most of the feathers used to line the nest (Robertson et al. 1992). Nest quality is an important component of reproductive success in Tree Swallows (Winkler 1993, Lombardo 1994, Lombardo et al. 1995). Specifically, chicks from nests with more feathers in the lining grow faster, fledge earlier, and have fewer nest parasites (Winkler 1993, Lombardo et al. 1995). In addition, nests with a larger grass mat hatch more eggs per clutch (Lombardo 1994). Toward understanding the influence of PCBs on reproductive success, we compared measures of nest quality of Tree Swallows from contaminated areas with those from Tree Swallows from an uncontaminated site.

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TABLE 1. Quality of Tree Swallow nests measured by nest mass and number of feathers lining the nest cup. Remnant, SA13, and Saratoga contain high concentrations of PCBs; Champlain is moderately contaminated; and Ithaca is uncontaminated. Values are $\bar{x} \pm$ SE, with n in parentheses; F values are from ANOVA testing the effects of colony site on nest quality. Within rows, sites that share a letter in the superscript do not differ significantly based on Fisher's PLSD post-hoc test. The effects of colony site on nest quality are significant using a sequential Bonferroni correction (Rice 1989) to correct for multiple comparisons.

	Colony site						
Variable	Remnant	SA13	Saratoga	Champlain	Ithaca	F	P
Nest mass at laying	$23.1 \pm 1.5^{A,B}$ (23)	20.1 ± 0.9^{A} (36)	$24.5 \pm 1.4^{B,C}$ (33)	28.4 ± 1.6^{C} (20)	34.7 ± 0.9^{D} (103)	30.2	<0.001
Nest mass at hatching	26.5 ± 1.5^{A} (22)	22.8 ± 1.1^{A} (30)	25.9 ± 1.5^{A} (25)	31.3 ± 2.2^{B} (15)	—	4.9	0.003
No. feathers at first egg	6.6 ± 1.0^{A} (27)	6.5 ± 0.6^{A} (41)	3.3 ± 0.4^{B} (33)	9.2 ± 1.8^{A} (24)	15.0 ± 1.6^{C} (23)	14.9	<0.001
No. feathers at last egg	$17.3 \pm 1.7^{A,B}$ (28)	$15.0 \pm 1.9^{A,C}$ (42)	$11.6 \pm 1.7^{A,C}$ (34)	23.5 ± 2.8^{B} (19)	33.6 ± 1.8^{D} (103)	21.7	<0.001
No. feathers at hatching	$50.7 \pm 4.3^{A,B}$ (23)	$46.6 \pm 2.7^{A,B}$ (30)	40.4 ± 3.2^{A} (25)	56.3 ± 5.9^{B} (17)	—	2.8	0.047

METHODS

In 1995, we monitored Tree Swallow colonies located downstream from the main PCB source at Hudson Falls, New York (43°18'N, 73°29'W). Sites were located at Remnant Deposit 4 (hereafter "Remnant") 3 km downstream from the main PCB source, Special Area 13 ("SA13") approximately 6 km downstream from the source, and Saratoga Battlefield National Historic Park ("Saratoga") about 45 river km downstream. A fourth site was located along the Champlain Canal ("Champlain") 5 km upstream from its confluence with the Hudson River. Some of the Tree Swallows at Champlain were moderately contaminated with PCBs (probably accumulated during migration along the Hudson River). We compared data from the Hudson River and Champlain sites with data collected from 1990 to 1994 at an uncontaminated Tree Swallow colony approximately 260 km west of the Hudson River near Ithaca, New York (42°30'N, 76°27'W; D. W. Winkler and J. P. McCarty unpubl. data).

At each site, 25 to 35 nest boxes (interior dimensions 12 × 12 × 20 cm) were placed within 100 m of the river's edge. All boxes along the Hudson River and at Ithaca were placed in large grassy areas with an abundance of suitable nesting material. A removable cardboard liner was inserted into each box, allowing us to remove and measure nests with minimal disturbance. Nest-box dimensions were the same at the Hudson River and Ithaca colonies, and nest liners were identical in all boxes. We used two measures of nest quality: nest mass, and the number of feathers lining the nest cup. The mass of each nest was measured on the day the first egg was laid and again on the day the eggs hatched. The number of feathers lining the cup was counted on the day the first egg was laid, after the clutch of eggs was completed, and on the day the eggs hatched. Feather numbers also were counted in 14 nest boxes of nonstandard dimensions (seven at SA13, five at Remnant, and two at Saratoga).

Reproduction was monitored through frequent nest checks begun prior to nest initiation. We defined the incubation period as the number of days between the laying of the penultimate egg and the hatching of the majority of eggs in the nest, and the fledging period as the number of days between the hatching of the majority of eggs and the departure of the last surviving nestling. All nests were equipped with predator guards, but some eggs and chicks were taken by predators. Losses of eggs and nestlings to predators were not included in analyses of reproductive success. Nestling mass was measured (±0.1 g) using a portable electronic balance on day 10 (where hatching = day 1). We compared the mean mass of all nestlings in a brood with nest characteristics to avoid problems of nonindependence among brood mates. Reproductive data obtained after eggs or nestlings were collected for chemical analyses were not included in the calculation of reproductive success. Adults were captured at the nest during the brood-rearing period, and the age class of females was determined using plumage criteria (Hussell 1983).

RESULTS

In general, nests built by Tree Swallows along the Hudson River were significantly lighter and had fewer feathers than nests at the Champlain and Ithaca sites (Table 1). Qualitatively, nest construction was similar at all sites, with a tightly woven grass mat filling the bottom of the nest liner and a nest cup lined with feathers as has been described elsewhere (Robertson et al. 1992). Post-hoc tests of differences among sites indicated that Ithaca nests had significantly higher mass and more feathers than Champlain nests, and Champlain nests in turn had higher mass and feather numbers than Hudson River sites. Among the three Hudson River sites, significant differences existed only in nest mass at first egg and number of feathers at first egg (Table 1). Nest quality tended to decline as PCB contamination increased (Fig. 1), but with a sample size of only five sites, only the relationship between nest mass and PCB contamination was significant (Kendall rank correlation, $\tau = -0.8$, $P = 0.05$).

Previous studies have shown that female age may affect the quality of nest construction, with yearling females (readily identified by their brown plumage) building inferior nests (Sheppard 1977, Lombardo 1994; but see Rendell and Verbeek 1996). Possible confounding effects of female age were examined by comparing the proportion of yearling females at each site. The Champlain site had a higher percentage of yearling females (45%) than did the Hudson River sites (21 to 25%), whereas the percentage of yearling females at the Ithaca site varied from 17 to 50% among years. The effects of female age on nest mass and feather number were examined using a two-factor ANOVA, controlling for nest site. Because the number of yearling females along the Hudson was small, data from all three Hudson River sites were pooled and compared with Ithaca and Champlain. The number of feathers and nest mass at clutch completion were the only variables with sufficient data for this analysis. In both cases, colony site, but not female age, had a significant effect on nest quality (Table 2).

The incubation period was significantly longer in nests with few feathers and nests that had relatively low mass at the beginning of incubation (Fig. 2), but both relationships were weak (number of feathers, $R^2 = 0.05$, $F = 6.4$, df = 1 and 112, $P = 0.013$; nest mass, $R^2 = 0.04$, $F = 4.4$, df = 1 and 102, $P = 0.038$). Length of the nestling period was not significantly related to the number of feathers present when the eggs hatched ($R^2 = 0.02$, $F = 1.3$, df = 1 and 77, $P = 0.26$) or to nest mass at hatching ($R^2 = 0.02$,

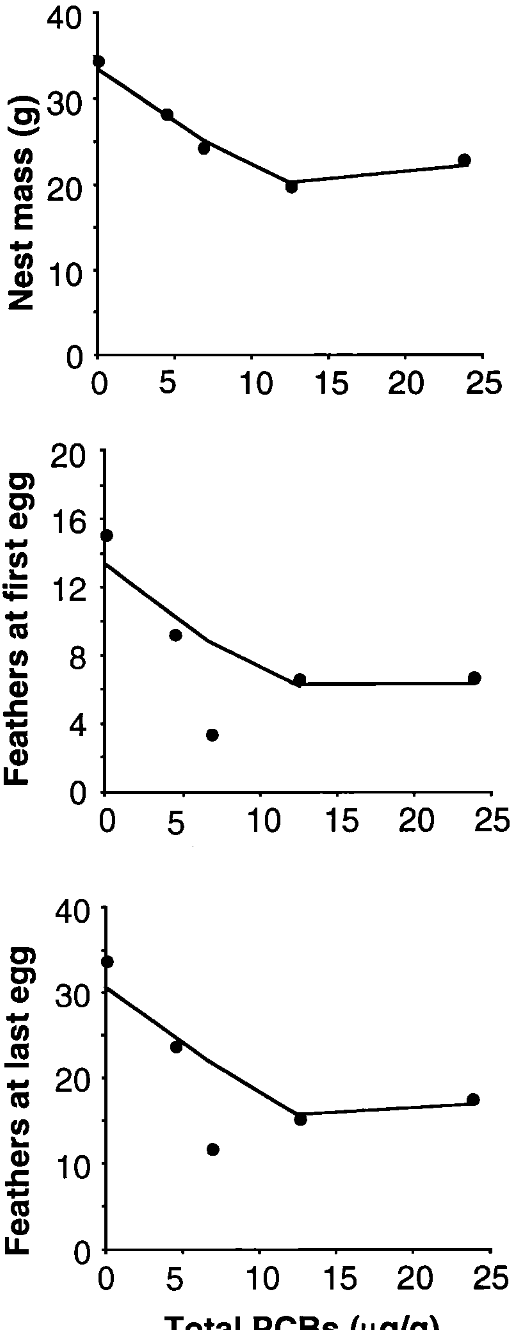

FIG. 1. Relationship between total PCBs in Tree Swallow eggs and nest quality. Mean total PCB concentrations (µg/g wet mass) in eggs are from Secord et al. (unpubl. data). Curves fitted using LOWESS (Cleveland 1981).

TABLE 2. Effect of female age and colony site on nest quality of Tree Swallows. Values are $\bar{x}$, with n in parentheses. "Hudson" colony sites include Remnant, SA13, and Saratoga, which contain higher levels of PCB contamination than Champlain and Ithaca.

	Colony site			Two-way ANOVA		
	Hudson	Champlain	Ithaca	Age effect	Site effect	Interaction
		Number of feathers				
Yearling females	18.5 (16)	24.3 (7)	26.4 (16)	0.1	12.7*	1.9
Older females	13.0 (68)	22.9 (9)	30.9 (29)			
		Nest mass				
Yearling females	23.0 (10)	28.7 (7)	36.8 (16)	0.2	36.9*	0.3
Older females	21.2 (63)	27.1 (10)	37.7 (29)			

* $P < 0.001$.

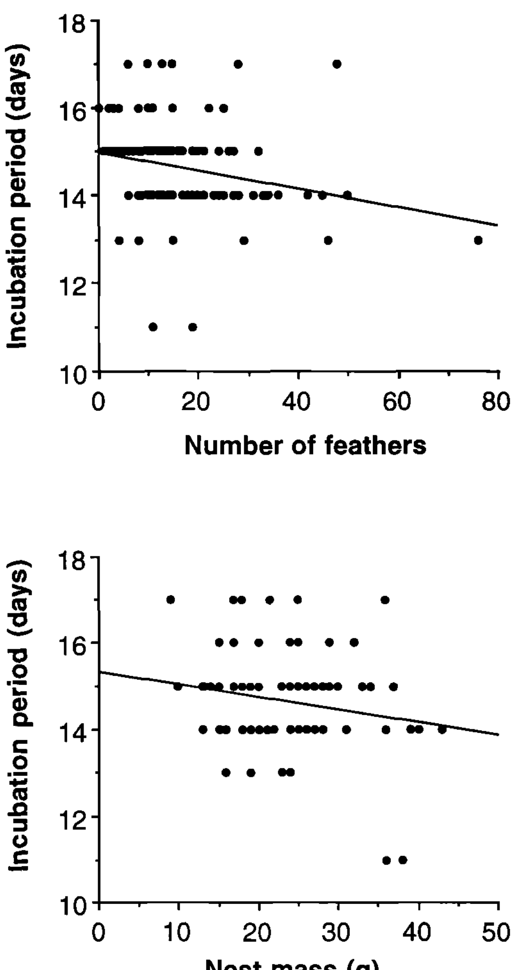

FIG. 2. Relationship between nest quality and the length of the incubation period in Tree Swallows in the Hudson River Valley (including Champlain Canal). Lines are from least-squares regression.

$F = 1.81$, df = 1 and 76, $P = 0.18$). Nestlings raised in relatively well-feathered nests were heavier on day 10 ($R^2 = 0.15$, $F = 6.5$, df = 1 and 38, $P = 0.015$), but nestling mass was not related to nest mass at hatching ($R^2 = 0.02$, $F = 0.7$, df = 1 and 36, $P = 0.39$; Fig. 3). The relationship between feathers and nestling mass shown in Figure 3 was heavily influenced by one poorly feathered nest where nestling mass averaged only 12.6 g. When this nest was excluded from the analysis, the relationship between feather numbers and nestling mass was no longer significant ($F = 1.32$, df = 1 and 37, $P = 0.26$). The number of fledglings produced was significantly correlated with the number of feathers in the nest at the start of egg laying ($R^2 = 0.05$, $F = 4.5$, df = 1 and 90, $P = 0.037$; Fig. 4), but none of the other factors examined was related to fledgling production (nest mass at initiation, $R^2 < 0.01$, $F = 0.29$, df = 1 and 90, $P = 0.59$; nest mass at hatching, $R^2 = 0.01$, $F = 0.41$, df = 1 and 76 $P = 0.53$; feathers at hatching, $R^2 = 0.01$, $F = 1.1$, df = 1 and 76, $P = 0.30$).

DISCUSSION

The quality of nests built by Tree Swallows at colonies along the Hudson River was significantly lower than at other sites in New York. Comparisons of both nest mass and the number of feathers lining the nest showed a consistent pattern of Ithaca nests having higher mass and more feathers than Hudson River nests, whereas nests from Champlain were intermediate in quality (Table 1). Because females are responsible primarily for building the grass nest cup, and males gather most of the feathers used in lining the nest cup (Robertson et al. 1992), it appears that nest-building behavior of both

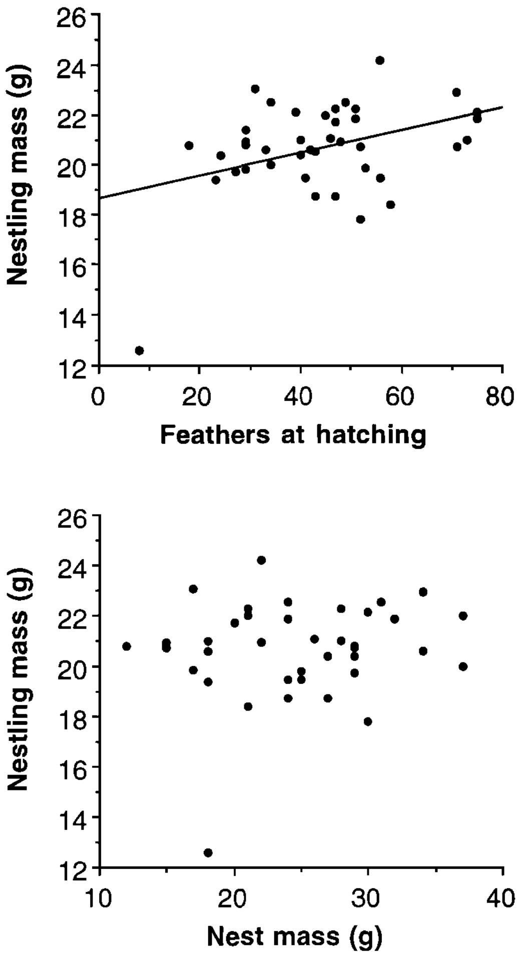

FIG. 3. Relationship between nest quality and mass of nestlings at day 10 for Tree Swallows in the Hudson River Valley (including Champlain Canal). Lines are from least-squares regression.

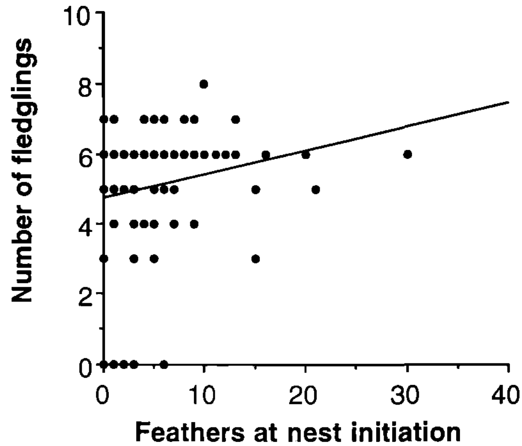

FIG. 4. Relationship between number of feathers in the nest at clutch initiation and the number of fledglings produced Tree Swallows in the Hudson River Valley (including Champlain Canal).

sexes was impaired at the Hudson River colonies.

The quality of nests may influence reproductive success either by attracting higher-quality mates (Collias and Collias 1984, Hoi et al. 1994, Evans 1997) or through direct effects on nesting success (Møller 1982, 1991; Slagsvold 1989; Winkler 1993). Data from this population support the relationships between nest quality and length of the incubation period (Lombardo et al. 1995), length of the nestling period (Winkler 1993), nestling mass (Winkler 1993, Lombardo et al. 1995), and number of fledglings produced (Lombardo et al. 1995) found in previous studies of Tree Swallows.

The differences in nest quality among sites were consistent with the hypothesis that PCB contamination had adverse effects on Tree Swallow behavior: nests from the uncontaminated site (Ithaca) had the highest quality, those from the highly contaminated sites (Hudson River) had the poorest quality, and those from the moderately contaminated site (Champlain) had intermediate quality (Fig. 1). Significant differences existed among the three Hudson River sites in two of the nest-quality variables. The pattern of nest mass at nest initiation followed the expected pattern, with swallows from Saratoga (located 45 river km downstream of the source of contamination) building heavier nests than those from the highly contaminated SA13 site located only 6 km downstream of the contamination source (Table 1). The opposite pattern occurred in the number of feathers in the nest at nest initiation: nests at Saratoga had fewer feathers than nests at the two Hudson River sites closer to the source of contamination (Fig. 1).

Only limited sampling for other environmental contaminants has occurred in the study area. Concentrations of organochlorines in Tree Swallow eggs collected from our sites in 1994 were below the analytical detection limits. Concentrations of polychlorinated dibenzo-*p*-dioxins, dibenzofurans, and heavy metals were below levels associated with biological effects in birds (Secord and McCarty 1997). Heavy metals are present in high concentrations in some Hudson River sediments (Chillrud 1996). Although heavy metals could influence nest-building behavior, our data suggest that PCBs are present at more significant biological concentrations in Tree Swallows than are heavy metals and at concentrations known to influence reproductive behavior in other bird species (Kubiak et al. 1989). It is likely that any contaminant effects in Hudson River Tree Swallows are due to PCBs because of the exceptionally high levels of these chemicals and their overwhelming contribution to the toxicity of the chemical mixture contaminating the Hudson River sites (based on toxic equivalency factors; Secord and McCarty 1997).

The mechanisms behind the observed differences in nest-building behavior among swallow colonies are not known, although the patterns observed are consistent with the expected effects of endocrine disruptors such as PCBs. The importance of interactions among hormones and other reproductive behaviors (e.g. Fivizzani et al. 1990, Wingfield and Farner 1993, Buntin 1996) suggests that behavioral studies may provide the link between endocrine disrupters and impaired reproduction in contaminated populations of wildlife. Although the role of the endocrine system in controlling nest-building behavior has not been studied in Tree Swallows, work on other species of birds clearly shows the importance of hormone levels in determining both the gathering of nesting materials and subsequent nest construction (Erickson and Hutchison 1977, Collias and Collias 1984, Adkins-Regan and Ascenzi 1987, Logan and Wingfield 1995).

In birds, the relationships among chemical contaminants, hormone levels, and reproductive behavior are best documented in Ringed Turtle-Doves (*Streptopelia risoria*). Nest building is under hormonal control in doves (Erickson and Hutchison 1977, Collias and Collias 1984). Experiments involving captive Ringed Turtle-Doves fed a mixture of endocrine-disrupting organochlorines, including PCBs, have shown that hormone levels are affected and courtship and reproductive behavior are abnormal (Haegele and Hudson 1973, 1977; Peakall and Peakall 1973; McArthur et al. 1983). In addition, nest-construction behavior was significantly reduced and occurred later in the reproductive cycle in individuals fed higher levels of contaminants (McArthur et al. 1983). Although results from distantly related species such as doves may not apply directly to Tree Swallows, such studies support the hypothesized link between endocrine-disrupting chemicals, hormones, and the poor quality of nests in Tree Swallows.

Several factors besides chemical contaminants could influence intraspecific variation in nest quality. Although the environment is thought to have effects on interspecific differences in nest construction (Collias and Collias 1984) and on populations living in different climates and habitats (Kern 1984, Kern and van Riper 1984, Morin 1992), few studies have quantified differences in nest quality among individuals in the same population. Nest quality can improve with the age and experience of adults in some species (Collias and Collias 1984, Evans 1997). However, in Tree Swallows, no consistent effect of female age on nest characteristics has been found in this or in previous studies (Lombardo 1994, Rendell and Verbeek 1996). Indeed, young females had higher nest mass and more feathers in their nests (although the differences were not significant) at Hudson River sites than at sites that were less contaminated (Table 2), suggesting that the influence of PCBs is greater on older individuals that have spent more time in contaminated areas. Given the number of factors that might interact to produce effects on nest quality, we cannot exclude the possibility that factors other than contamination levels contribute to variation in nest construction. Indeed, given the variation that exists within a site, it is surprising that differences among sites could be detected at all.

Our study documents a plausible link between PCB contamination and nest quality. Yet, like other such studies, it cannot demonstrate a causal link between chemical contaminants and behavioral effects (Peakall 1996). Given the obvious difficulties in experimentally introducing dangerous chemicals into the field, this constraint will continue to impede studies of behavioral effects in ecologically realistic settings. Although carefully controlled experiments are critical to assigning causality, field studies such as ours have been and will continue to be important in identifying possible effects of contaminants on natural populations (Blus and Henny 1997).

Several now-classic studies conducted during the last 25 years have documented the effects of chlorinated hydrocarbons on reproduction in birds and other wildlife (Fox 1993, Hoffman et al. 1996). Although the focus of much of this work has been on physical defects that result from abnormal levels of hormones (Colburn et al. 1993, Giesy et al. 1994, Guillette 1995), behavioral abnormalities have also been suggested for some nonpasserines (Fox et al. 1978, Conover and Hunt 1984, Fry et al. 1987, Kubiak et al. 1989, Peakall 1996). Our study provides the first evidence of behavioral abnormalities in a wild population of passerines associated with high concentrations of PCBs. Our results emphasize that behaviors with direct ties to reproductive success, such as nest building, are important for understanding the mechanism behind changes in demographic parameters in contaminated populations and as potentially important assays of biological effects of chemical contaminants.

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