The Auk 117(4):987–995, 2000

POSSIBLE EFFECTS OF PCB CONTAMINATION ON FEMALE PLUMAGE COLOR AND REPRODUCTIVE SUCCESS IN HUDSON RIVER TREE SWALLOWS

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ABSTRACT.—Chemical contaminants in the environment can influence both morphological and behavioral traits. Ornamental traits such as plumage color may be especially valuable in detecting the effects of toxic chemicals in the environment, although they have been little used to date. We examined patterns of plumage color in subadult female Tree Swallows (*Tachycineta bicolor*) breeding in an area on the Hudson River that had high levels of PCB contamination and compared them with specimens from other parts of the species' range and with data from two previous studies of plumage color. Tree Swallows are one of the few species of birds where females, but not males, have a distinctive subadult plumage during their first breeding season. Females from four breeding colonies in contaminated areas had significantly more adult-type blue-green coloring than females from the rest of the species' range. Subadult female plumage color at these sites formed a continuum between the normal dull brown plumage found elsewhere and the blue-green plumage of older females. Among these subadults, more colorful individuals bred earlier, and earlier breeding in turn led to larger clutches. The patterns of plumage anomalies described here are consistent with disruption of the endocrine system resulting in the early expression of an adult trait. This study supports recent suggestions that examining variation in ornamental traits of animals is an efficient means of detecting effects of chemical contaminants in the environment. *Received 24 June 1999, accepted 28 April 2000.*

THE KEY ROLE of ornamental traits in the social and reproductive biology of animals has been a subject of enormous interest to organismal biologists (see Andersson 1994). Studies of variation in plumage color of birds have provided some of the classic examples of how ornamental traits influence sexual (Hill 1990, Norris 1990) and nonsexual (Rohwer 1977, Järvi and Bakken 1984, Möller 1987) interactions within species and perhaps among individuals of different species (Johnson 1991, Dumbacher et al. 1992, Götmark 1992).

Humans have introduced a diversity of biologically active chemicals into the environment, some of which are associated with morphological and behavioral abnormalities in animals (Hoffman et al. 1996, Peakall 1996). Although the mechanisms behind many of these anomalies are not well understood, it is clear that chemicals such as dioxin and polychlorinated biphenyls (PCBs) can interfere with the development and functioning of the endocrine and neural systems (Colburn et al. 1993, Guillette 1995). The expression of many ornamental traits is influenced by environmental conditions and an individual's physiological condition, making ornamental traits potential indicators of the effects of chemical contaminants (Møller 1993, Hill 1995).

Tree Swallows (*Tachycineta bicolor*) have been used as monitors of environmental contaminants (Blancher and McNicol 1988, Ankley et al. 1993, St. Louis et al. 1993, Bishop et al. 1995, Nichols et al. 1995) because they are abundant and when nesting near water feed primarily on insects emerging from aquatic systems, thereby providing a pathway for transfer of contaminants from aquatic sediments to a terrestrial species (Larsson 1984, Robertson et al. 1992). Tree Swallows that breed along the Hudson River in New York accumulate high concentrations of PCBs (Secord et al. 1999) and might be expected to exhibit negative effects of contamination (McCarty and Secord 1999b). These PCBs were released over the course of three decades from two capacitor manufacturing plants near Hudson Falls, New York. As a result, the United States Environmental Protection Agen-

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cy declared the entire length of the Hudson River downstream from these plants (>300 km of river) to be a Superfund Site. PCBs are no longer produced in the United States, but levels of contamination in the Hudson River remain high. In fact, PCB levels in these Tree Swallows (721 to 62,200 ng per g in eggs and nestlings and up to 114,000 ng per g in adults) are the highest ever reported for the species (Secord et al. 1999).

As one indicator of the effects of PCB contamination on Tree Swallows, we examined patterns of plumage color in females. Within species, plumage color can vary between sexes and with age. Typically, young passerines obtain their adult plumage through a molt that occurs in the fall or spring of their first year. However, in some species, full adult plumage is not obtained until after the first breeding season has passed, even though subadults are sexually mature. This delayed plumage maturation usually occurs in sexually dichromatic species and involves young males that retain a female-like plumage until after their first breeding season (Lyon and Montgomerie 1986, Rohwer and Butcher 1988, Björkland 1991, Stutchbury 1991).

Tree Swallows are one of the few passerines in which females, but not males, show delayed plumage maturation (Lyon and Montgomerie 1986, Stutchbury and Rohwer 1990). Thus, females in their first breeding season (hereafter, "subadult" females) typically have brown upperparts that are distinct from the greenish-blue iridescent color of males and older females. Subadult females also are generally smaller and may have lower reproductive success (DeSteven 1978, Lozano and Handford 1995). Males may discriminate against younger females when choosing mates, and female plumage color may serve an important function in other aspects of the social system of Tree Swallows (Stutchbury and Robertson 1987, 1988; Robertson et al. 1992).

Not all subadult females are uniformly brown. Some individuals have scattered iridescent green or blue feathers, and the brown plumage of others is covered with a "faint greenish sheen" (Robertson et al. 1992). In previously studied populations, only a small minority (≤16%) of subadult females had the adult-type, iridescent blue-green plumage over more than half of their body (Cohen 1980, Hussell 1983). Here, we examine the extent of adult-type blue-green plumage in subadult female Tree Swallows for possible effects of environmental contaminants on this ornamental trait and also discuss the relationships between female plumage color and reproductive success.

METHODS

We studied three breeding sites along the Hudson River in 1994 and 1995. Sites were located between 2 and 40 km downstream of the PCB source at Hudson Falls, New York (43°18'N, 73°29'W). All nest boxes were located within 100 m of the river (see McCarty and Secord [1999b] for details of study site and monitoring of breeding activity). Tree Swallows at all of these sites have extremely high levels of total PCBs (Secord et al. 1999). A fourth site was added in 1995 along the Champlain Canal less than 3 km upstream from its confluence with the Hudson River. Although the Champlain Canal site was not adjacent to a contaminated site, adults still had abnormally high concentrations of PCBs (≥22,000 ng per g) that probably were obtained from feeding over the Hudson River during the prebreeding period (Secord et al. 1999). Because these females are part of the same Hudson Valley population, we include them in our analyses.

Nest boxes were equipped with predator guards, and predation was very low. Any losses of eggs or young to predators were not included in measures of reproductive success. In both years, we collected eggs and nestlings for chemical analysis and excluded these nests from calculations of reproductive success. We examined four components of reproductive success: (1) timing of breeding, (2) clutch size, (3) number of fledglings produced, and (4) number of fledglings produced per egg laid. Fledglings were defined as young that left the nest.

We trapped adults in their boxes during the nestling period and determined the sex of captured individuals by the presence or absence of an incubation patch (found only in females). Females were evaluated using plumage criteria described by Hussell (1983). All females classified as yearlings (SYs in Hussell [1983]) or intermediates by Hussell (1983) were considered subadults, and the extent of adult-type blue or green iridescent feathers on the upperparts was estimated to the nearest 5%. All females were scored by the same observer (McCarty). We banded adults, measured wing length to the nearest 1 mm, and measured body mass to the nearest 0.1 g.

We examined all female Tree Swallow specimens from the Cornell University Vertebrate Collections and from the United States National Museum. The extent of blue or green iridescent feathers on the upperparts was estimated to the nearest 5% following the same methods used on wild-caught females. All specimens were scored by the same observer (Mc-

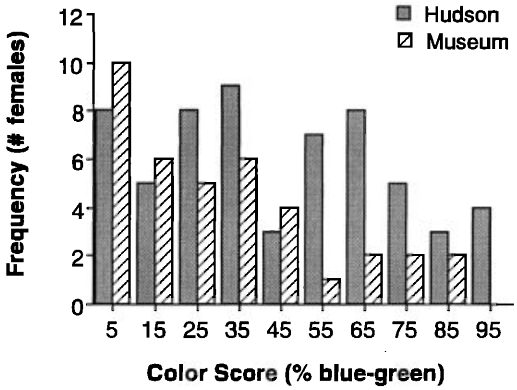

FIG. 1. Plumage color of subadult female Tree Swallows captured along the Hudson River and of museum specimens collected across North America. Hudson River swallows have significantly higher color scores than do birds from the rest of the species' range.

Carty). Except where noted, only females collected between 1 March and 15 July were included in the analyses to minimize complications caused by molt (Stutchbury and Rohwer 1990).

We evaluated the reliability of the plumage-scoring techniques for wild-caught females and museum specimens by calculating repeatability using intraclass correlation coefficients (Lessells and Boag 1987). Photographs of the dorsal plumage of wild-caught Hudson River females taken at the time of capture in 1994 were viewed several months later and scored by the same observer. Plumage scores of wild-caught Hudson River females were highly correlated with plumage scores estimated from photographs of the same individuals (repeatability = 0.67, $F = 5.05$, df = 28 and 57, $P < 0.001$). Specimens from the United States National Museum Collection were also scored twice by the same observer, who did not know the identity of the birds during the second scoring session. The two color scores were compared for all females to evaluate the repeatability of the scoring method, and again plumage scores were highly correlated (repeatability = 0.88, $F = 15.7$, df = 79 and 141, $P < 0.001$). Only the initial plumage score was used in all other comparisons.

RESULTS

Plumage color of Hudson River swallows and museum specimens.—Subadult female Tree Swallows captured along the Hudson River had significantly more adult-type blue-green plumage (median = 37.5%, 95% CI = 30 to 50, $n = 60$) than those examined in museums (median = 20.0%, 95% CI = 10 to 30, $n = 38$; Kolmogorov-Smirnov test, $\chi^2 = 10.4$, $P = 0.011$; Fig. 1). Color scores of subadult females from the Hudson River did not differ between the two years of study (Table 1). Color scores of museum specimens of subadults collected in New York (median = 15.0%, 95% CI = 2 to 25, $n = 5$) did not differ from those in the rest of the species' range (median = 25.0%, 95% CI = 10 to 35, $n = 32$) from March to June (Mann-Whitney U-test, $Z = 1.0$, $P = 0.32$) or for all collection dates (median = 12.5%, 95% CI = 0 to 40, $n = 8$ vs. median = 10.0%, 95% CI = 10 to 20, $n = 71$, respectively; $Z = 0.65$, $P = 0.51$), suggesting that the high level of blue-green plumage is a characteristic of Hudson River Tree Swallows and not of those from the region as a whole.

Although the prevalence of PCBs and other organochlorines in the environment has increased since the 19th century, we detected no effect of year of collection on color scores of female Tree Swallows in subadult or intermediate plumage ($r_s = -0.068$, $Z = -0.60$, $n = 79$, $P = 0.55$; Fig. 2). Wild-caught subadult females from the Hudson River showed no correlation between color score and body mass ($r_s = 0.15$, $Z = 0.98$, $P = 0.33$), wing length ($r_s = -0.13$, $Z = -0.92$, $P = 0.36$), or length of outer primary ($r_s = -0.05$, $Z = -0.37$, $P = 0.71$). Subadult females had significantly shorter wings and outer primaries than did older females (Table 1).

TABLE 1. Color and morphology of female Tree Swallows from the Hudson River. Data are from all females captured, including those excluded from analyses of reproductive success. Values are $\bar{x} \pm$ SD, with n in parentheses. Color score ($t = 0.19$, $P = 0.85$), wing length ($t = 1.77$, $P = 0.08$), and body mass ($t = 1.06$, $P = 0.29$) did not differ between years for subadults, but the outer primary was significantly longer in 1995 than in 1994 ($t = 2.52$, $P = 0.015$). Subadults and older females differed significantly in wing length ($t = 4.09$, $P < 0.001$) and length of outer primary ($t = 6.22$, $P < 0.001$) but not in body mass ($t = 1.79$, $P = 0.08$).

Age class	Color score (%)	Wing (mm)	Outer primary (mm)	Body mass (g)
Subadult 1994	41.6 ± 22.0 (29)	114.4 ± 2.8 (36)	88.3 ± 2.7 (34)	20.4 ± 1.3 (34)
Subadult 1995	40.3 ± 30.6 (31)	113.5 ± 2.3 (26)	90.0 ± 1.9 (25)	19.8 ± 1.2 (17)
Adult	—	115.8 ± 2.8 (93)	91.7 ± 2.7 (89)	20.7 ± 1.3 (62)

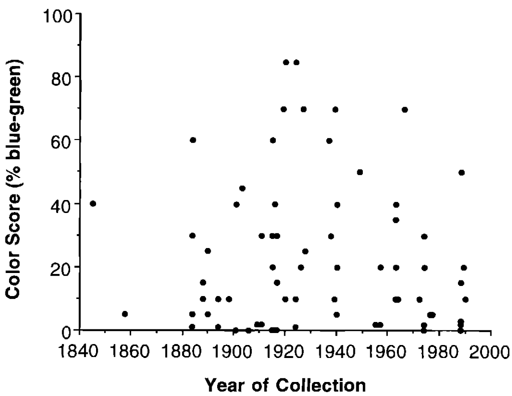

FIG. 2. Color scores of individual female Tree Swallows with subadult or intermediate plumage between 1845 and 1990. Individuals from all months included.

Eight females banded as nestlings in 1994 were recaptured in 1995. All eight were correctly classified as subadults and had a mean color score of 39.4 ± SD of 30.1%. Only 15 of the subadult females banded in 1994 were recaptured in 1995, and 14 of these were given a color score of 100 in their second season. One female retained some brown feathers on her head and rump and was given a color score of 90 in 1995. This female had the very low color score of 5 when captured in 1994 compared with a mean of 36.9 ± 21.2% for the other 14 individuals and a mean of 41.6 ± 22.0% for all subadult females captured in 1994.

Plumage color and reproductive success.—Among subadults, brighter females bred earlier when we controlled for the effects of year of breeding (ANCOVA, $F = 4.11$, df = 2 and 50, $P = 0.022$, $R^2 = 0.14$; standardized coefficient for color = −0.27, $P = 0.048$; standardized coefficient for year = 0.27, $P = 0.045$; Fig. 3A). Subadult females with higher color scores also tended to have larger clutches, but clutch size was also negatively correlated with breeding date ($F = 27.3$, df = 1 and 51, $P < 0.001$, $R^2 = 0.35$; Fig. 3B). When we controlled for the effects of initiation date and year, female plumage color no longer had a significant effect on clutch size (ANCOVA, $F = 8.96$, df = 3 and 49, $P < 0.001$, $R^2 = 0.35$; standardized coefficient for color = 0.73, $P = 0.55$; standardized coefficient for year = −0.33, $P = 0.79$; standardized coefficient for initiation date = −0.56, $P < 0.001$; Fig. 3C). We found no significant relationship between female color and the number of fledglings produced or the number of fledglings produced per egg laid (Spearman rank correlation, all P-values > 0.20).

DISCUSSION

Subadult Tree Swallows from the PCB-contaminated population along the upper Hudson River had an increased amount of adult-type blue-green color in their normally brown dorsal plumage (Fig. 1). This conclusion is based on comparisons of estimates of the extent of iridescent blue-green feathers in the plumage of wild-caught subadults from the Hudson River with those of museum specimens from throughout the species' range. Although this is a simple method of estimating color, it proved to be highly repeatable for museum specimens and wild-caught birds; because one person scored both samples of birds, variability among observers was not a factor.

Based on previous work with individuals of known age (Hussell 1983), it is likely that most of the females with intermediate-colored plumage are yearlings with excessive adult-type blue-green color. Some intermediate females are older adults with abnormal amounts of brown plumage. However, this does not change our conclusion that the proportion of intermediate females is greater along the Hudson River.

Previous studies from elsewhere provide additional support for the conclusion that female Tree Swallows along the Hudson River have an abnormal pattern of color in their subadult plumage. In his study in Ontario, Hussell (1983) found that 12 of 76 (16%) of the subadult females he examined had adult-type blue-green feathers over at least 50% of their upperparts ("intermediates"). Cohen (1980) examined 67 subadult females from Colorado and estimated that 19% of his sample were "approximately 50%" blue-green, and another 6% had more extensive adult-type feathers. If half of the birds classified as "approximately 50%" were no more than 50% blue-green (the classification used by Hussell [1983]), then 15.5% of Colorado subadults would have had ≥50% blue-green plumage, and the remainder would have had <50%. Both of these studies are consistent with our estimates of plumage color in museum specimens where 14% (11 of 80) of the subadults were given plumage scores ≥50%. In

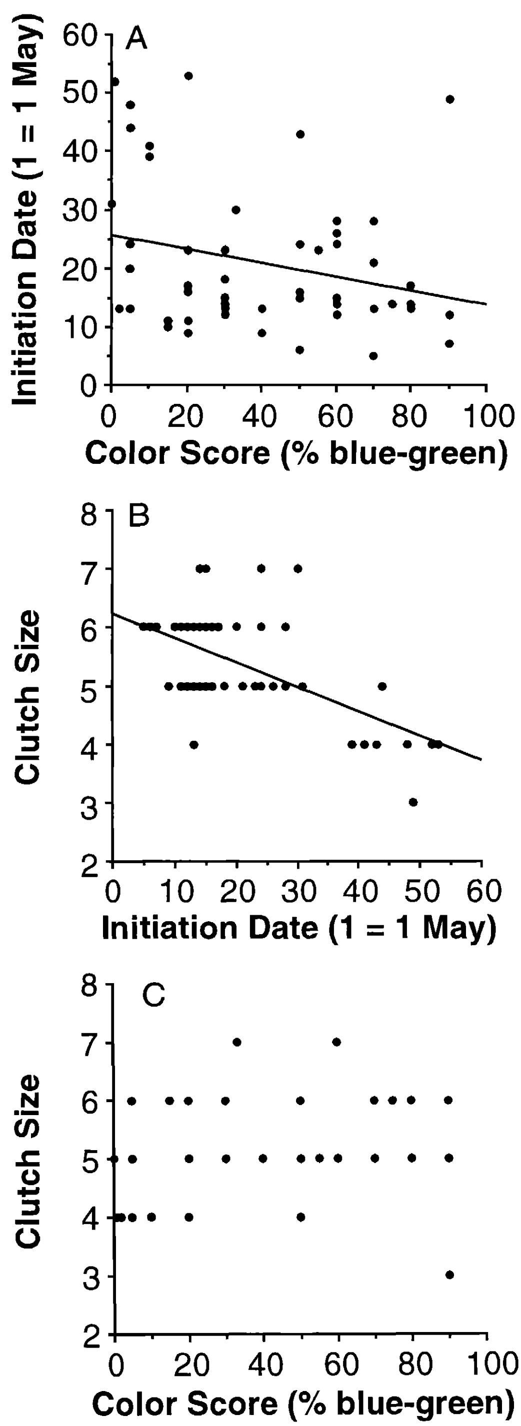

FIG. 3. Color, breeding date, and clutch size of subadult female Tree Swallows. Univariate relationships are illustrated, with lines drawn using least-squares technique. (A) Females with higher plumage color scores started nests earlier in the season, when controlling for the effect of year. (B) Clutch size decreased over the season. (C) Multivariate analysis of the relationship between female color and clutch size failed to find a significant effect of female color when controlling for the effect of initiation date and year.

contrast, 46% (29 of 63) of the Hudson River Tree Swallows were classified as ≥50% blue-green.

It is not known if this association between PCB contamination and plumage color of females exists in other populations of Tree Swallows. Previous studies of Tree Swallows have reported much lower levels of PCB contamination than found along the Hudson River (Ankley et al. 1993, Bishop et al. 1995, Nichols et al. 1995, Secord et al. 1999). The high concentrations of PCBs in the Hudson River, combined with the size of the contaminated area, have created a situation where such effects on populations would be more easily detected. Because the Hudson River dominates the landscape in the study area, it is likely that individuals from a large surrounding area are exposed to PCBs while feeding over the river prior to and during migration. This may not be true of other sites where contamination is more localized and where only birds breeding adjacent to the source of contaminants will be exposed.

Plumage color is important in the biology of birds in that it mediates a wide variety of interactions among individuals (Butcher and Rohwer 1989, Andersson 1994, Savalli 1995), including mate choice (Norris 1990, Hill 1990) and territoriality (Stutchbury 1991). Evidence from several species indicates that variation in plumage characters may be an indicator of an individual's social status (Rohwer 1977, Järvi and Bakken 1984, Möller 1987) and genetic or physiological quality (Hill 1991, 1992; Norris 1993). The function of subadult plumage in Tree Swallows is not fully understood, but plumage color may act as a signal of age and sex to conspecifics, reducing levels of aggression directed at brown subadult females (Lyon and Montgomerie 1986, Stutchbury and Robertson 1987). Numerous studies have shown that brown subadult females have smaller clutch sizes and lower reproductive success (De Steven 1978, Lombardo 1984, Stutchbury and Robertson 1988, Wheelwright and Schultz 1994, Winkler and Allen 1996; but see Lozano

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and Handford 1995), both because they are smaller and have lower fat and protein reserves than adult females (Lozano and Handford 1995), and because high-quality males may preferentially mate with iridescent blue-green adults.

Although these previous studies have documented differences between brown subadult females and older blue-green females, to our knowledge no study has examined the implications of variation among subadults. We found no relationship between the color of subadults and reproductive success as measured by number of fledglings or fledglings per egg, but brighter females bred significantly earlier in the season and laid larger clutches (Fig. 3). A robust relationship exists between early breeding and reproductive success in a wide range of birds (see Price et al. 1988, Winkler and Allen 1996), suggesting that breeding date is an important indicator of other aspects of an individual's quality. More colorful subadult females lay larger clutches, but this is confounded by the relationship between breeding date and clutch size in this and other Tree Swallow populations (Stutchbury and Robertson 1988, Winkler and Allen 1996). Multivariate analysis that included female color and breeding date suggests that the relationship between breeding date and color is responsible for differences in clutch size among subadults (Fig. 3).

The differences in subadult color we report are unlikely to result from natural differences among subpopulations because no subspecies of Tree Swallows have been recognized, nor has geographic variation in plumage been described. Moreover, birds from Ontario (Hussell 1983), Colorado (Cohen 1980), and the rest of North America (this study) generally had consistent patterns of plumage color, as did museum specimens collected in New York.

It also is unlikely that the difference between museum specimens and the Hudson River birds results from fading or other changes in museum specimens because the blue-green color of Tree Swallows is structural in origin, rather than pigment-based. Examination of male Tree Swallows more than 100 years old showed no signs of fading, and we found no relationship between the age of a museum specimen and its color score (Fig. 2). Another valid concern is that museum specimens represent a biased sample of the wild population (e.g. a collector might have avoided taking intermediate females). However, the fact that collections at two different museums, as well as the results of two independent field studies (Cohen 1980, Hussell 1983), consist of low numbers of intermediate females makes it highly unlikely that the patterns presented here result from a collection bias against intermediate females.

The one obvious difference between the Hudson River and elsewhere in the range of Tree Swallows where museum specimens have been collected is that the Hudson River is the most heavily contaminated PCB site in the United States (Limburg 1986). The locations where most of the adults in this study were born are not known. However, available data indicate that natal dispersal in Tree Swallows is limited and that the majority of surviving nestlings breed within 20 km of their natal nest site (Cohen et al. 1989, Robertson et al. 1992), suggesting that most of the individuals we captured were born in the Hudson River Valley.

During both the prebreeding and postbreeding period, we observed large concentrations of Tree Swallows feeding on the abundant insects emerging from the Hudson River. It is likely that birds from a wide area are exposed to PCBs from the Hudson River prior to and during molt. Molt in female Tree Swallows occurs after the breeding season and generally before migration (Stutchbury and Rohwer 1990). The persistent nature of PCBs in the body means that even individuals molting months after exposure to Hudson River PCBs will be contaminated (Stickel et al. 1984).

Field biologists usually focus on traits such as reproductive success or gross morphological changes when screening for effects of environmental contaminants on wildlife. Although a relationship appears to exist between PCB contamination and reproductive success and behavior in this population of Tree Swallows (McCarty and Secord 1999a,b), changes in plumage color may prove to be a reliable means of screening for effects of contamination. Environmental disturbances may have a stronger effect on ornamental traits, such as the plumage dimorphism in Tree Swallows, than on traits under strong natural selection (Møller 1993, Hill 1995). In condition-dependent traits such as tail length, pigments derived from food sources, or the degree of asymmetry in bilateral traits, the quality of ornamental traits is expected to decrease under environmental stress. The direction of effects on ornamental traits that are not condition dependent, such as subadult plumage, cannot be predicted without a detailed understanding of the mechanisms that determine the expression of the trait. The patterns described here are consistent with hormonal abnormalities that result in the early expression of an adult trait.

We report a positive correlation between plumage color and timing of breeding and suggest a role for PCBs in increasing the average color of subadult females, but it is important to note that this does not suggest that PCB contamination leads to overall higher reproductive success in Tree Swallows. Indeed, we have evidence that Tree Swallows in this population suffer from decreased reproductive success (McCarty and Secord 1999b). Any positive benefits to individual subadult females associated with their abnormally bright plumage color simply acts to moderate the other negative effects of contamination, such as reduced hatchability of eggs. In fact, evidence for an adaptive benefit of brown plumage in young females (Lyon and Montgomerie 1986, Stutchbury and Robertson 1987) emphasizes that abnormally colorful plumage in young birds is likely to be detrimental.

The correlational nature of our study makes it impossible to establish a causal relationship between PCB contamination and female plumage color. Logistical and ethical difficulties associated with experimentally introducing toxins into the environment make establishing causality difficult in most field studies of effects of contamination on behavior (Peakall 1996). However, a plausible link exists between PCBs and plumage color because PCBs are suspected to interfere with normal functioning of the endocrine system (Guillette et al. 1995, Eisler and Belisle 1996). The hormonal basis for subadult plumage in Tree Swallows has not been studied, but sex-specific differences in plumage generally are under hormonal control (Fivizzani et al. 1990, Collis and Borgia 1992, Owens and Short 1995, Lank et al. 1999). Although field studies such as ours seldom have been able to demonstrate a causal link between contaminants and their effects, they have been important in identifying possible effects of contaminants that would not be identified from carefully controlled laboratory experiments (Blus and Henny 1997).

Acknowledgments

We extend our thanks to the New York Thruway Authority and the staff of Saratoga National Historical Park for allowing us to establish Tree Swallow colonies on lands they administer. We are grateful to Kevin McGowan at the Cornell University Vertebrate Collections and Richard Banks at the United States National Museum for allowing us to examine specimens under their care. G. A. Fox, R. D. Montgomerie, W. Rendell, L. L. Wolfenbarger, and two anonymous reviewers provided many helpful comments on an earlier draft of this paper.

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Associate Editor: R. D. Montgomerie