

Use of tree swallows in studies of environmental stress

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Abstract. Tree swallows (*Tachycineta bicolor*) are common North American song birds and are increasingly targets of studies of the effects of environmental change on wildlife. This review examines previous work on use of tree swallows to study the ecological importance of environmental contaminants and other sources of environmental change. Exposure of tree swallows to chemical contaminants has been monitored at sites throughout the species' range. Major studies of environmental contaminants have been conducted on Green Bay, the Great Lakes, and the Hudson River where tree swallows are exposed to high levels of PCBs through their diet of insects with aquatic larvae. Additional studies have been completed examining possible effects on tree swallows of exposure to agricultural pesticides in orchards and effluent from pulp mills. In general these studies document that tree swallows are good indicators of exposure to chemical contaminants and their use as a model species has increased our understanding of the importance of biological transport of contaminants from aquatic sediments to the terrestrial food chain. Tree swallows appear to be less sensitive to the effects of PCBs and related chemicals than previously studied species. Evidence of behavioral and developmental effects of PCBs is found in tree swallows exposed to high levels of PCBs along the Hudson River. In addition to studies of contaminants, tree swallows have been used in studies of acid deposition, radiation, and climate change. These studies show that tree swallows are sensitive to the ecological changes that can result from anthropogenic stressors impacting both terrestrial and aquatic ecosystems.

1. Introduction

Field studies of the impacts of environmental stressors on birds and other wildlife play a key role in identifying unexpected impacts of chronic exposure to stressors [1, 2]. As environmental fields in general have come to place increased emphasis on non-game species the number of studies using terrestrial songbirds (Passeriformes), especially migratory species, as model organisms has also increased. Species differ in their suitability for different types of studies. Information about the advantages and disadvantages of different species of migratory passerines as monitors of environmental stress is needed to select among the possible species during planning for field studies.

The purpose of this review is to provide an overview of how a common passerine, the tree swallow (*Tachycineta bicolor*), is being used to study exposure to environmental stressors and the possible effects of that exposure. This review begins with a broad overview of tree swallow ecology and the importance of natural

and anthropogenic sources of environmental stress. This information should provide a guide to factors that should be considered in both designing a study using tree swallows as a model organism and as an aid in interpreting the results of field studies.

The second part of this review describes the exposure of tree swallows to a variety of chemical contaminants. The procedures of ecological risk assessment provide a useful framework for evaluating the effects of environmental stressors [3]. I adopt ecological risk assessment's emphasis on dividing the study of environmental stressors into characterization of exposure and characterization of effects. Even if a contaminant is known to exist in the environment, the complex biotic and abiotic interactions that determine the magnitude of exposure make exposure characterization a critical step in ecological risk assessment.

In the third section of this review, the diverse endpoints that have been considered in studies using tree swallows are described. This overview of past work is intended to assist in interpretation of measures of effects and as an aid to risk assessors and other field workers during the planning phase (problem formulation) of studies considering use of tree swallows [3]. Choice of endpoints will depend in part on the goals of the study and criteria exist for selection of endpoints for ecological risk assessment. The ecological risk assessment guidelines for the U.S. Environmental Protection Agency describe three criteria: ecological relevance, susceptibility, and relevance to management goals [3]. Since the choice of endpoints is likely to be specific to each risk assessment, this review will focus primarily on description of the endpoints used to date in tree swallows rather than evaluation of these or other criteria for selecting among those endpoints.

Birds are widely used to monitor chemical contaminants in the environment as well as other sources of environmental change [4, 5, 6]. The use of birds as indicators and monitors as environmental change carries some disadvantages as well as many advantages. Their long life cycle may make it more difficult to study effects of short-term perturbations on reproductive success and population size, and their ability to move across relatively large spatial scales sometimes makes it difficult to study localized impacts. Balanced against these disadvantages is the compelling reason that birds are relatively well studied, familiar to the public, and protected by existing legislation [7]. Observational studies of birds may have a limited ability to determine the impact of specific stressors since so many interacting variables influence reproduction and population size [8, 9]. However, this is not a shortcoming of studying birds *per se*, since the same is true of observational studies of other types of organisms.

Tree swallows are increasingly important among the ranks of birds used as model species in ecological field studies (Table 1). Careful choice of species can improve the balance between advantages and disadvantages but picking a species or group of species for an ecological field study involves a virtually unlimited number of considerations. No single species can adequately represent the diversity of responses that will occur in a natural community but the depth of knowledge that can be

Table 1

Studies using tree swallows to evaluate environmental stress. Includes completed work and on-going studies measuring uptake of chemical contaminants or studying the effects of anthropogenic stress on tree swallows. Map codes refer to locations indicated on Fig. 1. Major stressor(s) are indicated; studies may have evaluated additional variables. Major endpoints evaluated are listed but inclusion does not signify that an impact of the stressor was found.

Map Code	Location	Major Stressor(s)	Effects Endpoints	References
1	New Brunswick	PCB, DDT, PCDD, PCDF		N. Burgess pers. comm.
2	Acadia Natl. Park	mercury		www.pwrc.usgs.gov
3	se Massachusetts wetlands	organophosphate / carbamate pesticides		H. Czech pers. com.
4	Housatonic River, MA	PCB, PCDD, organochlorines		C. Custer pers. comm.
5	New Jersey	metals		107
6	Hudson River	PCBs	reproduction, behavior, development	27, 47, 54, 97, 135, 151
7	Adirondack Mtns.	acid deposition, black fly control	reproductive success	177, M. Wasson pers com,
8	Lower Great Lakes and St. Lawrence River	PCB, organochlorines	reproduction, biomarkers	80, 91, 103
9	Ontario Orchards	organophosphorus insecticides	reproduction, behavior, biomarkers	29, 99, 100, 102, 141, 156
10	SE Pennsylvania	PCBs	biomarkers, reproduction	26
11	Patuxent NWR	none - reference site	biomarkers, reproduction	26
12	Central Indiana	PCBs		26
13	Saginaw Bay	PCBs	reproductive success, nestling growth	81, 89, 90
14	Sudbury, Ontario	acid deposition	reproductive success	13, 14, 163
15	Green Bay and Fox River Valley	PCB, PCDF, PCDD	biomarkers, reproductive success	28, 87, 88, 123
16	Wisconsin River	PCB, PCDD		C. Custer pers. comm.
17	upper Mississippi River Pool 15	organochlorines		79
18	upper Mississippi River	trace elements		C. Custer pers. comm.
19	Herculeaneum MO	lead	biomarkers	C. Custer pers. comm.
20	Agassiz NWR	trace elements		C. Custer pers. comm.
21	Experimental Lakes Area	acid deposition	reproduction, ecology, metal uptake	18, 106, 162, 164, 165
22	Whiteshell Nuclear Research Establishment	ionizing radiation	reproductive success, development	113, 114, 115, 140
23	South Dakota	trace elements		C. Custer pers. comm.
24	Arkansas River, Colorado	lead	reproductive success	C. Custer pers. comm.
25	nw Colorado	DDE, PCB	eggshell thickness	95
26	s Colorado	DDE, PCB, organochlorines		32
27	Colorado	DDE, PCB, organochlorines		33
28	ne Colorado	DDE, PCB, organochlorines		32
29	N. Platte River, WY	petroleum	biomarkers	105
30	w Montana	DDE, PCB, organochlorines		32
31	n. Idaho	Lead and Cadmium		108
32	Saskatchewan	pulp mill effluent	reproductive success, biomarkers	15
33	Central Alberta	DDE, PCB, organochlorines		94
34	Western Alberta	pulp mill effluent	reproductive success, biomarkers	15
35	British Columbia Orchards	DDT, DDE	reproductive success	96
36	Fraser River, BC	pulp mill effluent	reproductive success	92, 93
37	s Oregon	DDE, PCB, organochlorines		32

gained through careful study of a few model species is irreplaceable in understanding anthropogenic influences on ecological patterns.

2. Tree swallow ecology

Tree swallows belong to a family of approximately 90 species of swallows and martins (family *Hirundinidae*) in the songbird order Passeriformes. The tree swallow is one of the most abundant swallows throughout its range in North America, and can be found breeding from the western edge of Alaska to eastern Newfoundland, as far north as the tree line. Tree swallows breed across much of the continental United States, except for the southeastern states and the tree-less Great Plains and deserts of the west (Fig. 1). In winter, they migrate to the gulf coast of the United States, Mexico, Central America, and the Caribbean [10]. Although not colonial in the same sense as many gulls and terns, tree swallows will nest in close proximity to each other (15 to 20 m spacing) allowing fairly high densities of breeding birds to be attracted to specific areas [10]. Although tree swallows will nest in virtually any open area, they are especially attracted to marshes and open bodies of water. In these situations they may prove to be appropriate indicators of overall ecosystem health at the watershed level, integrating conditions of both terrestrial and aquatic habitat conditions. Populations of tree swallows appear healthy throughout most of their range and the species appears to be spreading to areas where artificial cavities are provided for nesting [10, 11].

2.1. Foraging, diet, and trophic level interactions

A good understanding of diet is critical for many studies, especially those involving contaminants since the best documented route of exposure is through foraging. During the breeding season, tree swallows feed almost exclusively on flying insects [10, 12, 13, 14]. Depending on where the birds are feeding, adults of aquatic insect larvae may dominate the diet [13, 15]. However, most flying insects large enough to be seen and small enough to be swallowed will be eaten if encountered. Prey items come from at least 10 insect orders and over 70 families [14, 16]. All quantitative studies have focused on the diet consumed by nestlings but qualitative observations suggest that the diets of adults are similar to those fed nestlings.

Insects are caught during feeding flights, often over water and are seldom taken from the ground or vegetation. When feeding nestlings, adults usually remain within a hundred meters of the nest and collect a mouth-full of small insects bound together with saliva (a bolus), or one or two larger insects [16]. These insects are fed whole, and often alive, to nestlings. Adults have not been observed to remove wings or legs prior to feeding even large insects such as dragonflies. Most observers also find snail shells in the diet of growing nestling tree swallows, however, snails are probably sought out as a source of calcium for developing young rather than as an energy

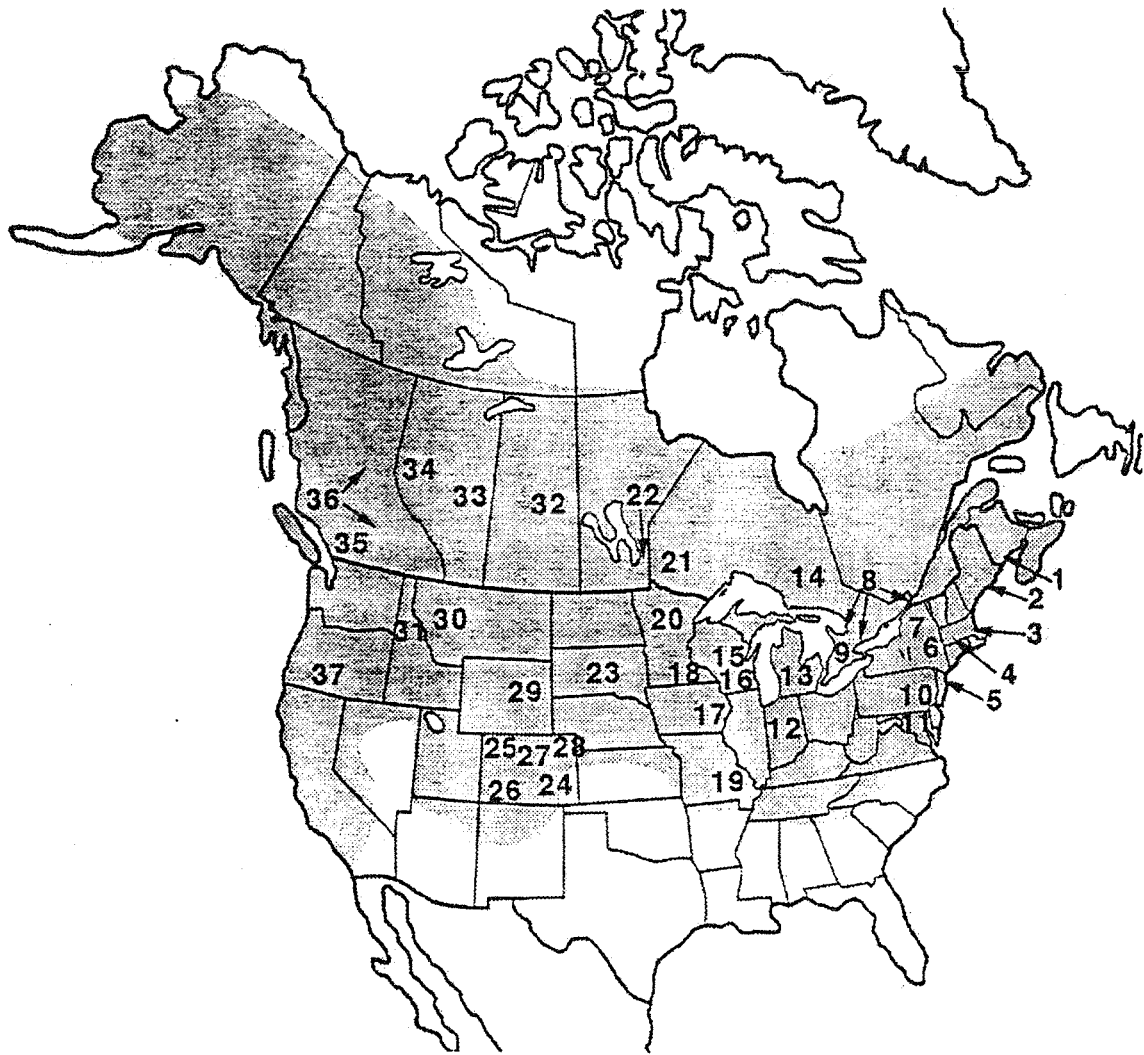


Fig. 1. Locations of studies using Tree Swallows to monitor environmental stress. Shaded area represents that breeding range of Tree Swallows. Numbered sites refer to studies listed in Table 1 that are published or in progress.

source [13, 14, 17, 18]. During the non-breeding season, tree swallows will supplement their diet with fruit, especially *Myrica*, when insects are not available [19].

In most areas the diet of tree swallows is dominated by Diptera [12, 14, 20, 21]. These include taxa from both aquatic and terrestrial habitats. Diptera with aquatic larvae, especially nematoceran diptera such as chironomids, are especially common in many tree swallow diets [12, 20, 21, 22]. Most aquatic diptera larvae feed on dead organic matter or living aquatic plants, especially periphyton, for a period ranging from two weeks to a year before emerging as adults [23]. In areas near water, Odonata, including both Anisoptera (dragonflies) and Zygoptera (damselflies) can form an important part of tree swallow diets since individuals are large relative to most prey items [12, 21]. Odonata larvae are predators and spend from many weeks to a year or more before emerging as adults [23]. Odonates are most vulnerable during the teneral stage shortly after emerging when their wings are not fully hardened and they are poor flyers. Ephemeroptera and Trichoptera adults can be

come important prey items during emergence events [13, 15]. The aquatic stages of these orders lasts from three months to a year, and they tend to feed on either periphyton or dead organic matter, though some species of Trichoptera are predatory [23]. Important groups of terrestrial insects eaten include brachycerous Diptera and Hemiptera (Homoptera plus Heteroptera) [12]. In upland areas far from sources of aquatic insects the diet changes in predictable ways, with more emphasis on brachycerous Diptera and Homoptera, and fewer aquatic forms such as Odonata and Ephemeroptera [24]. While the composition of tree swallow diets depends on available insects, comparisons of available insects to those captured by foraging adults do reveal some preferences. Adults generally prefer insects greater than 3 mm in length [12, 22], and avoid large stinging Hymenoptera such as wasps and bees.

For a bird with a diet that consists almost entirely of a single food source (aerial insects), defining the trophic level of tree swallows is not a simple matter. When feeding on adults of aquatic insects, tree swallows will be consuming a cross section of a complex aquatic food web that includes detritivores, herbivores and predators. The mix of trophic levels consumed is likely to vary from place to place and with time as different groups of insects emerge. Thus a group of swallows feeding heavily on emerging chironomids are at the top of a detritivore food chain. These same birds may feed the next day on emerging odonates that had been top predators in an aquatic community, only to feed the next day on a large hatch of mayflies that had been grazing on algae. This already complicated food web is further complicated by the inclusion of insects of terrestrial origin. It may be possible to obtain an integrated picture of the trophic status of tree swallows through use of stable isotope techniques [25] but any method employed is likely to reflect only the specific place and time measured.

Fortunately, diet samples can be efficiently collected from tree swallows, allowing for a specific description of the types of food being eaten at a given time and place. For the purposes of obtaining a general overview of diet for ecotoxicology studies, the best methods for collecting diet samples are to collect boluses directly from parents captured while feeding young or through use of neck collars on nestlings [13, 14, 15, 16, 22, 26, 27]. Stomach contents of nestlings collected for chemical analysis can be analyzed to provide information on the contaminant levels in food, though identification of types of prey eaten is difficult [13, 28]. Information about insects available to foraging tree swallows can be obtained through use of emergence traps, sweep nets, or passive drift nets [13, 15, 22, 27, 29]. Suction traps are more expensive but provide a more accurate sample of aerial insects, are less sensitive to wind conditions, and provide an accurate indication of food abundance [12, 16, 30, 31]. In addition, the larger biomass of insects collected by suction traps relative to drift nets may be useful when samples are to be analyzed for contaminants.

While tree swallows and related species are important predators, they in turn are eaten by a variety of predators. Tree swallow nests are less vulnerable to predators than ground or cup nesting birds but are still subject to a host of predators known to take eggs, nestlings, and adults. Snakes (e.g. *Elaphe obsoleta*) can gain access to

cavities and can be important predators. Mammals such as raccoons (*Procyon lotor*) and mink (*Mustela vison*) can take large numbers of eggs and nestlings and may kill adults on the nest. Adults are eaten by a range of predators, including other birds such as peregrine falcons (*Falco peregrinus*) [32, 33]. Tree swallows thus form a potentially important link in the transfer of chemical contaminants from aquatic to terrestrial food webs.

2.2. Breeding behavior and ecology

An understanding of the breeding behavior and ecology of tree swallows is an important component to interpreting studies of environmental stressors both because commonly used endpoints such as reproductive success are influenced by behavior and because behavior itself is an increasingly important endpoint [34, 35].

Nest site selection – Tree swallows are obligate cavity nesters, relying on cavities excavated in trees by other species. In at least some areas, cavities are believed to be a limiting resource for tree swallows [36, 37]. Natural nest sites occur in cavities in trees adjacent to open bodies of water, and in trees flooded by beaver (*Castor canadensis*) but tree swallows have willingly adopted nest-boxes as a preferred nest site.

Preferred nest sites for tree swallows are open, grassy areas (ideally > 2.5 ha) near water and far from trees and other tall vegetation (ideally > 30 m) [38, 39]. When provided with a choice, tree swallows prefer nests placed far from forest edges [40]. Tree swallows nesting close to forest edges can suffer significant losses of eggs through nest-site competition with house wrens (*Troglodytes aedon*), while nest-boxes close to human dwellings can attract house sparrows (*Passer domesticus*) which may kill nestlings and adults [38, 41]. Bluebirds (*Sialia spp.*) and chickadees (*Poecile spp.*) will also use nest boxes set up for tree swallows but seldom interfere with successful breeding [42].

For studies monitoring reproductive success, the size of nest box used must be standardized. For tree swallows using natural cavities, the size of the cavity influences the number of eggs laid [43]. Female tree swallows prefer larger nest boxes and lay larger clutches in large nest boxes [44, 45]. Nest boxes 20 cm deep with a floor area of 12 cm by 12 cm are appropriate for studies using tree swallows. Boxes can be spaced approximately 20 m apart and mounted on poles (1.5–2.0 m high) with predator guards [10].

Time of breeding – Tree swallows are the first swallow to arrive in the north each spring and the first to begin breeding. The timing of the onset of breeding in tree swallows varies geographically and with year-to-year changes in climate [46]. In upstate New York, tree swallows typically arrive in the last week in March. Nest construction lasts for several weeks in late April and early May and egg laying occurs as early as 1 May, and continues until late May. Breeding dates become later as one moves north and west through the species range [46]. Tree swallows rarely attempt to raise two broods but they may renest if eggs are lost [10].

Clutch size, hatching success, fledging, and survival – Reproductive success and ultimately population size is determined by demographic parameters such as the number of eggs laid and survival of offspring. One egg is laid per day until the clutch is completed. Typical clutches consist of five or six eggs, with a normal range of from two to seven eggs [10, 47], which the female incubates for 14–15 days. Young generally hatch within a 24 hour period, and are naked, blind, and helpless (i.e. altricial). Only the female broods the nestlings, but both parents share in the feeding of the young [10]. The hatchability of eggs is a function of fertilization success, intrinsic properties of the embryo, and parental care behavior, especially incubation. Under most conditions hatching success of eggs is high and in the absence of natural or anthropogenic disturbance can be expected to approach 95 % of eggs [10].

Tree swallows are typically socially monogamous, though many nests contain eggs fathered by males other than the one in attendance [48]. Under some conditions males will attend more than one nest or two females will share a single nest-box with a male [49]. This may be more common when nest sites are in short supply and food is abundant [49, 50].

Survival of nestlings is generally high. Over 90 % of hatchlings survive as long as food remains abundant, but loss of nestlings is high in years with poor weather conditions [10, 16]. Nestlings leave the nest (fledge) after approximately 21 days. A fledgling's first flight usually carries it out of sight of the nest, to which most young never return. Parents sometimes continue to provide some food to the young for at least several days after fledging.

Survival of adults and fledglings is not accurately known. Mortality of young between leaving the nest and the next breeding season may be 80 % or more, while mortality of adults after the first breeding season probably ranges between 40 and 60 % [10]. As our ability to distinguish between dispersal and mortality of marked birds improves these estimates will become more accurate.

Variation in the reproductive success – Reproductive success of tree swallows can be strongly influenced by environmental conditions [50, 51, 52]. Cool, weather reduces the available food supply and may lead to reduced nestling growth and starvation [16, 53].

There is a robust relationship between early breeding and higher reproductive success at a given site [15, 54, 55]. Nests initiated late in the season are typically re-nests and tend not to be successful, thus they are typically excluded from calculations of nest success.

As in other passerines, clutch size of tree swallows is larger at higher latitudes [56]. Clutch sizes and reproductive success is sometimes lower in first year females than in older females [10, 15, 54, 55], making it important to note female age in studies monitoring reproductive success.

Tree swallow nestlings are sometimes subject to infestation with ectoparasites including mites (*Dermanyssus*, *Ornithonyssus*, et al.), bird fleas (*Ceratophyllus*), and blowflies (*Protocalliphora*). Infestations may be worse in nest-boxes with old,

used nests present [57], and females prefer clean nest boxes [58]. However, there is little evidence that ectoparasite infestations have a significant impact on nestling growth or survival [57, 59, 60].

Tree swallows are relatively resistant to disturbance from researchers at most stages of the reproductive cycle. Nests can be checked daily with little or no impact on success. Females lay eggs in the first few hours after sunrise disturbance during this time should be minimized. Adults can be safely captured at the nest after nestlings have hatched using nest box traps [61, 62, 63].

3. Exposure

As a first step in analysis of risk, exposure to the stressor must be evaluated. For terrestrial species like tree swallows, exposure to chemical contaminants is possible through eating contaminated food. In many of the studies conducted to date, chemical contaminants in aquatic sediments are taken up by insect larvae, which emerge as flying adults and are eaten by swallows [64, 65, 66, 67]. Terrestrial insects can also accumulate contaminants from soil [68]. Other possible routes of exposure include contact with contaminated air, water or sediment deposits. In orchards and other agricultural settings, direct exposure to pesticide sprays may be important for adults and nestlings and there is evidence that some pesticides can diffuse through eggshells [29].

3.1. Exposure to PCBs

Previous work has provided evidence for a range of effects of PCBs, dioxins, and related chemicals on birds and other wildlife. PCBs are ubiquitous in wild birds and concentrations above background levels are still found in many areas and are associated with adverse effects [69, 70]. Among the effects of PCBs observed in birds are developmental abnormalities (especially deformed feet and bills), liver damage, physiological and metabolic changes, reduced reproductive success and embryonic and adult mortality [69, 70, 71]. The impact of PCBs on normal functioning of the endocrine system has been recognized for at least 30 years [72]. Concentrations in brain tissue greater than 300,000 ng/g have been found in dead or dying adults and are indicative of acute toxicity [70, 73].

PCBs were used and typically released as mixtures of congeners. Thus they are often evaluated under the generic name PCBs. However, it is recognized that individual congeners differ in their effects [74]. Planar congeners are structurally similar to TCDD and are considered especially toxic [69, 74, 75, 76].

There are substantial differences among species in their susceptibility to the effects of PCBs [77]. In general, birds are more resistant to acute toxic effects than are mammals [70]. Among birds, effect levels vary across at least two orders of magnitude [77, 78].

To document the source of chemical contamination found in wild birds, both egg and nestling samples are typically collected. Contaminant levels in eggs represent chemicals deposited from the female's body. Nestlings are usually collected between nestling day 12 and 15 (where day 1 = hatch day) when they contain contaminants from food the parents deliver, as well as any remaining maternal PCBs from the egg [27]. The difference in body burdens between nestlings and eggs provides evidence of local accumulation of contaminants. This is an especially conservative estimate in passerines because the large investment in a clutch of eggs, relative to body size, requires that a significant portion of the nutrients (and presumably contaminants) that females deposit in eggs reflect recently acquired, rather than stored nutrients. If the age of nestlings collected is known with certainty, the difference in body burden between eggs and nestlings can also be used to estimate daily accumulation rates by dividing contaminants accumulated by age [26, 27, 79].

Hudson River – Average total PCB levels in tree swallow eggs from the Hudson sites during 1994–95 ranged from 9,320 ng/g wet mass at the Saratoga site 45 km downstream of the PCB source to 29,500 ng/g wet mass at Special Area 13 located just 6 km downstream (Table 2) [27]. The highest level was found in an egg sample from Special Area 13, which had 56,800 ng/g wet mass. Nestling contamination levels were higher than those in eggs, ranging from an average of 3,710 ng/g wet mass at Saratoga to 62,200 ng/g wet mass at Remnant Site 4 (Table 2). A single adult from Special Area 13 had 114,000 ng/g wet mass while an adult from the Champlain Canal had a total PCB concentration of 22,200 ng/g wet mass [27].

The higher concentration of PCBs in nestlings compared to eggs on the Hudson is somewhat unusual. Typically nestlings accumulate contaminants at a lower rate than they gain mass; a process referred to as growth dilution [80, 81]. The lack of growth dilution at the Remnant and Special Area 13 sites is indicative both of the high overall levels of contamination present and the domination of the food supply by contaminated insects from the Hudson River.

At all the sites studied along the Hudson River, the total PCB body burden of nestlings was greater than in eggs. Since tree swallows feeding nestlings forage primarily within 100 m of the nest [12], the increase in PCB content confirms that contaminants were being drawn from the area around the nest. The insects being fed to nestlings had significant concentrations of PCBs (as high as 17,700 ng/g wet mass at Remnant Site 4). Mean accumulation rates of PCBs were highest at the sites near the PCB source, ranging from 44 $\mu\text{g}/\text{day}$ at Special Area 13 in 1994 to 158 $\mu\text{g}/\text{day}$ at Remnant Site 4 in 1995 [27]. Accumulation rates were an order of magnitude lower at Saratoga, ranging from 3.5 to 7.3 $\mu\text{g}/\text{day}$. Even reference nestlings along the Champlain Canal accumulated PCBs at 0.10 to 1.70 $\mu\text{g}/\text{day}$ [27].

Nestlings collected from Special Area 13 in 1997 still had elevated levels of contamination ($13,300 \pm 4800$ ng/g wet mass, $n = 11$) [26]. This level is slightly lower than that documented in 1994 and 1995 ($29,500 \pm 9200$ ng/g wet mass) [27]. While this difference could reflect a change in contaminant levels over time, it is likely that at least part of the difference between years is due to slightly different collection and analysis

Table 2
Concentrations of PCBs and DDE in the eggs and nestlings of tree swallows. Concentrations given are means for sites based on wet mass. Ranges of means are given for regions where multiple sites were studied. Values reported as below detection limits are shown as < reported detection limit.

Region	Site - year	Eggs		Nestlings		Ref.
		Total PCBs ng/g	DDE µg/g	Total PCBs ng/g	DDE µg/g	
Hudson River, NY	Champlain Canal 1994-95	5940	<0.05	721		27, 97
	Remnant 1994-95	15800	<0.05	62200		27, 97
	SA13 1994-95	29500	<0.06	39800		27, 97
	SA13 1997			13270		26
	Saratoga 1994-95	9320	<0.05	3710		27, 97
Lake Huron	Georgian Bay 1991-94	255	0.458	11- 54	0.022-0.035	80
Lake Erie	3 sites 1991-95	256- 932	0.693-4.376	140- 639	0.105-1.484	80
Lake Ontario	2 sites 1991-95	914- 2470	0.625-1.601	615- 755	0.133-0.290	80
St. Lawrence R.	2 sites 1991-94	4010-11168	0.470-1.440	1387-5469	0.112-0.175	80
Ontario	Orchards 1994-97	270- 610	0.360-2.290			29
Pennsylvania	5 sites 1995-97	948- 4600		170-2180		26
Maryland	Patuxent 1995-97	695		290		26
Indiana	Contaminated 1996			18460		26
	Reference 1996			131		26
Saginaw River	4 sites 1991	563- 1373		171-1027		81
Green Bay	Kidney Island 1988			2970		87, 88
	Kidney Island 1994-95 ¹	3300	0.20	3770	0.07	28
Fox River	Lower 1988	4120		2490		87, 88
	Arrowhead 1994-95 ¹	2500	0.19	1460	0.07	28
	High Cliff 1994-95 ¹	500	0.15	200	0.02	28
	Lake Poygan 1994-95 ¹	200	0.11	80	0.03	28
Mississippi River, IA	3 sites 1998	280- 540	0.11 -0.17	130-140	0.02-0.04	79
Colorado	1977 - 1980	300	2.1	340	6.2	33
Alberta	1978- 79	430- 490	0.86 -2.23	140	0.31	94
British Columbia	Orchard 1990-91	190	9.4			96
	non-orchard 1990-91	160	3.3			96
Fraser River, BC	2 upstream sites 1994			<0.10	0.090-0.178	92, 93
	2 downstream sites 1994			16- 32	0.087-0.165	92, 93

¹ Egg data from collected from eggs in the process of hatching ("pipers").

techniques used in the two studies. Specifically, the exact age of nestlings collected in 1997 was not known and livers were removed prior to analysis, both of which could affect contaminant concentrations [26].

The majority of PCBs in Hudson River tree swallows were congeners from the tri-, tetra-, and pentachlorinated homologue groups [27]. The pattern of homologues in insects collected at the same sites was similar to that found in eggs and nestlings, while contaminants in sediments tended to contain relatively higher levels of the less chlorinated congeners [27]. The pattern of accumulation of different PCB congener homologue groups by tree swallows was a good indicator of the patterns in nearby sediments and in insects, though tree swallows did tend to preferentially accumulate more highly chlorinated congeners as would be expected based on previous studies of birds.

In general PCB congeners 118, 105, and 77 were most prevalent. Concentrations of PCB 77 were as high as 1,000 ng/g; higher than any avian samples in the literature [27]. In most previous studies of PCB congeners in birds, PCBs 138 and 153 have predominated [74]. PCB congeners vary in the relative toxicity to birds. For comparative purposes we calculated the 2,3,7,8-tetrachlorodibenzo-*p*-dioxin equivalents (TEQs) using the World Health Organization's toxic equivalency factors (TEFs) for birds [82]. The pattern of overall TEQs generally mirrored that of total PCB concentrations with samples from Saratoga (1,370–1,730 pg/g) being less contaminated than the Remnant and Special Area 13 sites (7,520–25,400 pg/g) [27]. PCB 77 was an especially important contributor to overall TEQs, accounting for over 80 % of the total toxicity [27].

Fox River Valley and Green Bay. Studies along the lower Fox River and Green Bay, Wisconsin, have contributed greatly to our understanding of the effects of contaminants on birds [83, 84, 85, 86]. Tree swallows have been used for several years to monitor exposure to contaminants in this area. Total PCB levels in eggs and nestlings collected in Green Bay and along the lower Fox River in 1988 were high (2,970 ng/g wet mass in nestlings from Green Bay and 4,120 ng/g wet mass in eggs from the Lower Fox River Table 2) [87].

In 1994 and 1995 total PCBs in nestlings from the same site in Green Bay were actually higher than in 1988 (3,800 ng/g wet mass Table 2) [28]. At a contaminated site on the Fox River total PCB concentrations of 2,500 ng/g wet mass and 1,600 ng/g wet mass were found in eggs measured at hatching ("pipers") and nestlings respectively [28]. At two Fox River reference sites total PCB concentrations were ≤ 500 ng/g wet mass in eggs and ≤ 200 ng/g wet mass in nestlings (Table 2). Accumulation rates of 1.3 to 6.7 $\mu\text{g}/\text{day}$ were estimated for contaminated areas, while tree swallows nesting later in the season had total PCB levels greater than early nesters, showing that exposure levels increase the longer adults spend in contaminated areas [28].

Compared to other species in the area, tree swallows accumulated greater levels of PCBs than red-winged blackbirds (*Agelaius phoeniceus*), but significantly less than fish eating Forster's terns (*Sterna forsteri*) and common terns (*S. hirundo*) [87, 88].

PCB congener 105 was the largest contributor to the TEQs for Green Bay tree swallows, while PCBs 105, 118/106, and 138 were the largest contributors to TEQs for tree swallows from contaminated sites on the Fox River [28, 87, 88]. At contaminated sites along the Fox River and Green Bay, TEQs in eggs and nestlings ranged from 62 pg/g to 589 pg/g depending on the TEFs used [28]. These levels are significantly elevated above the TEQs of ≤ 110 pg/g from reference sites. Custer et al. note the important correlation between total PCBs and TEQs, and conclude that total PCBs are a reliable indicator of toxicity as calculated from congener-specific analyses.

Saginaw River and Bay – Sediments in Saginaw Bay, Michigan are highly contaminated with PCBs. Tree swallow colonies have been studied at four sites on the Saginaw River: one at the mouth of the river where it empties into the bay (COPO) and the remaining three at increasing distances upriver and away from the major industrial areas [81, 89]. Eggs and nestlings at the COPO site at the mouth of the river averaged 1,370 ng/g wet mass and 1,030 ng/g wet mass total PCBs respectively [81]. The first upstream site (AIRP) had total PCBs of 1,140 and 620 ng/g wet mass in eggs and nestlings, while the two sites furthest upstream had total PCBs in eggs of 840 ng/g wet mass and 560 ng/g wet mass and total PCBs in nestlings of 330 ng/g wet mass and 170 ng/g wet mass [81]. Of the planar PCB congeners examined, PCB 118 was most prevalent [81]. Total lipid-corrected TEQs for these sites are estimated at 90 pg/g lipid for eggs and 110 pg/g lipid for nestlings [90].

Eastern Great Lakes and the St. Lawrence River – In recent years, the Canadian Wildlife Service has made extensive use of tree swallows to monitor PCB contaminated sites near Georgian Bay off Lake Huron, Lake Erie, Lake Ontario and the St. Lawrence River (Table 2). Between 1991 and 1995 levels of PCBs and other contaminants in tree swallows were surveyed [80, 91]. The highest levels of total PCBs were found along the St. Lawrence River, where eggs contained average concentrations of 11,100 ng/g wet mass total PCBs in 1992. Nestlings from two sites on the St. Lawrence averaged 1,390 and 5,470 ng/g wet mass in 1994 [91]. Sites at the east end of Lake Ontario were also highly contaminated (Table 2), with average total PCBs in eggs from these sites ranging from 910 ng/g wet mass to 2,470 ng/g wet mass [80, 91]. Nestlings and eggs from sites on or adjacent to Lake Erie averaged 256 ng/g wet mass to 932 ng/g wet mass for eggs and 140 ng/g wet mass to 640 ng/g wet mass for nestlings [91]. Tree swallows from Georgian Bay had the lowest levels of total PCBs, with eggs averaging 260 ng/g wet mass and nestlings ≤ 54 ng/g wet mass (Table 2) [80, 91].

Southeastern Pennsylvania – Tree swallows at six sites in southeastern Pennsylvania have been evaluated for contaminants [26]. Five sites were near known sources of PCBs and had PCB concentrations in sediment ranging from 120 to 16,000 ng/g. Reference sites were monitored in both Pennsylvania and Maryland (Patuxent Wildlife Research Center) and low levels of PCB contamination in sediment were found at those sites (≤ 30 ng/g). PCBs were found in eggs from all sites, with levels from two contaminated sites near Philadelphia significantly higher than the reference sites (Table 2). Nestlings from all sites accumulated significant levels of

PCBs, with mean levels at contaminated sites in Pennsylvania ranging from 740 ng/g wet mass to 2180 ng/g wet mass. Reference sites averaged ≤ 290 ng/g wet mass [26].

There was a significant correlation between levels of PCBs in eggs and in sediment from different sites ($R^2 = 0.92$). Samples of the insect food delivered to nestlings were collected at three Pennsylvania sites and at the Pennsylvania and Maryland Reference sites. The importance of insects with aquatic larvae varied both within and among sites but a significant proportion of all diets was aquatic in origin. Insects at contaminated sites contained 10 to 110 ng/g of PCBs. Levels in the food supply at the reference sites were below detection limits [26].

Accumulation rates of PCBs in nestlings at contaminated sites in Pennsylvania ranged from 1.51 $\mu\text{g}/\text{day}$ to 5.2 $\mu\text{g}/\text{day}$, while accumulation rates at reference sites were ≤ 0.49 $\mu\text{g}/\text{day}$. Accumulation rates by nestlings were significantly correlated with PCB levels in the food supply [26].

PCBs at other sites – Tree swallows monitored at other sites across North America contain variable levels of PCBs. Navigation Pool 15 in the upper Mississippi River is known to be contaminated by PCBs and eggs collected from nests adjacent to the PCB source averaged 540 ng/g wet mass [79]. Eggs collected upstream from the source had total PCB levels of 280 ng/g wet mass, while eggs from a downstream site averaged 400 ng/g wet mass (Table 2). Nestlings were available from only the upstream and downstream sites and had total PCB levels of 130 ng/g wet mass and 140 ng/g wet mass respectively [79]. Accumulation rates at the upstream and downstream sites were calculated to be 0.18 $\mu\text{g}/\text{day}$ and 0.21 $\mu\text{g}/\text{day}$, similar to the rates found at the Champlain Canal reference site in the Hudson River Valley [27].

Nestling tree swallows downstream of pulp mills in British Columbia showed signs of elevated levels of PCBs relative to upstream control sites [92, 93]. Total PCB concentrations ranged from 16 to 31 ng/g wet mass in nestlings downstream of mills compared to < 0.1 ng/g wet mass in nestlings upstream of mills (Table 2). Levels of individual PCB congeners were higher at the downstream sites than the upstream reference sites [92, 93]. Upstream concentrations of PCB 77 were 0.018–0.059 ng/g wet mass upstream and 0.08–0.163 ng/g wet mass in nestlings downstream [92, 93]. Concentrations of congeners 37, 81, 126 and 169 were lower than PCB 77 but followed the same pattern among sites [92, 93].

Nestling tree swallows collected from a PCB contaminated site near Bloomington, Indiana contained total PCB concentrations of 18,460 ng/g wet mass while nestlings from a nearby reference site contained 130 ng/g wet mass [26].

Measurements of tree swallows collected in areas without identified contaminated sites are an important indicator of background levels of PCB exposure. Reference sites such as the Champlain Canal and Patuxent National Wildlife Research Center in Maryland [26] still contain detectable levels of PCBs (Table 2). In the late 1970's, analysis of adult tree swallows from Colorado and northern New Mexico contained an average of 420 ng/g wet mass PCBs [33], while nestlings from Alberta contained 2,000 ng/g wet mass and eggs contained 640 ng/g wet mass PCBs [94]. Tree swallows collected in

Colorado, Oregon and Montana during the early 1980's averaged 450 ng/g wet mass PCBs, with a range of ≤ 280 ng/g wet mass to 4370 ng/g wet mass [32, 95]. Tree swallow eggs from orchards in British Columbia in the early 1990s had mean PCB levels > 160 ng/g wet mass [96].

Other aerial insectivores have also been used to monitor uptake of PCBs. In the late 1970's violet-green swallows (*Tachycineta thalassina*) and cliff swallows (*Petrochelidon pyrrhonota*) from Colorado contained total PCB concentrations of 550 ng/g wet mass and 120 ng/g wet mass respectively [33]. Samples of other swallow species (including cliff swallows, barn swallows (*Hirundo rustica*), violet-green swallows, and rough-winged swallows (*Stelgidopteryx serripennis*) collected in Colorado, Oregon and Montana during the early 1980's had detectable levels of PCBs ranging from 150 ng/g wet mass in cliff swallows to $> 3,000$ ng/g wet mass in violet-green swallows [32].

3.2. Exposure to dioxins and furans

Dioxins and furans (polychlorinated dibenzo-*p*-dioxins (PCDDs) and polychlorinated dibenzofurans (PCDFs) do not have commercial uses and are released in the environment as contaminants of other chemicals and through combustion [71]. Dioxins and furans share many of the same effects as the more toxic PCB congeners [69, 71].

Although they are toxic and widespread, PCDDs and PCDFs have seldom been detected above background levels in tree swallows. The most important exception to this pattern is found in the Green Bay and Fox River area where significant levels of TCDD and PCDD have been found (Table 3). Along the upper Hudson River both PCDDs and PCDFs were detected in tree swallow samples but when compared to PCB levels using TEFs these contaminants were of minor importance [97]. The same is true of the Fraser River Valley of British Columbia where low but detectable levels of PCDDs and PCDFs were found (Table 3) [92, 93].

3.3. Exposure to pesticides and their residues

Organochlorine pesticides are persistent in the environment and tend to accumulate in organisms and concentrate along the food chain [98]. Levels of DDE and related chemicals tend to be low, with the exception of tree swallows collected in the late 1970's in Colorado and samples from British Columbia orchards in the 1990s [96] where DDE concentrations between 2.1 and 9.4 $\mu\text{g/g}$ wet mass have been found (Table 2). The average DDT level in eggs from four orchard areas in British Columbia was 0.033 $\mu\text{g/g}$ wet mass compared to 0.005 $\mu\text{g/g}$ wet mass at four non-orchard sites [96]. DDD levels were 0.284 $\mu\text{g/g}$ wet mass in orchards compared to 0.067 $\mu\text{g/g}$ wet mass at non-orchard areas [96].

Adult tree swallows collected in Colorado in the late 1970's averaged of 32.8 $\mu\text{g/g}$ wet mass DDE [33]. Tree swallows collected at roughly the same time in

Table 3
Concentrations of organic contaminants in tree swallows (based on wet mass). Values given are means for sites. Ranges of means are given for regions where multiple sites were studied. Values reported as below detection limits are shown as < reported detection limit

Region	Age	Dieldrin µg/g	Oxy µg/g	HE µg/g	<i>t</i> -nonchlor pg/g	TCDD pg/g	PCDD pg/g	TCDF pg/g	HCB µg/g	βHCH µg/g	mirex µg/g	Ref.
Hudson R.	egg	<0.06	<0.33	<0.06	<0.07	<0.07		5-29	<0.06		<0.08	97
	nestling											80, 91
Lake Huron	egg	0.008	0.021	0.010	0.007				0.012	0.004	0.013	80, 91
	nestling	0.004	0.004	0.002							<0.001	80, 91
Lake Erie	egg	0.019-0.057	0.039-0.046	0.021-0.036							0.026-0.036	80, 91
	nestling	0.009-0.024	0.011-0.018	0.007-0.010							0.002-0.003	80, 91
Lake Ontario	egg	0.019	0.044	0.016							0.040	80, 91
	nestling	0.211	0.114	0.116							0.003	80, 91
St. Lawrence R.	egg	0.050	0.059	0.029							0.040	80, 91
Green Bay	egg		<0.02	<0.02								28
	nestling					2.8	132	<24				87, 88
Fox River	egg		<0.02	<0.02		5.2	398	<40				28, 87, 88
	nestling					2.3	136	<26				87, 88
Mississippi R.	egg	0.03	0.02-0.04	0.05-0.07	0.01-0.03	0.012-0.026		0.14-0.22				79
	nestling	0.03-0.04		0.01-0.07								79
Western States	adult	<0.01	0.05-0.13	0.06-0.13					0.01	0.12-0.18		32
Alberta	egg			0.08								94
	nestling			0.02								94
BC orchards	egg	0.003	0.012	0.005	0.002					0.042	0.002	96
BC nonorchard	egg	0.006	0.016	0.010	0.002					0.058	0.001	96
Fraser River	nestling	0.001	0.001	<0.001	<0.001	<0.001	0.004-0.078	0.58-3.17	0.002	<0.001	<0.001	92, 93

central Alberta averaged 1.4 $\mu\text{g/g}$ wet mass DDE in eggs and 5.5 $\mu\text{g/g}$ wet mass in nestlings [94]. Adult tree swallows collected at several sites in western North America in the early 1980's had average DDE levels ranging from ≤ 1.0 $\mu\text{g/g}$ wet mass to ≥ 150.0 $\mu\text{g/g}$ wet mass [32, 95]. Males tended to have higher concentrations of DDE than females (10.8 $\mu\text{g/g}$ wet mass vs 5.1 $\mu\text{g/g}$ wet mass), though the difference was not significant [32].

Eggs and nestlings of tree swallows collected in 1998 from the upper Mississippi River contained average DDE levels in eggs ranged from 0.11 to 0.17 $\mu\text{g/g}$ wet mass, while nestlings contained 0.02 to 0.04 $\mu\text{g/g}$ wet mass [79]. In the Fox River Valley and Green Bay, DDE levels ranged from 0.11 to 0.20 $\mu\text{g/g}$ wet mass in eggs and were < 0.10 $\mu\text{g/g}$ wet mass in nestlings for tree swallow samples collected in 1994 and 1995 [28].

DDE levels in tree swallows from the lower Great Lakes and St. Lawrence River were highest in eggs from the Mud Creek site on Lake Erie (2.6 to 4.4 $\mu\text{g/g}$ wet mass) [80, 91]. Nestlings from this site had DDE concentrations of 0.6 $\mu\text{g/g}$ wet mass to 1.5 $\mu\text{g/g}$ wet mass. Lowest levels were found at the Wye Marsh site at Georgian Bay (0.5 $\mu\text{g/g}$ in eggs and < 0.05 $\mu\text{g/g}$ wet mass in nestlings) [80, 91]. Other sites along Lake Erie and Lake Ontario had DDE levels averaging 0.4 $\mu\text{g/g}$ wet mass to 2.5 $\mu\text{g/g}$ wet mass in eggs and 0.1 $\mu\text{g/g}$ wet mass to 0.6 $\mu\text{g/g}$ wet mass in nestlings [80, 91].

DDE residues in tree swallow eggs from four orchards were compared to three reference sites in Ontario. Eggs from the two types of sites were similar: orchards averaged 0.66 to 2.29 $\mu\text{g/g}$ wet mass while reference sites contained 0.36 to 2.23 $\mu\text{g/g}$ wet mass DDE [99].

While swallows are the most frequently used aerial insectivore used to monitor contaminants, other species in this guild also accumulate pesticides and organochlorines. Adult violet-green swallows collected in Colorado in the late 1970's contained 5.9 $\mu\text{g/g}$ wet mass and cliff swallows 2.0 $\mu\text{g/g}$ wet mass DDE [33]. The white-throated swift (*Aeronautes saxatalis*) and common nighthawk (*Chordeiles minor*) in western North America both accumulated significant levels of contaminants. Average DDE levels in white-throated swifts ranged from 1.2 to 1.9 $\mu\text{g/g}$ wet mass [32, 33]. Common nighthawks had lower levels of DDE, averaging 0.35 $\mu\text{g/g}$ wet mass [33]. DDE levels in other species of swallows ranged from an average of 3.2 $\mu\text{g/g}$ wet mass in cliff swallows to 10.4 $\mu\text{g/g}$ wet mass in rough-winged swallows [32].

Organophosphorus and carbamate pesticides are relatively short-lived and rapidly metabolized by most animals so they do not bioconcentrate. Effects vary widely with both the type of pesticide used and the species exposed [100, 101]. Exposure typically occurs through direct contact during pesticide application or through ingestion of sprayed insects. Bishop et al. have proposed toxicity scores based on the number of spray events and the type of pesticides used [29, 100]. Direct exposure to pesticide spray in orchards was evaluated by placing filter papers in empty nest boxes during spray events to determine if pesticides entered nest cavities. Low but detectable levels

of azinphos-methyl were found on filter papers from nests in sprayed areas indicating that some direct exposure of eggs and nestling to pesticides is possible [102].

Other organochlorines and pesticides detected in tree swallows include Heptachlor epoxide (HEP), dieldrin, hexachlorocyclohexane (HCH), oxychlorodane, toxaphene, Hexachlorobenzene, *trans*-nonachlor, and mirex (Table 3) [28, 32, 80, 94, 95, 96, 103]. Even in actively sprayed orchards, levels of these other chemicals tend to be low [99, 100].

3.4. Exposure to PAHs

Polycyclic aromatic hydrocarbons (PAHs) and aliphatic hydrocarbons (ALHs) enter the environment largely through release or burning of petroleum products or natural organic material [104]. Total PAH concentrations in tree swallow nestlings on the North Platte River in Wyoming were elevated downstream of a refinery, relative to an upstream reference site, with total PAH concentrations as high as 0.17 $\mu\text{g/g}$ wet mass near the refinery and below the detection limit of 0.01 $\mu\text{g/g}$ wet mass at the reference site [105]. The lack of methylated PAHs and the distribution of ALHs found suggests that this is not a result of direct exposure to petroleum, but derived from combustion sources [105]. Total ALH levels were similar at the two sites (range 5.0–8.1 $\mu\text{g/g}$ wet mass at the refinery and 8.1–9.5 $\mu\text{g/g}$ wet mass at the reference) [105].

3.5. Exposure to trace elements

A few studies have focused primarily on the uptake of metals by tree swallows (Table 4). The effects of experimental lake acidification on the movement of metals through the food chain has been evaluated using tree swallows and uptake of copper, zinc and cadmium was found [106]. Nestling tree swallows accumulated detectable levels of Chromium, Nickel, Cadmium, Copper, and Lead from the Hackensack River Estuary in northeastern New Jersey [107], while a survey of number of bird species from northern Idaho found little evidence of elevated levels of lead and cadmium contamination [108]. In the lower Great Lakes and St. Lawrence River, total mercury levels of 0.04 to 0.08 $\mu\text{g/g}$ wet mass are found in tree swallow eggs [80]. Mercury levels in tree swallow eggs from the North Platte River in Wyoming were 0.3 $\mu\text{g/g}$ dry mass [105]. North Platte River eggs and livers of nestlings also contained significant levels of boron, selenium, and strontium (Table 4) [105].

Related species have also been studied. Barn swallows breeding along a busy highway in Maryland in 1979 had elevated levels of lead compared to those breeding in areas with less automobile traffic [109]. Adults breeding under a highway overpass contained lead concentrations of 7.0 $\mu\text{g/g}$ dry mass while those in less traveled areas had average lead concentrations of 4.3 $\mu\text{g/g}$ dry mass. Nestling lead concentrations averaged 1.5 $\mu\text{g/g}$ dry mass at the highway site compared to 0.7 $\mu\text{g/g}$ dry mass at the reference site [109]. Barn swallows were also used to evaluate a se-

Table 4

Concentrations of trace elements in tree swallow tissues. Concentrations given are means for sites based on wet mass. Ranges of means are given for regions where multiple sites were studied. Samples with less than detection limit are not shown.

Region	Site	tissue	As µg/g	B µg/g	Cr µg/g	Cd µg/g	Cu µg/g	Fe µg/g	Hg µg/g	Mg µg/g	Ni µg/g	Pb µg/g	Se µg/g	Zn µg/g	Ref.
Hudson R.	Champlain Canal	egg	0.55	2.04			0.48	24.1	0.095	72.3				14.6	97
	Remnant	egg	0.82				0.47	25.9	0.051	72.6				15.3	97
	SAI3	egg	0.75	2.55			0.44	23.6		71.7				15.6	97
	Saratoga	egg	0.66				0.45	16.9	0.066	71.6				15.3	97
New Jersey	Hackensack R.	egg shell			173.6	1.8	2.4				31.4	90.9			107
		egg contents			6.5						1.6	2.3			107
		nestling brain			211.7						27.6				107
		nestling liver			101.8						23.8	63.6			107
		nestling muscle			56.1		1.6				7.6				107
Lake Huron		nestling feather			25.5		4.7				4.3	4.3			107
		egg							0.066						80
		egg							0.076-0.079						80
		egg							0.043						80
Ontario	Acid Lakes	liver ¹					0.06-0.11	3.6-12.6						21.1-32.1	106
		kidney ¹					0.04-0.14	3.1- 4.9						21.7-26.1	106
	Reference Lakes	liver ¹				0.06	5.1							21.1	106
Idaho	contaminated sites	kidney ¹				0.05	3.1							22.9	106
		blood										0.19			108
		liver										0.15			108
Wyoming	North Platte	kidney				0.07									108
		egg ¹		11.5			0.4	28.5	0.06	64.4			1.4	11.3	105
		liver ¹		4.8			7.7	293.7		237.6			6.2	26.1	105

¹ approximate wet mass concentrations converted from dry mass based on moisture values presented in [105].

lenium contaminated lake in Texas [110]. Eggs from nest adjacent to the contaminated lake contained an average selenium concentration of 2.8 $\mu\text{g/g}$ dry mass while those from a reference site had levels of 1.5 $\mu\text{g/g}$ dry mass. Liver and kidney tissue from adults had higher levels of selenium; 14.0 $\mu\text{g/g}$ dry mass and 5.8 $\mu\text{g/g}$ dry mass at the contaminated and reference sites respectively [110].

3.6. Exposure to pulp mill effluent

Effluent from pulp and paper mills adds significant levels of nutrients and contaminants to aquatic ecosystems [15, 111]. How the changes in the aquatic ecosystem impact wildlife in riparian zones is not as well understood. In western Canada tree swallows breeding upstream and downstream of pulp mills have been compared. In western Alberta nest boxes for tree swallows were provided along the Wapiti River 3–25 km downstream from a bleached kraft pulp mill releasing 50,000–60,000 m^3 day^{-1} while additional boxes were provided 12–20 km upstream of the mill [15]. In eastern Saskatchewan boxes were provided along the North Saskatchewan River 25 km upstream and 7–18 km downstream of a bleached kraft pulp mill releasing approximately 100,000 m^3 day^{-1} [15]. Effluent at both sites was treated prior to release and contained 7.80–12.50 mg/l adsorbable organic halides, 0.22–0.61 mg/l NO_x , 0.90–1.00 mg/l total Phosphorus, and 20–34 mg/l total suspended solids [15]. On the Thompson River in British Columbia, tree swallows nesting downstream of a pulp mill were exposed to elevated levels of chlorinated contaminants, especially highly chlorinated PCB congeners [92]. Average TEQs of nestlings upstream of the mill were 5.2 pg/g wet mass, compared to 14.9 pg/g wet mass for nestlings downstream (based on WHO TEFs) [93]. Tree swallow nestlings upstream of a pulp mill on the Fraser River B. C. had lower TEQs (1.9 pg/g wet mass) than those downstream of the mill (11.8 pg/g wet mass) due in part to elevated levels of PCDDs [93].

3.7. Exposure to ionizing radiation

Compared to other types of environmental contaminants, radioactive contaminants have been studied in only a few areas and studies have tended to focus on experimental manipulations rather than monitoring existing contamination [112]. In 1979 and 1980 Zach and Mayoh exposed breeding tree swallows to a continual gradient of gamma radiation from a 3.7×10^{14} Bq cesium (^{137}Cs) source mounted on a tower at the Whiteshell Nuclear Research Establishment in southeastern Manitoba. Nest-boxes were provided across a gradient of potential exposure ranging from 38.7 $\text{mC} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ to background levels of 0.05 $\mu\text{C} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ but mean exposure at boxes actually selected for breeding was 9.3 $\mu\text{C} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ (based on wet mass) [113]. The highest exposure experienced was 37.4 $\text{mC} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ [113]. Eggs and nestlings were also exposed in the lab to 0.4 Gy to 4.48 Gy doses of radiation from a ^{60}Co source, and then returned to nests exposed to only background levels of radiation [114, 115]. Finally, in 1990 Zach et al. conducted a field study using

Table 5
Advantages and limitations of using tree swallows to evaluate environmental stressors

Advantages	Disadvantages
<ul style="list-style-type: none"> • Abundant • Familiar to casual observers • Large geographic range • Uses nest-boxes • Tolerates disturbance • Tolerates contaminants • Sensitive to overall ecological integrity • Integrates terrestrial and aquatic ecosystem • Strict aerial insectivores 	<ul style="list-style-type: none"> • Not rare, threatened or endangered • Not a game species • Breeding not limited to a few large colonies • Cavity-limited population size • • Not most sensitive indicator of effects • Sensitive to overall ecological integrity • • Difficult to rear in captivity

unirradiated uranium fuel pellets (UO_2) mounted in the bottoms of experimental nest boxes. Background radiation was measured at $0.13 \mu Gy/h$ while experimental nests received doses as high as $9.6 \mu Gy/h$ [115].

The studies of Zach et al. have focused on experimental exposure to radiation but few studies have looked at terrestrial habitats with unintentional radioactive contamination [112]. However, barn swallows have been used in the field to study the effects of the massive release of radiation from the Chernobyl area in the Ukraine where atmospheric radiation levels were 300–500 μR [116, 117, 118].

4. Effects of Exposure

4.1. Population/Community/Ecosystem level effects

One goal of ecological toxicology, and applied ecology in general, is to understand the impacts of human actions on higher levels of biological organization such as population sizes, community dynamics and ecosystem functioning. For mobile, terrestrial species like birds, it can be very difficult to evaluate these relationships, especially when the spatial or temporal scale of disturbance differs from the scale at which ecological interactions take place. The appropriate ecological endpoints for use in assessment of environmental stress will be specific to each study and the limitations of evaluating higher levels of ecological organization need to be carefully evaluated [119]. Even the large sites may not be at an appropriate scale to consider population and community level endpoints. For example, the Hudson River Superfund site extends for 320 km but is no more than a few km wide. Tree swallows are not restricted to the river zone itself, making it difficult to determine impacts of contamination on higher levels of ecological organization.

Population size. Population dynamics of mobile species such as tree swallows can be dominated by dispersal among different breeding sites. In this way, tree swallow colonies function as a metapopulation of interacting breeding groups. The majority of new breeders at a given breeding site are individuals reared elsewhere ([10], McCarty pers. obs.). At sites along the Hudson River the origin of breeding

individuals is unknown, as is the fate of the majority of young produced at these sites since less than 5 % of individuals banded as nestlings were recaptured as adults [47].

The spatial structure of tree swallow populations and their dispersal abilities means that it is likely that some breeding sites act as sources of individuals for other sites that have low reproductive success ("sinks"). The implications of this are that a local stressor could cause extensive, or even complete mortality without having an effect on the number of breeding pairs settling at the site each year as individuals from the surrounding area continually replenish the breeding population [8]. Data on the dispersal of individuals from natal sites and survival during the non-breeding season are needed as a first step in addressing the population dynamics of tree swallows. This is in marked contrast with many studies of freshwater aquatic systems where dispersal is limited and the spatial scale of the stressor often encompasses the entire population in a lake.

Added to the difficulties inherent in studying population sizes of spatially structured population like tree swallows is the fact that population size in a given area appears to be limited by the availability of nest sites [10]. One of the advantages of using tree swallows in field studies is that they do not appear to be undergoing a dramatic reduction in population size and remain abundant through much of their range [11] and that they can be attracted to appropriate sites in large numbers by providing nest-boxes (Table 5). The implication of this is that the dominant factor determining population size in an area around a contaminated site may be the number of nest-boxes provided by researchers [36, 37]. Unfortunately, the presence of breeding tree swallows at nest-box colonies in highly contaminated areas has occasionally been used to suggest that there are no ecologically-relevant effects of stressors on wildlife. Such arguments are fundamentally flawed and based on the naive assumption that simply counting breeding adults in a local area is a reliable indicator of population-level or higher effects.

The dependence of tree swallow populations on the availability of nest sites could be turned to the advantage of long-term monitoring schemes at well established sites, if the availability of sites is carefully controlled. Under such conditions and with care, it may be possible over the course of years to infer changes in population size from fluctuations in nest box occupancy or the age distribution of females. Such a scheme would require sites that have been established for a number of years, effective exclusion of predators, consistent control of vegetation height through mowing, and controls on the abundance of nest-site competitors like house sparrows, in addition to consistent numbers, size and quality of nest boxes.

Although difficult to study, population-level effects of local stressors are still of interest for tree swallows and similar species. Over-all population size could be impacted by local events occurring in areas where a large portion of the population congregates. For example, tree swallows could be vulnerable to impacts on the wintering ground where up to a million tree swallows congregate in relatively few marshes. Under these conditions effects similar to those observed in species such as

fish eating seabirds where only a few large breeding colonies are used each year might be expected.

For tree swallows, understanding the effects of local stressors on the breeding grounds will be based on a thorough understanding of effects on reproductive biology of individuals, combined with additional information on meta-population dynamics. Tree swallow populations are likely impacted by regional events, such as those caused by adverse weather during the breeding season and by factors that alter habitat quality [10, 16, 46].

Community interactions and ecosystem functioning. The impact of tree swallows on the interactions among members of an ecological community and their role in ecosystems is unknown and a subject that will first need to be addressed by basic ecological studies. Tree swallows do consume an enormous number of insects but their impact on the community is unknown [16]. Likewise tree swallows are a prey source for numerous other species. In areas where tree swallows have elevated levels of contamination they are likely sources of contamination for sensitive avian and mammalian predators that eat them [32, 33]. For example, this may be of some concern in the Hudson River valley where peregrine falcons have been reestablished adjacent to the river and where large numbers of highly contaminated tree swallows pass by during migration.

In contrast, the import impacts of community and ecosystem characteristics on tree swallows is documented. It is known that variation in climate and food supply, as well as the chemical and biological characteristics of aquatic communities can impact tree swallow ecology [46, 53, 120]. Disruption of aquatic communities by human activities, especially acid deposition, has wide ranging consequences for tree swallow ecology (see discussion below)

Pesticides may have direct effects on populations through toxic effects but less explored have been indirect effects on insectivores like tree swallows due to changes in the insect community. Spraying insecticides causes broad changes in the insect community and these changes can be associated with shifts in the diet of forest insectivores [121]. These changes can in turn negatively affect the nutritional condition of insect eating birds [122]. The food supply of tree swallows can be measured with accuracy, especially when suction traps are used [53, 16], so it should be possible to investigate indirect effects due to changes in the insect community. Insect abundance was low in orchards relative to control sites but temporal variation in insect abundance within orchards was not related to spray events [102].

4.2. *Reproductive success*

The success and efficiency of reproduction is a fundamental life history parameter that has been widely used in evaluating the impacts of various stressors on wildlife. Within the broad heading of reproductive success there are numerous specific endpoints that can be evaluated. For birds such as tree swallows the number of eggs

(clutch size), hatchability of eggs, and survival of young to independence (fledging) are relevant measures of reproductive success.

Clutch size. Average clutch size of tree swallows is approximately 5.4 eggs with a typical range of 4 to 7 eggs [10]. There is little evidence from field studies that chemical contamination influences mean clutch size. Clutch size has been examined at contaminated sites at Saginaw Bay, Green Bay, and the Fox River and in every case mean clutch size was within the normal range for tree swallows [28, 89, 123]. Slightly smaller clutch sizes were found at one contaminated Pennsylvania site (Fort Mifflin) but overall average clutch sizes at the Pennsylvania sites (4.4 to 5.8 eggs) were within the range typically encountered in tree swallows [26]. Exposure to pesticides in orchards did not have a significant effect on clutch size in studies from Ontario and British Columbia [96, 100]. Sites upstream and downstream of pulp mill effluent discharges had similar clutch size [92] and clutch mass [15].

None of the sites that make up the Hudson River study differed significantly in mean clutch size, with a range from an average of 5.2 to 6.0 eggs [47]. However, the Hudson River sites did have an unusual number of large clutches (> 7 eggs) [47]. Although tree swallows are not determinant layers like gulls and terns, this situation is analogous to the "supernormal" clutches described in gulls from areas contaminated with organochlorines [124, 125].

Hatching success. The proportion of eggs that hatch reflects both fertilization success and survival of embryos. In the first year of the Hudson River study, the percent of eggs hatching at the Hudson River sites was low relative to studies at uncontaminated sites [10, 47, 97]. In fact the only other sites with comparable elevated levels of hatching failure were contaminated areas of Green Bay and the St. Lawrence (Cornwall Island) [91, 123]. The low hatching success along the Hudson in 1994 was not observed in 1995, suggesting that PCB contamination may be interacting with other environmental variables [47].

Hatchability of tree swallow eggs from Ontario orchards was not correlated with organochlorine residues but in some years there was a decline in egg fertility related to cumulative toxicity scores that based on exposure to current pesticide sprays [100]. Similar patterns were observed in eastern bluebirds (*Sialia sialis*) nesting in the same orchards [29]. In British Columbia, hatching success was over 90 % for both control and orchard nests [96].

Eggs irradiated with acute doses up to 3.2 Gy in the laboratory hatched normally although chronic exposure may reduce hatching [114].

Nestling survival and fledglings produced. Nestling tree swallows can be protected from predation mortality when metal predator guards are used on support poles of nest-boxes. Removal of predation as a major source of mortality leaves weather-related deaths as the major source of nestling loss [10, 16]. Losses of nestlings not explained by known sources of mortality are generally low in uncontaminated areas.

Survival of nestlings that hatched was within normal ranges at all Hudson River sites [47]. Field studies at other contaminated sites also found no differences in pro-

duction of fledglings between contaminated and reference sites [91]. In British Columbia orchards fledging success was higher in orchards (82 %) than control sites (70 %) [96]. No effect of organochlorine residues on nestling survival was found in Ontario orchards, but in some years survival was lower among nestlings exposed to more frequent spraying of insecticides [100]. Nestling survival was not different among sites upstream and downstream of pulp mills [15].

In experimental field studies of the effects of radiation exposure, swallows tended to choose nests with lowest exposure [113]. The mechanism behind this choice was unclear but may have been related to the effects of radiation on vegetation. The result was the exposure to ionizing radiation was below levels that caused interference with reproductive success [113]. Subsequent studies also found no effects of ionizing radiation on reproductive success [114, 115].

4.3. Developmental Effects

Organisms may be especially susceptible to the effects of contaminants during rapid development. A variety of endpoints have been used in birds to examine changes in development including overall growth rates, presence of malformations, and changes in morphological characters [69, 71, 74, 77, 78, 126].

Female plumage color. Typical adult tree swallows have a distinctive iridescent blue-green plumage on their head, back, and rump that contrasts with their white undersides. However, female tree swallows are unique in that they retain the dull brown color of juveniles on their upper-parts through their first breeding season. This retention of juvenile plumage, referred to as a sub-adult plumage, is an indicator of age and probably reduces aggression directed towards the first year breeding females [10, 127].

In previously studied populations, most breeding females can be easily classified as either first year breeders or older birds based on plumage color [10, 127, 128]. However, observations of females breeding at the Hudson River sites suggested that there were a large number of females with plumage intermediate in color between sub-adult and full adult categories [54]. We were able to compare the proportion of sub-adult females with intermediate plumage color to those in two previous studies and to females in museum collections. The proportion of intermediate females was similar between the two previous studies and the museum collections but the contaminated Hudson River had significantly higher numbers of females with intermediate plumage [54]. Plumage development in birds is controlled by hormone levels, suggesting a plausible link between the abnormal development of female plumage and the high levels of contaminants known to interfere with normal endocrine function.

Eggshell thickness. Given the historical importance for environmental toxicology of the discovery of the impact of DDT/DDE on development of eggshells in birds [129, 130], it is not surprising that eggshell thickness of birds from contaminated sites continues to be of interest. Although there is some suggestion that PCBs are also associated with eggshell thinning, analyses of field data are generally complicated by

correlations between levels of PCBs and DDT and its metabolites. The balance of evidence suggests that PCBs impact eggshell thinning only at very high doses [131].

Eggshell thickness was measured in 1994 in birds from the Hudson River and shell mass was used to calculate an index of shell thickness [130]. The two measures of shell thickness were correlated [97]. Shell thickness and the shell index did not differ among eggs from the Hudson River, the Champlain Canal Reference site or the uncontaminated Ithaca site [97]. DeWeese et al. also measured tree swallow egg shells from Colorado and compared them to eggs collected prior to the widespread use of DDT but found no evidence of thinning associated with DDE levels in eggs averaging 2.1 $\mu\text{g/g}$ [95]. Hudson River swallows had significantly thicker shells than those from Colorado [95, 97]. The absence of an effect on egg shell thickness associated with the high levels of PCBs on the Hudson River suggests that the conclusion that PCBs do not cause eggshell thinning is supported in tree swallows [70, 131].

Developmental anomalies. Contaminants are associated with a range of deformities in birds [84, 132]. PCBs are thought to be associated with a range of developmental malformations, including deformities of legs and feet, brain, eyes, and bill. Other possible anomalies attributed to PCBs include edema, jaundice, hemorrhage, and "wasting syndrome" [77, 78, 83, 97, 132, 133, 134].

On the Hudson River, we have noted a number of unusual developmental anomalies. These include possible cases of jaundice and edema [97], leg abnormalities, underdeveloped eyes, and crossed bills in at least one adult and nestlings (unpublished observations). Yorks also noted one nestling with a "crooked beak" near a PCB contaminated site at John Heinz National Wildlife Refuge [26]. At the Special Area 13 site on the Hudson River a single nestling was observed with fully inflated air sacs: the sacs were stretched thin and produced a fully round chick. Finally, several females collected for chemical analyses from along the Hudson River were found to have some development of both ovaries (female birds typically only develop ovaries on their left side).

Unfortunately, no systematic data have been collected on the types and frequency of abnormalities in tree swallows. Until such data are compiled, both from contaminated and uncontaminated sites, the impact of chemical contamination on the frequency of developmental anomalies will remain unclear.

Mutation rates. The possible mutagenic effects of high concentrations of PCBs were evaluated by comparing Hudson River tree swallows to individuals from uncontaminated sites using minisatellite DNA fingerprinting [135]. Tree swallows from the Hudson River averaged 0.010 mutations per fragment scored, while swallows from reference sites in Wisconsin, Alberta and Ontario averaged 0.011 mutations per fragment scored [135].

There is limited evidence of higher mutation rates from areas with high levels of chemical contamination. For example, herring gulls (*Larus argentatus*) from Hamilton Harbor in Ontario were found to have higher levels of mutation using multilocus DNA fingerprinting [136]. Evidence for higher rates of mutation associated with elevated levels of radiation are better documented. Barn swallows nesting near Chernobyl, Ukraine, were evaluated by comparing microsatellite DNA fingerprinting to control ar-

eas [137]. Barn swallows in areas impacted by radiation from the Chernobyl site had mutation rates elevated by as much as ten times over control sites and had higher levels of gross phenotypic aberrations [118, 137].

Nestling growth rates. Numerous studies have looked at nestling growth. Tree swallow growth is sensitive to a variety of environmental factors [52, 53, 138, 139], but there is no indication that PCBs impair growth of tree swallow nestlings. Hudson River tree swallows grow at normal rates [47]. Yorks found low nestling mass at one of her contaminated sites but this was not consistent across sites and the heaviest nestlings were found at the most heavily contaminated site on the Hudson River [26]. Nestlings experimentally dosed with PCBs grow to normal mass [26]. Normal growth was also observed at other field sites with chemical contamination or other stressors [15, 28, 89, 102, 113, 115]. High levels of acute radiation exposure (> 2.7 Gy) in the lab did result in delayed growth [140] and chronic exposure was found to have more severe effects [114].

Other measures of development. Development of testes in nestlings from pesticide sprayed orchards in Ontario was evaluated by Bishop et al. [141]. Testes were weighed and measured and histological preparations examined. Sertoli cells, seminiferous tubules, spermatogonia, Leydig cells, and the presence of heterophils were evaluated. A decrease in the developmental organization of Sertoli cells was observed as the number of pesticide mixtures sprayed increased [141]. No other gross or histological measures of testes were correlated with spray exposure variables [141]. No differences in gross development of other organs were observed between spray treatments [99]. At a cellular level, sprayed orchards did show higher levels of inflammation of the bursa of fabricius and more cellular activity in the thymic cortex indicating delayed maturation of the thymus [99]. Immune function was also evaluated in these orchard colonies. Nestlings from sprayed sites had significantly stimulated T- and B-cell blastomeric response suggesting a stimulated immune system, in contrast to the suppressed immune system that might be expected with exposure to harmful chemicals [99].

Gross and histological gonad morphology in nestling tree swallows from PCB contaminated sites was evaluated but no evidence of abnormal development was found [26]. Skeletal development in pipped embryos and 12 day old nestlings was also examined. Cleared and stained specimens were examined for symmetry and the degree of bone ossification but no effects of PCB exposure were found [26].

4.4. Behavior

Behavior is a possibly sensitive, ecology relevant endpoint that increasingly used in environmental toxicology [34, 35, 142]. Chemical contaminants such as PCBs can impact behavior through several pathways. For example, exposure to PCB and related compounds during development can cause permanent changes to the nervous system, while disruption of the endocrine system can change circulating levels of hormones in adults, thereby altering behavior [143, 144].

Nest building behavior. Nest building involves a complex set of behaviors that are under hormonal control and that have broad implications for reproductive success [145, 146, 147, 148]. In tree swallows nest quality is known to be associated with reproductive success [149, 150]. Higher quality nests tend to have a larger and heavier grass cup lining the bottom of the nest-box and have more feathers lining the nest cup where the eggs are laid. In the first year of the Hudson River study, an unusual number of low quality nests were observed. In 1995 this was studied quantitatively by weighing nests and counting feathers [151]. Nests from contaminated sites on the Hudson River were significantly lighter and had fewer feathers than those at reference sites. These patterns were correlated with the average level of contamination at each site [151].

Poor nest construction at PCB contaminated sites in Pennsylvania was noted, including both low numbers of feathers and smaller grass cups [26], but nests in sprayed orchards and control sites had similar numbers of feathers [29].

Incubation behavior. Reduced reproductive success in Hudson River tree swallows was largely a result of abandonment and burial of eggs in the nest [47, 97]. In both 1994 and 1995 incidences of abandonment and egg burial were elevated at the Hudson River sites relative to other, uncontaminated locations [47]. It is also possible that the low hatchability of eggs in 1994 is a result of impaired incubation behavior. European starlings (*Sturnus vulgaris*) nesting in PCB contaminated sites also showed reduced nest attentiveness, however, mallards fed PCBs did not have abnormal incubation [152, 153]. Incubation behavior of tree swallows was not affected by spray events in Ontario orchards [29]. Abandonment of nests downstream of pulp mills was noted in British Columbia, though the authors suggested this was probably not directly related to contaminant exposure [92].

Parental care behavior. Like many other behaviors, parental care of dependent nestlings is influenced by a variety of environmental factors, including hormone levels. Cholinesterase inhibiting insecticides are associated with poor parental care in some passerines [154]. Feeding behavior and nestling hunger responses in tree swallows exposed to organophosphorus insecticides in orchards has been studied. Increased begging behavior was observed in nestlings in sprayed sites, which may reflect low food availability in orchards rather than a direct effect of pesticides on behavior [102]. The frequency of adult feeding trips declined after pesticide spraying in one year. Insect abundances were consistently low in sprayed orchards and did not significantly decline after spray events leading Bishop et al. to conclude that the observed decline in feeding frequency was most likely a result of direct effects of pesticides on the adults, rather than an indirect effect caused by a sudden decline in prey availability [102].

4.5. Biomarkers

Several studies have examined the development of biomarkers for use with tree swallows exposed to environmental contaminants. Biomarkers measure the physio-

logical response of organisms exposed to contaminants. A measurable response indicates that exposure is sufficient to cause a biological response [86]. Advantages of biomarkers include the ability to quantify the response, typically through measurement of biochemical changes, and the possibility that physiological responses will provide a sensitive indicator of biological effects.

Cytochrome P450 induction. The enzyme systems responsible for metabolism of toxicants provide a logical avenue for development of biomarkers. The Cytochrome P450 system has been widely applied in studies of wildlife exposure to chemicals in the environment [69, 71, 74, 86]. Exposure to toxicants that result in increases in Cytochrome P450 activity indicate that exposure is sufficient to cause a response in the organism. In tree swallows measures of monooxygenase activity associated with P450 such as EROD (ethoxyresorufin-*O*-dealkylase) and BROD (benzyloxyresorufin-*O*-dealkylase) are used to assess exposure to Ah-active PCBs [28, 88, 91].

Among pippers from sites in Green Bay and the Fox River valley, EROD and BROD activities were induced at the two most contaminated sites (Kidney Island and Arrowhead) relative to the least contaminated site (Pagan), but total P450 activity was not correlated with total PCB content of siblings [28]. EROD and BROD activities were higher in older nestlings from more contaminated sites than less contaminated sites and P450 activity was correlated with EROD ($r^2 = 0.69$) and BROD ($r^2 = 0.61$) in older nestlings [28]. EROD induction was also measured at heavily contaminated sites on the St. Lawrence River [91]. Tree swallows breeding in orchards sprayed with pesticides did not show EROD induction [99] but elevated levels of EROD and BROD were detected in tree swallows exposed to PAHs near a refinery in Wyoming [105]. EROD levels in young tree swallows from nests upstream and downstream of pulp mills did not vary among sites [15].

Hepatic Cytochrome P450 monooxygenase activity in nestlings from sites in Pennsylvania, Indiana, and Maryland was measured [26]. Both EROD and BROD values were significantly higher at the highly contaminated sites in Pennsylvania and Indiana (Fort Mifflin, PA and Winston-Thomas site, IN). For the Pennsylvania and Maryland sites, there was a correlation between BROD and EROD activity and contaminant levels in nestlings (for the 1995 and 1996 samples pooled, $r = 0.53$ for BROD and $r = 0.52$ for EROD). It is interesting to note that the highly contaminated Hudson River samples did not show elevated activity and PCB levels in nestlings were not correlated with EROD and BROD activity. Cytochrome P450 activity was not consistently induced by experimental exposure to PCBs [26]. The relatively low percentage of variation in Cytochrome P450 activity explained by PCB exposure, especially in controlled dosing experiments, raises questions about the usefulness of this biomarker in Tree Swallows exposed to PCBs. However, Yorks did find evidence from controlled dosing experiments that other contaminants do induce Cytochrome P450 in Tree Swallows (specifically BNF), suggesting that additional work in this area will be valuable. In particular, the possibility that Cytochrome P450 is induced and then inhibited by PCBs, and the effects of specific PCB congeners should be investigated [26].

Other possible biomarkers. High levels of porphyrins are also thought to indicate exposure to PCBs and related chemicals [77, 86, 155]. Nestling tree swallows from Lake Ontario showed severe porphyria, leading Fox et al. [155] to suggest that porphyrin patterns may be especially useful for monitoring exposure and effects at low to moderately contaminated sites. Measurements of highly carboxylated porphyrins (HCPs) did find elevated levels in some contaminated sites in the lower Great Lakes, especially in association with PCB congener 118 [91]. A pilot study measuring porphyrin levels in tree swallows experimentally dosed with Aroclor 1260 has been conducted but did not produce consistent trends in HCP [26].

HCP levels in nestlings immediately downstream of a pulp mill on the North Saskatchewan River were elevated 1.4–1.6 times above levels found elsewhere on the river [15]. No effect of pulp mill effluent on HCP levels was detected on the Wapiti River [15].

Other biomarkers explored for use in tree swallows include measures of vitamin A in the form of retinol and retinyl palmitate. Vitamin A metabolism is considered sensitive to organochlorines, however, depressed levels of vitamin A were not correlated with high levels of PCBs in tree swallows from the lower Great Lakes and St. Lawrence River, although vitamin A was correlated with EROD activity [91]. Endocrine activity in tree swallows in pesticide sprayed orchards was also examined [141]. Specifically, concentrations of the sex hormones 17β -estradiol and testosterone were measured and thyroid function was evaluated by measuring Triiodo-L-thyronine (T3) concentrations. T3 concentrations in male nestlings were positively correlated with the number of spray events in orchards but there were no differences observed for sex hormones [141]. Hormone levels of female nestlings and adults were not correlated with any measures of exposure. Levels of persistent organochlorines were generally low and not correlated with endocrine response [141]. Levels of 17β -estradiol in incubating females at sites exposed to pulp mill effluent on the Wapiti River in Alberta were only 0.6 times the levels found elsewhere in 1995 [15]. The opposite pattern was seen in 1996, when 17β -estradiol levels in females downstream of the pulp mill were elevated relative to upstream sites [15].

Brain and plasma cholinesterase (ChE) activity was measured in tree swallows from orchards sprayed with organophosphorus insecticides [156]. ChE activity in plasma of adult tree swallows was significantly inhibited by 19–41 % after application of insecticides [156]. There was some indication of inhibition in nestlings but ChE activity changes rapidly during nestling development, making it difficult to partition out the effects of pesticide exposure [156].

The possible use of immunohistochemistry response as a biomarker has been explored but Yorks concluded that this was not a useful for Tree Swallows exposed to typical levels of PCBs [26]. There was some indication that individuals experimentally dosed with BNF did show an immune system response, suggesting that this system may be useful for other types of contaminants [26].

5. Effects of other Environmental Stressors

Use of tree swallows as indicators of environmental conditions has not been limited to studies of chemical contaminants. A wide range of anthropogenic stressors may impact the ecology of tree swallows. The ease with which they can be studied combined with their ability to integrate conditions in both the aquatic and terrestrial ecosystems make tree swallows especially suitable for these studies.

Climate change. In recent years it has become increasingly clear that ongoing climate change, possibly due to human disturbance of greenhouse gas levels, is causing significant stress on a wide range of plants and animals [157]. Dunn and Winkler used a large collection of nesting records of tree swallows collected throughout the species range over the past 30 years to document a significant change in the timing of breeding of tree swallows [46]. Their analysis shows a strong correlation between the time of breeding and local climate, with the onset of breeding having advanced by up to 9 days between 1959 and 1991. The broader implications of these changes are unknown. It is clear that the time of onset of breeding is an important factor in reproductive success and the dramatic shifts in this fundamental life-history characteristic are an important early-warning of the broad effects of climate [46].

Acid deposition and calcium in ecosystems. Deposition of sulfur and nitrogen-based acidic compounds resulting from burning of fossil fuels has been recognized as having a broad range of ecological changes, especially in areas where water and soils have low buffering capacity [158, 159, 160]. A wide range of effects of acidification have been described for both aquatic and terrestrial ecosystems, including increased bioavailability of trace elements such as aluminum and mercury. Calcium metabolism can be impaired under acidic conditions and the availability of Ca in the environment reduced, leading to negative impacts across several trophic levels [161].

At the Experimental Lakes Area of northwestern Ontario artificially acidified lakes have been used to study the ecological impacts of acid deposition. Tree swallows nesting near acidified lakes did have smaller eggs and had lower hatchability [162]. Growth of nestlings was also impaired near experimentally acidified lakes, include lower mass and shorter wing length [162].

Tree swallows breeding near wetlands impacted by emissions from smelting operations at Sudbury Ontario were studied [163]. Tree swallows breeding at more acidic sites laid fewer and smaller eggs and produced fewer fledglings. Nestling growth was also impaired at the most acidic sites [163].

In experimentally acidified lakes, the biomass of Chironomids (a major food supply for tree swallows) either increased or did not change [164]. However, the types of prey insects available may change under acid conditions [13, 165]. Chironomids from acid lakes have lower calcium concentrations and accumulated more metals such as Al, Mn, and Zn [164]. The uptake of metals by insects could have negative impacts for wildlife that feed on them [106].

The decrease in calcium resulting from acidification may be the most important ecological impact on tree swallows. Calcium is a critical resource for egg production and reduced reproductive success has been observed in birds resulting from acid deposition [166]. Tree swallows do not store sufficient calcium to lay eggs [167] and need supplemental calcium to reproduce. Adults often seek out calcium rich items to supplement the diets of their nestlings [17, 18]. Low levels of calcium in the diet and the difficulty in finding high calcium supplements may be the mechanism behind the low reproductive success in acidified areas [18, 162, 163].

6. Conclusions and future directions

The wide use of tree swallows to monitor environmental stressors and the large number of studies currently in progress speaks to the advantages many researchers have found in working with this species (Fig. 1; Table 1). Work in progress includes evaluation of pesticide exposure and effects of *in situ* contaminants across North America (Fig. 1). For example, work using tree swallows is in progress at another major PCB contaminated river, the Housatonic River downstream from Pittsfield, Massachusetts (C. Custer pers. comm.). Previous monitoring of closely related barn swallows in this area estimated that daily PCB intake rates could be as high as 0.52 $\mu\text{g/g}$ and found that clutch size and the number of young hatched was smaller in contaminated areas than at reference sites [168].

Evaluating exposure – One of the key reasons to undertake a field study is to document and quantify exposure to contaminants [169]. Even when contaminants are known to be present in the environment it can be unclear to what extent wildlife will come in contact with them. For example, results of the Hudson River study effectively refute the hypothesis that PCBs buried in aquatic sediments are not available to terrestrial wildlife. As a result of the work on tree swallows, no reasonable doubt remains that there is a steady flow of PCBs from aquatic sediments to terrestrial ecosystem.

Tree swallows are effective indicators of exposure to a variety of contaminants. Across sites, a broad correlation between contaminants in the environment and uptake of contaminants by swallows is well documented [26, 27, 28, 81]. For PCBs, the uptake of individual congeners is consistent with site contamination, though the effects of differential metabolism are seen when comparing across trophic levels [27, 28, 81, 87, 90].

To date all available evidence supports that hypothesis that elevated levels of contaminants in tree swallows are acquired locally. Since it is possible that a migratory species could accumulate contaminants over a broad geographic range, the source of chemical contaminants must be documented. Comparisons of contaminants in eggs and nestlings demonstrates significant uptake of PCBs and other contaminants, while collection of individuals from reference areas suggests that background levels of most persistent chemicals are low [26, 27, 28, 32, 79, 81].

Tree swallows are likely to be representative of a wide range of insectivorous birds for studies designed to determine exposure to contaminants. Quantitatively, other aerial insectivores including other swallow species, swifts, and nighthawks are most likely to have exposure levels similar to tree swallows [32, 33], while insectivorous birds with other foraging modes such as red-winged blackbirds and house wrens will tend to diverge in the degree of exposure, depending on their diet [80, 87, 88, 96]. The foraging ecology of tree swallows is broadly similar to that of many insectivorous bats, including threatened and endangered species. The possible use of tree swallows as a surrogate for measuring exposure to bats may be a valuable area to pursue.

Measuring effects – The ability to detect effects of chemical contamination on tree swallows varies depending on the types of chemicals involved, the degree of exposure, and the choice of endpoints. Effects of contaminants on reproduction have been detected in both the Hudson River tree swallows [47, 97] and in Ontario apple orchards [29, 100]. However, tree swallows can tolerate relatively high levels of PCBs and other chemicals and still successfully reproduce; including levels of exposure that would cause reproductive failure in more sensitive species [97]. Thus, in making statements about effects of exposure the choice of endpoints is critical. Work described here suggests that behavioral, physiological, and developmental endpoints are more sensitive than indices of reproductive success.

Importance of indirect effects – It is difficult to estimate the importance of indirect effects in ecological systems, especially when evaluating population or community level endpoints. The interacting and indirect effects of stressors on tree swallows may even challenge some of the basic tenants of toxicology, such as the assumption that effects will increase as contamination increases. For example, while there are broad correlations between sediment contamination and the contaminant levels in breeding tree swallows [26, 27], this may not always be the case. Exposure to contaminants from aquatic sediments will depend on the proportion of the diet derived from aquatic insects as well as the concentration of contaminants in the insects. If contaminants levels become high enough to cause a decrease in the abundance of aquatic insects, exposure could decrease as tree swallows are forced to search out other sources of aerial insects. This in turn could impact tree swallow reproduction since the effects of reduced food supply on tree swallows are well documented [16, 51, 52, 53]. Thus, it is possible for contaminants to have negative impacts on tree swallow reproduction in a situation where direct exposure to the contaminants is limited by the lack of emerging insects. In other cases, such as near pulp mill effluent discharges, nutrients released along with contaminants will increase insect abundance and the increased food supply may offset some of the negative effects of elevated contaminants on tree swallows [15, 170].

Choice of species and endpoints – No single species will fulfill all the criteria for the ideal study species [9]. Indeed, many criteria are mutually exclusive (Table 5). The final decision about selecting tree swallows or another species as a target of a field study will depend on the goals of the study.

Numerous criteria have been proposed for selecting species for field studies. Characteristics important for target species include: 1) ecological attributes such as geographic range, population size, and diet appropriate for the study; 2) preexisting information about the species' ecology and natural history; 3) ability to easily obtain sufficient samples; 4) ability to maintain and breed in captivity for experimental purposes; and 5) preexisting knowledge about effects of contaminants and other environmental stressors [171].

Tree swallows meet many of these criteria (Table 5). They are abundant through most of their range (Fig. 1) and they use nest boxes so nests are easy to find and samples easy to obtain. However, this also means that since tree swallows are not rare, threatened or declining they may be of less interest to policy makers.

Both the basic ecology of tree swallows and their response to environmental stress has been extensively studied. Tree swallows' relatively small body size (20 g) does mean that analyses that require large samples of tissue will be more difficult to perform. The fact that tree swallows and related species are strict aerial insectivores simplifies the accurate identification of the route of exposure.

If the demands of a study place a high priority on a species showing dramatic responses in reproductive success or population size to contaminant exposure, tree swallows will present difficulties. They appear to tolerate contaminants better than many previously studied species (Table 5). However, for many studies, a more significant short-coming of using tree swallows is that they have not been successfully kept and bred in captivity, limiting the types of experimental work that can be performed. This difficulty may be overcome through creative, field based experiments.

6.1. Priorities for future work

Ongoing work on tree swallows will increase their usefulness in field studies of environmental conditions. Comparative studies across species and within species at different sites will greatly increase our abilities to interpret results from contaminated sites. Less is known about the sensitivity of other related aerial insectivores to contaminants [109, 110] so studies integrating other species will help to draw generalizations from studies of tree swallows.

Assessment of exposure – Tree swallows have been especially useful in evaluating exposure to environmental contaminants. Chemicals such as organochlorine pesticides are persistent in the environment and tend to accumulate in organisms and concentrate along the food chain so exposure can be evaluated with standard chemical assays [98]. Methods of evaluating exposure to other stressors needs additional work. For example, organophosphorus and carbamate pesticides are relatively short-lived and rapidly metabolized by most animals so they do not bioconcentrate. Exposure typically occurs through direct contact during pesticide application or through ingestion of sprayed insects [101]. Future studies of tree swallows in agricultural areas need to improve methods of quantifying exposure.

The complex mixture of PCB congeners present in the environment can make exposure assessment an especially important step for studies involving PCBs. As Custer et al. point out, future studies at PCB sites will need to balance the benefits provided by understanding patterns of different PCB congeners, against the expense of congener-specific analysis. The general lack of understanding about the relative toxicity of different congeners to birds may make the added expense of congener specific analysis difficult to justify [28]. This may be especially true if bird species differ in their sensitivity to different congeners, which would call for species-specific data [172]. If the correlation between total PCBs and calculated TEQs observed in some field studies [27, 28, 88] proves to be a general one, the use of less expensive analyses may be justified [28].

Biomarkers – Biomarkers hold great promise for evaluating exposure to contaminants [26, 28, 155, 156, 173]. Results from some studies that fail to find strong correlations among biomarkers and between biomarkers and contaminant levels emphasize the need for additional field data to help interpret results of biomarker analyses [26, 91].

Behavioral endpoints – Behavioral endpoints are recognized as being sensitive toxic response indicators [174] and may detect effects well below the lethal dose. Sufficient background information on tree swallow behavior and its link to ecology and reproduction exists to allow for informed use of behavioral endpoints. Of concern for future studies is how these endpoints contribute to assessment of risk from human impacts.

Reproductive success and populations – The implications choosing population and community level endpoints over endpoints at the individual level needs to be thoroughly discussed in light of the ecology of mobile, terrestrial organisms such as tree swallows [119]. There will be conditions where it is important to understand the implications of human effects on reproductive success and population dynamics. It is possible that population models will prove a useful tool for evaluating effects on higher levels of ecological organization, but development of models will be limited by the availability of accurate values for parameters [175]. Future progress in this area is especially limited by empirical data on dispersal and survival.

Experimental studies – The importance of indirect effects in ecological relationships combined with the variation in the response of individuals and species to levels of contaminants [176] make ecologically relevant experimental studies an especially important complement of observational field studies [2]. Such studies, along with future observational field studies will serve to increase the value of tree swallows as environmental monitors. The ability of researchers' to control for other influences on the ecology of the target populations through use of creative field-based manipulations will improve our ability to link causes to observed effects.

6.2. Integrating tree swallows into environmental toxicology

Much of our understanding of the environmental toxicology of birds comes from field studies of colonial fish-eating birds, predatory raptors, and game birds [70, 74]. These groups of birds all tend to be larger and longer-lived than typical passerines like tree swallows. Reproductive strategies also vary among groups; colonial

fish-eating birds and raptors typically rear only one or two young a year while tree swallows typically lay five or six eggs. These differences in life history will likely contribute to interspecific differences in the responses of birds to contaminants. As our knowledge of tree swallows and other passerines increases, the implications of interspecific differences need to be integrated into generalization about the effects of contaminants on ecosystems.

The fact that tree swallows integrate conditions of both aquatic and terrestrial ecosystems may make them especially valuable in studies of environmental health at the watershed or ecosystem level. Tree swallows are proving to be excellent model organisms for learning more about how contaminants and other sources of anthropogenic stress influence wildlife.

Abbreviations

PCB, polychlorinated biphenyl; TCDD, 2,3,7,8-tetrachlorodibenzo-*p*-dioxin; TCDF, 2,3,7,8-tetrachlorodibenzofuran; BNF, β -naphthoflavone; BROD, benzyloxyresorufin-*O*-dealkylase; EROD, ethoxyresorufin-*O*-dealkylase; TEQ, 2,3,7,8-tetrachlorodibenzo-*p*-dioxin equivalents; TEF, toxic equivalency factors; HCPs, highly carboxylated porphyrins; PAH, polycyclic aromatic hydrocarbons; ALH, aliphatic hydrocarbons; HEP, heptachlor epoxide; HCH, hexachlorocyclohexane

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