Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous chimney swifts

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Numerous environmental pressures have precipitated long-term population reductions of many insect species. Population declines in aerially foraging insectivorous birds have also been detected, but the cause remains unknown partly because of a dearth of long-term monitoring data on avian diets. Chimney swifts (*Chaetura pelagica*) are a model aerial insectivore to fill such information gaps because their roosting behaviour makes them easy to sample in large numbers over long time periods. We report a 48-year-long (1944–1992) dietary record for the chimney swift, determined from a well-preserved deposit of guano and egested insect remains in Ontario (Canada). This unique archive of palaeo-environmental data reflecting past chimney swift diets revealed a steep rise in dichlorodiphenyltrichloroethane (DDT) and metabolites, which were correlated with a decrease in Coleoptera remains and an increase in Hemiptera remains, indicating a significant change in chimney swift prey. We argue that DDT applications decimated Coleoptera populations and dramatically altered insect community structure by the 1960s, triggering nutritional consequences for swifts and other aerial insectivores.

Keywords: aerial insectivores; dichlorodiphenyltrichloroethane; diet reconstruction; guano

1. INTRODUCTION

A wide spectrum of recent environmental stressors, such as climate change, altered prey abundance, habitat loss and pesticide use, have negatively affected populations of many insects [1] and their predators [2–4]. In particular, populations of aerially foraging insectivorous birds have been declining for several decades [5], particularly in northeastern North America [6]. The reasons for declining population abundance of aerial insectivores, however, remain speculative [6,7], largely because of the general absence of long-term monitoring data. Aerial insectivore populations are probably affected by stressors on their wintering grounds [8], but these stressors are unlikely to be solely responsible for guild-wide population declines because of the diversity and distance between wintering ranges. For example, the eastern phoebe (*Sayornis phoebe*) overwinters in the southern US and eastern Mexico, whereas the eastern wood-pewee (*Contopus virens*)

overwinters more than 2000 km away in northern South America. However, insectivory is a feature common to all aerially foraging insectivores, and it is therefore probable that historical changes in prey populations had a role in delimiting populations of these birds. Data on historical diets of many bird species are unavailable, but a variety of proxy approaches have been used to obtain this information, including examination of fossilized egg-shell deposits [9], lake and pond sediments [10,11], guano deposits [9,12,13] and tissue biochemistry [14]. Such studies provide insight into past evolutionary and environmental conditions; however, none have yet elucidated how specific dietary shifts in recent decades might be associated with changing pesticide use.

Here, we examine a unique dietary archive from a major chimney swift (*Chaetura pelagica*) roost in Kingston (Ontario, Canada), which contains a geochronologically dated deposit of guano and egested insect remains (hereafter, collectively referred to as simply 'guano'; figure 1). This opportunity is rare because the chimney has been a major, long-term roost site, which was decommissioned but not destroyed, allowing a guano deposit to accumulate over five decades until it was capped in 1992, thus

Figure 1. (*a*) Roost chimney and (*b*) guano deposit of chimney swifts (*Chaetura pelagica*). At the base of a major roost chimney located in Kingston, Ontario, a 2-m-deep chronostratified deposit of chimney swift guano was discovered and studied to reconstruct the historical diet of chimney swifts and assess relative prevalence of prey remains, stable isotopes and pesticides.

capturing a critically important temporal window in which chimney swift populations steadily decreased by approximately 90 per cent [15]. We examined the strata in the deposit for temporal changes in diet and potential drivers behind those changes, particularly the link between shifts in prey abundance, relative trophic position and historical pesticide deposition.

Chimney swifts are a model aerial insectivore for diet studies because they are accessible on their breeding grounds, congregate in large roosts and migrate long distances, which exposes them to numerous stressors en route. The guano deposit serves as a unique natural archive of ecologically relevant indicators of diet composition by storing arthropod exoskeletons, and stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) that provide insight into possible food web shifts, and information on past levels of persistent environmental contaminants such as dichlorodiphenyltrichloroethane (DDT) and its major metabolites (e.g. dichlorodiphenyl-dichloroethylene, DDE).

2. MATERIAL AND METHODS
(a) *Guano deposit*
We studied a 2-m-deep deposit of chimney swift guano (figure 1), located in a chimney attached to Fleming Hall at Queen's University in Kingston, Ontario, Canada ($44°13'35''$ N, $76°29'38''$ W). The chimney was idled in 1928, and was thereafter a major roost site and a subject of previous banding studies [16]. Thousands of swifts roosted here nightly during that period with little variation in abundance across years (estimates for the 1930s and 1940s can be found in [16] and for the 1970s in [17]), allowing the deposit to accumulate and produce a stratigraphic environmental record. The guano deposit ceased accumulating in 1992, when the chimney was capped. Microscopic inspection of the guano revealed that more than 99 per cent of the material was ornithogenic and composed almost entirely of non-digestible insect remains (thus reflecting the diet of swifts). We collected a stratigraphic sequence of the deposit by excavating into and up through the guano from the access door at the bottom (figure 1*b*). We removed material from a portion of the chimney's 120×120 cm interior to create a smooth vertical face. We then used a stainless steel

tray ($1 \times 18 \times 22$ cm) with one open end to slice 1 cm layers off the top of the deposit, working down the exposed face. The tray was flushed with acetone after every five samples to reduce cross-contamination.

(b) *Radiochronology*
The guano deposit was dated using standard approaches applied to dating stratigraphically intact lake sediment cores [18]. Here, we measured ^{137}Cs, an artificial radionuclide associated with above-ground nuclear weapons testing, which in North America began in the late 1940s and peaked in 1963, just prior to the signing of a test ban treaty [18]. Briefly, layers of guano were freeze-dried, ground to a fine powder and placed in centrifuge tubes (8.4 cm height and 1.5 cm outer diameter) up to a height of approximately 2 cm (between 1 and 2 g). After the deposits had settled, the tubes were sealed with epoxy and allowed to equilibrate for three weeks before counting on a digital, high-purity germanium spectrometer (DSPec, Ortec). The resulting spectrum files show ^{137}Cs at 662 keV. The spectrum files were processed by DOS-based software [18] that included calculations for efficiency and self-absorption corrections. A peak in ^{137}Cs activity was recorded at a depth of 70 cm, indicating 1963, the year of maximum atmospheric ^{137}Cs fallout [18]. Given this, and that the bottom layer of the deposit represented 1928 (the year the chimney was idled) and the top layer represented 1992 (the year it was capped), we estimated that approximately 2.2 cm of guano accumulated annually.

(c) *Stable isotopes*
Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) of the guano remains might be used as dietary tracers in swifts. Typically, δ^{13}C provides information on the source of food, whereas δ^{15}N can be used to characterize trophic structure. To analyse stable-carbon and stable-nitrogen isotopes, we washed all guano samples with a 2 : 1 chloroform : methanol solution and air-dried them for 72 h under a fume hood. We then loaded 0.70–0.80 mg of homogenized samples into tin capsules and combusted them in an elemental analyser (NCS 2500) in-line with an isotope-ratio mass spectrometer (Finnigan Delta^{plus}XP). Stable-carbon and stable-nitrogen isotope ratios are expressed in per mil units (‰) as $\delta = (R_{sample}/R_{standard} - 1) \times 1000$, where $R = {}^{13}$C/^{12}C or ^{15}N/^{14}N, and $R_{standard}$ is either the international

standard V-PeeDee Belemnite (carbon) or atmospheric N_2 (nitrogen). We randomly repeated measurements for 10 per cent of all the samples and determined the precision of our isotope estimates to be $\pm 0.9‰$ for $\delta^{15}N$ and $\pm 0.3‰$ for $\delta^{13}C$.

(d) Entomological remains

We removed 10 ml subsamples from each centimetre of sampled guano and sorted each subsample under a dissecting microscope, using needles to separate the identifiable insect parts (e.g. heads, elytra and wings) from otherwise assimilated chitin fragments. These retained insect parts were identified at least to order, to family where possible, and to genus or species in some instances. The counting protocol included heads (either whole or part) that allowed identification, single elytra with less than half missing or broken and bodies with double elytra. The predominant prey items were Coleoptera (beetles) and Hemiptera (true bugs). Coleoptera were identified by examining the mandibles and head capsule. Hemiptera were identified by the presence of mouthpart stylets if visible, or the clypeus. Dried specimens from a single section were placed into a watch glass and the insect parts were counted under a dissecting microscope. Sections were assessed in a random order to prevent systematic bias.

(e) Pesticides

Deposit samples were homogenized and mixed with Hydromatrix, which was pre-cleaned with petroleum ether. This mixture was spiked with surrogate recovery standards of polychlorinated biphenyl (PCB) 30 and PCB 205, and extracted in an accelerated solvent extractor (ASE, Dionex). The samples underwent two extractions at 2000 PSI and 100°C each, first with acetone/hexane, followed by dichloromethane (DCM). The two extracts were then combined and exchanged in DCM for gel permeation chromatography to isolate the pesticides from pigments, lipids and sulphur. The resulting volume of 20 ml was reduced to 1 ml in a TurboVap (at 15 psi using ultra-high-purity nitrogen gas, with a 35°C water-bath temperature) and exchanged into iso-octane. Further, clean-up and fractionation were accomplished by passing the extracts through a chromaflex column packed with 8 g of activated silica gel topped with 1 g of sodium sulphate. The DDT isomers and metabolites (DDE, DDD) were eluted with 50 ml of hexane and evaporated to a final volume of 500 µl in iso-octane. A known concentration of octachloronaphthalene (OCN) was added as an internal standard. All solvents used were Omnisolv high-purity grade from Fisher Scientific (Ottawa, Ontario, Canada). Pesticides and metabolites were analysed on an Agilent 6890 gas chromatograph with a ^{63}Ni micro-electron-capture detector, using splitless injection with an inlet temperature of 250°C. Extract (1 µl) was separated on a 30×0.25 mm (0.25 µm film) DB-5MS column (J&W Scientific) using hydrogen carrier gas at 2 ml min^{-1} on constant flow. The oven ramping programme was as follows: initial temperature of 80°C held for 2 min, climbing to 110°C at 10°C min^{-1}, then to 280°C at 3°C min^{-1} and held for 5 min. The detector temperature was at 350°C using constant column flow and make-up nitrogen gas at 30 ml min^{-1}. The instrument was calibrated using a five-point calibration curve, using standard concentrations ranging from 1 to 500 pg µl^{-1} with a correlation coefficient of greater than or equal to 0.99. Chromatographic peaks were interpreted using CHEMSTATION software (Rev. A.06.03, Agilent, Mississauga, Ontario, Canada). Compounds were identified by running sets of standards with known concentrations and comparing their retention times with those of the sample compounds. Concentrations of sample compounds were calculated by taking the ratio of their peak areas and the peak area of the internal standard (OCN), which was added prior to injecting the sample.

(f) Statistical analyses

Inter-annual patterns of prey consumption, stable isotopic compositions and pesticides were strongly non-parametric (figure 2). Therefore, we modelled these data using local (loess) regression [20]. For each model, we chose the smoothing parameter (i.e. span) that minimized a bias-corrected Akaike information criterion [21]. All loess models were generated with a first-degree polynomial; although a higher-degree polynomial has less bias, it also increases variability (because there are more coefficients to estimate) and thus risks underfitting when sample sizes are not large.

Coleoptera and Hemiptera often constituted up to 98 per cent of the sample, and not surprisingly were highly inversely correlated $(F_{1,88} = 983.01, \ p = 2.2 \times 10^{-16}, \ r = -0.96)$. Therefore, to reduce the number of analytical comparisons, we used the ratio of Coleoptera to Hemiptera remains as a single variable in further analyses. The relationships between prey consumption, stable isotopes and pesticides were relatively linear (see the electronic supplementary material). We thus built simple linear regression models to assess the relationships between: (i) $\delta^{15}N$ and the ratio of Coleoptera to Hemiptera remains; (ii) $\delta^{15}N$ and the C:N ratio; and (iii) ratio of Coleoptera to Hemiptera remains and p,p'DDE levels. Because sample sizes were small for some assays (e.g. DDT metabolites), we sought to reduce type II error and set $\alpha = 0.10$. To further describe the direction and magnitude of correlations revealed by linear regression, we calculated Pearson's correlation coefficient (r) [22] for all pairwise variable combinations (see the electronic supplementary material).

All statistical analyses were performed in R v. 2.12.2 [23].

3. RESULTS

Examination of the proportion of the orders present in insect remains in the deposit revealed a major shift in the diet of swifts between the 1940s and early 1950s. During this period, the prevalence of true bug remains increased (figure 2a), whereas that of beetle remains decreased (figure 2b). Beginning in the late 1950s and continuing into the 1970s, swifts then consumed more beetles and fewer true bugs, a change that might be associated with a potential decrease in the trophic level of swift diet as interpreted from changes in stable isotope ratios of nitrogen ($\delta^{15}N$; figure 2c). A decrease in $\delta^{15}N$ from 19.9‰ to 9.8‰ in swift prey occurred between the early 1960s and late 1970s (figure 2c).

Nonetheless, the relative changes we observed in $\delta^{15}N$ values corroborate the change we observed in prey abundance in the deposit, because ^{15}N is preferentially incorporated into consumer tissues with each trophic level [24]; abundance of beetles relative to true bugs was negatively correlated with $\delta^{15}N$ ($F_{1,88} = 7.88$, $p = 0.006$; $r = -0.29$), such that when swifts consumed more beetles and fewer true bugs, their $\delta^{15}N$ values
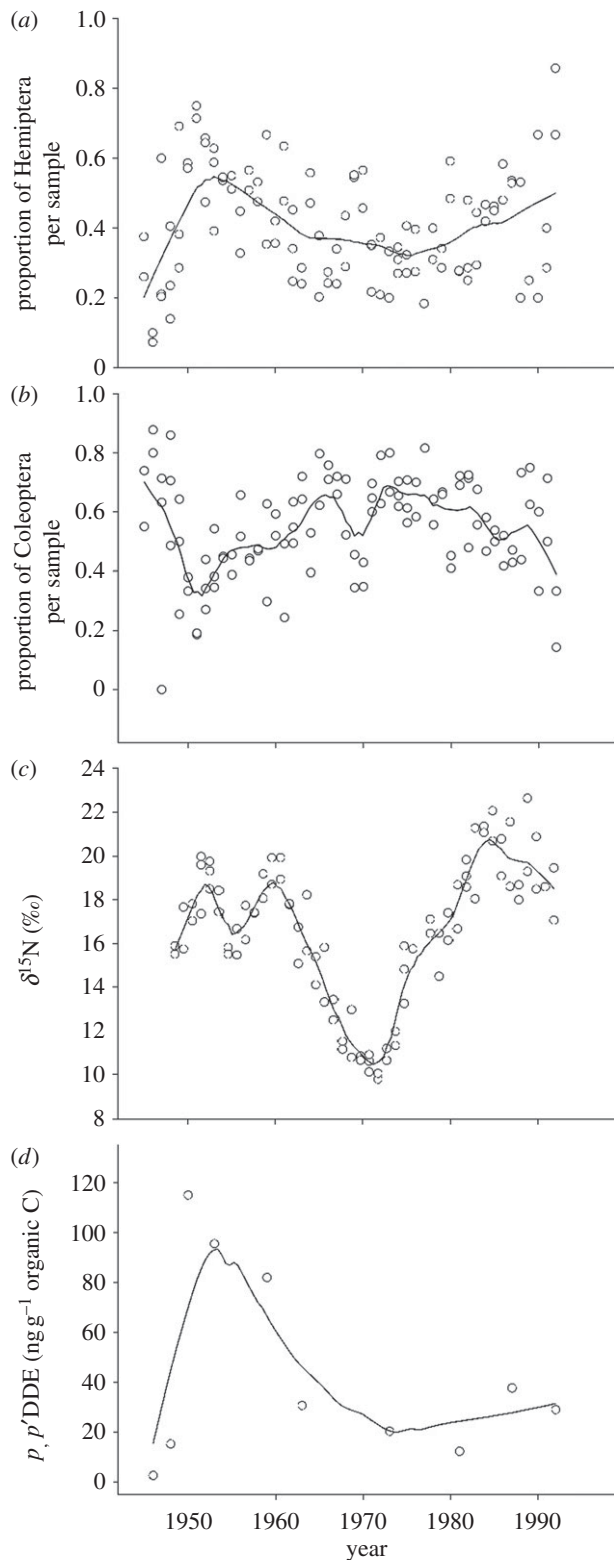
Figure 2. Four components of historical diet of chimney swifts (*Chaetura pelagica*). (*a*) Proportion of Hemiptera remains per sample; (*b*) proportion of Coleoptera remains per sample; (*c*) levels of $\delta^{15}N$; and (*d*) *p,p'*DDE from a chronostratified deposit of chimney swift guano in Ontario, Canada. For reference, the insecticidal properties of DDT were first discovered in 1939; it was in widespread use by 1945 and was banned in North America in 1973 [19]. Chronostratigraphy of guano was verified by analysis of ^{137}Cs content and known dates of chimney opening and closure. Trend lines are loess curves with a sampling proportion (span) of (*a*) 3.0 for, (*b*,*c*) 1.5 for and (*d*) 7.0 for; further details on curve fitting are provided in the electronic supplementary material.

decreased. This relationship is expected given that, in many systems, there are more predatory species among true bugs than there are among beetles [25,26]. The ratio of Coleoptera to Hemiptera is negatively correlated with an increase in metabolites of DDT, particularly DDE (figure 2*b–d*; $F_{1,8} = 4.04$, $p = 0.08$; $r = -0.58$), present in the insect remains. The predominance of DDE over other forms of DDT in this archive is not surprising because DDE is the stable metabolite of DDT and is also the predominant DDT metabolite found in local food webs [27,28]. See the electronic supplementary material for data on total DDT and minor component metabolites. A comparison of figure 2*a* with 2*d* reveals that the proportion of true bugs in the guano and DDE concentration have remarkably similar curves, including a slight increase from the late 1970s to the early 1990s. The proportion of beetles in the guano (figure 2*b*) showed the opposite pattern.

Stable isotope ratios of carbon ($\delta^{13}C$) in the guano strata showed no temporal trends (see the electronic supplementary material), indicating no systematic shifts in carbon source of the prey (e.g. terrestrial versus aquatic). Conversely, we note that the magnitude of the change in $\delta^{15}N$ is remarkably large and, although partly representative of diet composition differences, is unlikely to be solely attributable to such differences. Aside from three outliers in the topmost guano layers, $\delta^{15}N$ was strongly positively correlated ($F_{1,85} = 43.7$, $p = 3.2 \times 10^{-9}$, $r = 0.84$) with the C : N ratio (a measure of food quality [27]) throughout the deposit and thus negatively correlated with overall N concentrations ($F_{1,85} = 25.6$, $p = 1.8 \times 10^{-6}$, $r = -0.44$), indicating that $\delta^{15}N$ is subject to variation from post-depositional processing or differing sources of nitrogen.

4. DISCUSSION
Increased DDT use, beginning in the late 1940s (figure 2*d*), may have dramatically depressed beetle prey in the diet of swifts (figure 2*b*), as beetle populations are particularly subject to negative long-term population impacts from DDT [29–31]. This negative relationship is supported by beetle populations that inversely track DDE concentrations; the proportion of beetles in the guano rebounded in the decades after DDT use started to decline, and they declined slightly in the most recent decades coincident with a marginal increase in DDE concentrations. The reduction in prey availability of beetles may have thus caused swifts to consume a greater proportion of true bugs (figure 2*a*), which were less affected by DDT applications than beetles [32,33]. Although there might be alternative explanations for why many birds prefer to consume beetles over true bugs when given a choice [34–36], including that true bugs have greater chemical defences [37], such a shift in diet for swifts has energetic consequences because beetles can provide greater caloric value than true bugs [38].

True bugs exhibit resilience to DDT sprays [39,40] and they have also been observed to quickly rebound beyond pre-spray levels [41]. This pattern may result because some true bugs can develop resistance mutations within a few generations [42], quickly rendering populations impervious to pesticides such as DDT. Not surprisingly, some DDT was detected in guano samples as late as the 1990s (figure 2*d*), reflecting the strong environmental persistence

of the insecticide. Swift populations were thus experiencing residual exposure to DDT well after it was banned for agricultural use in most developed countries in the 1970s, perhaps partly owing to the fact that it was not banned until much later in several of the countries through which swifts migrate or in which they overwinter. It is difficult to determine whether the DDT burden we detected in the swift guano is indicative of local- or broad-scale exposure; the temporal patterns of DDT we observed in guano match those observed in sediments of nearby Lake Ontario [43] and global use estimates [44].

After DDT exposure reached its lowest point in the early 1970s, true bugs again began to constitute a greater part of the diet of chimney swifts (figure 2a), which paralleled a corresponding increase in $\delta^{15}N$ throughout the late 1970s and the 1980s (figure 2c), and a slight rise in DDE concentrations. Although this increase in $\delta^{15}N$ could be construed as a rise in trophic position, the correlations we observed between $\delta^{15}N$ (overall N concentration) and the C : N ratio suggest that $\delta^{15}N$ could also be responding to changes in nitrogen provenance or post-depositional processing such as ammonification or nitrate utilization, which has been observed in palaeolimnological studies tracking seabird populations [45,46]. Relationships between $\delta^{15}N$, overall N concentration and the C : N ratio have been quantified in some aquatic taxa [47], and may also be related to nutritional stress [48].

Despite the diminishment of DDT as a stressor relative to its peak in the 1950s, chimney swift populations have been declining at least since the Breeding Bird Survey was initiated in 1968 [15]. Their population declines are probably a product of the general decrease in relative abundance of Coleoptera from the early 1970s to 1992 (figure 2c), and multiple environmental stressors, ranging from climate change to habitat loss [49,50]. Although reduced populations should result in the benefit of greater resource availability per bird, this does not seem to be the case for chimney swifts as their population decline continued unabated. One possible explanation is that swifts may have regained their relative trophic position after DDT declined but their more recent diet is not composed of the same species or functional groups as their historical diet. Forensic genetic analyses would be required to determine this. Alternatively, the prey base may once again be representative of historical diet insofar as species presence/absence, but certain prey populations may not be as abundant as before. A final possibility is that swift populations were brought below a recovery threshold beyond which they could not rebound. If this were the case, then swifts may have regained their relative trophic position (figure 2c) after DDT declined only because their populations are so low as to not create any appreciable competitive interference.

Non-fossilized guano deposits, such as those considered here, represent an unprecedented dietary archive with untapped potential to provide valuable information on population dynamics on decadal scales or longer. Our examination of swift guano reveals an important link between the diet of an aerial insectivore, food quality and type, and anthropogenic pesticides (figure 2). Given that populations of many aerial insectivores are declining [6], the historical population declines in these species are very likely to be related to the types of dietary changes we observed here, having been induced by altered prey abundance and the

historical use of pesticides. The problem has become increasingly compounded by the recent reductions in availability of an insect prey as a result of climate-induced changes in the phenology of insect emergence, at numerous spatial scales and across taxa [50,51].

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