Environ Monit Assess (2015) 187:119
DOI 10.1007/s10661-015-4333-9

The effects of a remediated fly ash spill and weather conditions on reproductive success and offspring development in tree swallows

Michelle L. Beck · William A. Hopkins · Brian P. Jackson · Dana M. Hawley

Received: 12 August 2014 / Accepted: 26 January 2015

Abstract Animals are exposed to natural and anthropogenic stressors during reproduction that may individually or interactively influence reproductive success and offspring development. We examined the effects of weather conditions, exposure to element contamination from a recently remediated fly ash spill, and the interaction between these factors on reproductive success and growth of tree swallows (*Tachycineta bicolor*) across nine colonies. Females breeding in colonies impacted by the spill transferred greater concentrations of mercury (Hg), selenium (Se), strontium, and thallium to their eggs than females in reference colonies. Parental provisioning of emerging aquatic insects resulted in greater blood Se concentrations in nestlings in impacted colonies compared to reference colonies, and these concentrations remained stable across 2 years. Egg and blood element concentrations were unrelated to reproductive success or nestling condition. Greater rainfall and higher ambient temperatures during incubation were later associated with longer wing lengths in nestlings, particularly in 2011. Higher ambient temperatures and greater Se exposure posthatch were associated with longer wing lengths in 2011 while in 2012, blood Se concentrations were positively related to wing length irrespective of temperature. We found that unseasonably cold weather was associated with reduced hatching and fledging success among all colonies, but there was no interactive effect between element exposure and inclement weather. Given that blood Se concentrations in some nestlings exceeded the lower threshold of concern, and concentrations of Se in blood and Hg in eggs are not yet declining, future studies should continue to monitor exposure and effects on insectivorous wildlife in the area.

Keywords Element · Interactive effects · Nestling growth · Reproductive success · Tree swallow · Weather

Electronic supplementary material The online version of this article (doi:10.1007/s10661-015-4333-9) contains supplementary material, which is available to authorized users.

M. L. Beck (✉) · W. A. Hopkins
Department of Fish and Wildlife Conservation, Virginia Tech, 106 Cheatham Hall, Blacksburg, VA 24061-0321, USA
e-mail: beckmic@vt.edu

B. P. Jackson
Department of Earth Sciences, Dartmouth College, 6105 Fairchild Hall, Hanover, NH 03755, USA

D. M. Hawley
Department of Biology, Virginia Tech, 2125 Derring Hall, Blacksburg, VA 24061-0406, USA

Introduction

Animals are exposed to a variety of natural and anthropogenic stressors that can affect the number and/or quality of offspring that they produce. Natural stressors include variation in biotic and abiotic factors such as food availability (Zanette et al. 2006; Brown and Shine 2007), exposure to parasites (Brown and Brown 1986; Gooderham and Schulte-Hostedde 2011), and weather conditions (Pipoly et al. 2013; McDonald et al. 2004). Anthropogenic stressors include exposure to

Published online: 18 February 2015

contaminants (Savage et al. 2002; Berglund et al. 2010), habitat loss and fragmentation (Nystrom et al. 2007; Hinam and Clair 2008), and global climate change (Salafsky et al. 2008; Cunningham et al. 2013; Plard et al. 2014). These sources of stress may interact to further affect health and reproduction in the wild (Fischer et al. 2013; Holmstrup et al. 2010; Barrett et al. 2013). Of particular concern is the interaction between global climate change and contaminants (reviewed in Moe et al. 2013; Hooper et al. 2013; Noyes et al. 2009). Climate change will directly influence physiology and behavior due to increased frequency and intensity of droughts, storms, and other extreme weather events (IPCC 2013). Environmental changes associated with climate change may in some cases increase the availability of contaminants (Gouin et al. 2013), alter degradation rates (Noyes et al. 2009), increase contaminant toxicity (Holmstrup et al. 2010), or simply subject wildlife to the cumulative insults of both anthropogenic changes. These interactive effects could be especially important for developing young who may be more sensitive to stressful conditions than adults. Thus, it is important to determine how weather conditions may interact with contaminant exposure to affect wild populations so that these interactions can be considered in future risk assessment frameworks (Hooper et al. 2013).

Avian species are excellent models for addressing the individual and interactive effects of contaminant exposure and climatic conditions on reproduction because they are frequently used in studies of the effects of contaminants or climate change on reproductive biology (Saether et al. 2004; Møller 2013; Custer 2011). Only a few studies have addressed the combined effects of contaminant exposure and weather conditions on avian reproduction, and these studies indicated that natural variation in weather conditions may intensify or mask the effects of contaminant exposure on reproduction. For instance, unfavorable environmental conditions, such as periods of intense cold, drought, or high temperatures, may increase the effect of contaminant exposure on reproduction (Eeva and Lehikninen 1995; Gentes et al. 2006; Hallinger and Cristol 2011; Hill et al. 2008; Brasso and Cristol 2008). Alternatively, unfavorable weather conditions may mask the effects of contaminants by reducing reproductive success equally in reference and contaminated areas (Custer et al. 2003). Further research is needed on a greater array of pollutants and ecological contexts to determine how weather, and potentially climate change, may interact with contaminant exposure to affect avian reproductive success.

Inorganic contaminants, such as metals and metalloids (hereafter collectively referred to as elements), are globally widespread contaminants and have diverse effects on reproduction in birds and other taxa. Maternal exposure to elements such as arsenic (As), cadmium (Cd), and selenium (Se), can reduce egg size in European songbirds (Nyholm and Myhrberg 1977; Eeva and Lehikninen 1995). Some elements can be maternally transferred to eggs, exposing developing young to element contamination (Bryan et al. 2003; Harding 2008; Weech et al. 2012; Brasso et al. 2010). Maternally transferred Se and mercury (Hg) can reduce hatching success and cause severe developmental malformations (Ohlendorf 2011; Heinz and Hoffman 2003; Burger and Gochfield 1997; Heinz et al. 2011). Growth abnormalities, such as malformed tarsi or wings, are associated with exposure to As, copper (Cu), nickel (Ni), Se, lead (Pb), and zinc (Zn) (Eeva and Lehikninen 1996; Janssens et al. 2003; Ohlendorf and Heinz 2011). Maternally transferred elements and/or dietary exposure posthatch can reduce fledging success (Eeva et al. 2009), and nestlings raised in contaminated areas may exhibit reduced growth or poor body condition which reduces their likelihood of survival after fledging (Janssens et al. 2003; Eeva and Lehikninen 1996; Eeva et al. 2009). The relative importance of maternally transferred elements and dietary exposure posthatch are not well understood in birds, particularly if maternally transferred elements continue to influence aspects of development posthatch. However, in some amphibians and reptiles, maternally transferred elements can negatively influence offspring body mass and reduce offspring survival postparturition (Hopkins et al. 2006; Bergeron et al. 2011). Thus, it is important to determine if exposure prehatch and posthatch, coupled with weather conditions throughout development, influence reproductive success or offspring phenotype.

The coal fly ash spill in Kingston, TN, provided an opportunity to examine the combined consequences of element exposure and weather conditions on avian reproduction and offspring development. In December 2008, a coal fly ash impoundment wall at the Tennessee Valley Authority fossil plant ruptured releasing 4.13 million m^3 of coal fly ash slurry into the Emory River, part of which subsequently flowed into the Clinch and Tennessee Rivers (TVA 2009). Fly ash contains elevated concentrations of a complex mixture of elements (Table 1) including

Table 1 Geometric means and 95 % confidence intervals for egg element concentrations among tree swallow colonies μg/g dry weight

Element	R1	R2	R3	MD	SS	D1	D2	D3	D4
Ba 2011	4.51^{a} (3.53–9.35)	4.38^{a} (4.08–6.26)	3.41^{a} (2.85–5.47)	5.98^{a} (5.67–7.81)	4.64^{a} (4.82–7.47)	5.70^{a} (3.93–9.36)	4.03^{a} (3.75–5.71)	4.39^{a} (3.98–6.06)	3.87^{a} (3.05–5.92)
Ba 2012	5.94^{ab} (5.48–11.26)	6.16^{ab} (6.06–9.52)	6.23^{ab} (6.48–9.99)	6.88^{b} (7.00–9.87)	4.09^{a} (4.27–6.06)	5.91^{ab} (5.48–8.03)	5.24^{ab} (4.97–7.69)	4.46^{ab} (4.41–6.25)	7.01^{b} (6.91–11.38)
Cu 2011	2.07 (1.97–2.19)	2.32 (2.21–2.49)	2.12 (1.93–2.44)	2.27 (2.17–2.44)	2.11 (2.05–2.23)	2.02 (1.82–2.29)	2.05 (1.94–2.23)	2.07 (1.98–2.20)	2.17 (1.97–2.43)
Cu 2012	1.82 (1.71–2.01)	1.85 (1.77–1.98)	1.92 (1.85–2.08)	1.84 (1.79–1.94)	1.94 (1.88–2.09)	1.93 (1.83–2.09)	1.80 (1.72–1.93)	1.90 (1.83–2.04)	2.11 (1.98–2.35)
Fe 2011	98.0^{ab} (91.8–107.8)	113.9^{b} (107.6–123.9)	89.5^{a} (82.8–100.3)	103.8^{ab} (99.7–110.6)	103.8^{ab} (100.8–111.0)	111.7^{ab} (101.0–125.4)	102.3^{ab} (97.5–109.3)	98.3^{ab} (91.2–109.8)	101.4^{ab} (93.2–111.7)
Fe 2012	87.5^{ab} (82.9–97.5)	90.7^{ab} (86.7–98.6)	83.3^{a} (80.2–90.7)	91.7^{ab} (89.0–102.1)	102.1^{bc} (99.0–109.6)	91.3^{ab} (85.6–103.8)	85.1^{a} (80.7–93.6)	84.3^{a} (80.6–92.3)	83.4^{a} (79.1–95.6)
Mn 2011	3.46^{a} (3.15–4.19)	4.55^{abc} (4.15–5.46)	4.69^{abc} (4.28–5.40)	5.18^{c} (4.88–6.13)	4.10^{ab} (3.97–4.55)	5.28^{bc} (4.49–6.42)	4.61^{abc} (4.23–5.48)	4.28^{abc} (3.96–5.40)	4.25^{abc} (3.58–5.42)
Mn 2012	3.59^{a} (3.32–4.12)	4.06^{ab} (3.84–4.71)	3.96^{ab} (3.76–4.62)	3.64^{a} (3.52–4.17)	4.30^{ab} (4.19–4.98)	5.12^{b} (4.78–5.84)	4.36^{ab} (3.98–5.38)	4.43^{ab} (4.18–5.23)	3.59^{a} (3.34–4.34)
Hg 2011	0.08^{a} (0.076–0.111)	0.10^{a} (0.095–0.134)	0.10^{a} (0.090–0.113)	0.15^{bc} (0.138–0.180)	0.23^{d} (0.229–0.265)	0.16^{bc} (0.142–0.174)	0.15^{bc} (0.131–0.184)	0.19^{cd} (0.178–0.224)	0.13^{ab} (0.110–0.147)
Hg 2012	0.08^{c} (0.071–0.098)	0.12^{ae} (0.114–0.132)	0.12^{a} (0.114–0.130)	0.17^{b} (0.164–0.183)	0.30^{d} (0.289–0.344)	0.21^{b} (0.190–0.246)	0.19^{b} (0.178–0.210)	0.20^{b} (0.187–0.225)	0.15^{be} (0.144–0.167)
Se 2011	2.35^{a} (2.20–2.58)	2.54^{abf} (2.42–2.71)	2.37^{ab} (2.24–2.54)	2.75^{bc} (2.65–2.93)	3.41^{d} (3.31–3.59)	3.12^{cdf} (2.83–3.49)	2.79^{bc} (2.65–2.99)	2.58^{abc} (2.45–2.78)	2.76^{abc} (2.54–3.04)
Se 2012	2.10^{ac} (2.01–2.23)	2.11^{ac} (2.03–2.25)	1.99^{c} (1.92–2.14)	2.29^{ab} (2.22–2.43)	2.92^{d} (2.81–3.18)	2.52^{bd} (2.42–2.67)	2.46^{ab} (2.31–2.71)	2.33^{ab} (2.23–2.50)	1.97^{c} (1.90–2.07)
Sr 2011	3.31^{a} (2.97–4.02)	3.02^{a} (2.82–3.35)	2.82^{a} (2.57–3.24)	3.15^{a} (2.93–3.65)	5.47^{c} (5.28–6.17)	5.12^{bc} (4.19–6.83)	3.58^{a} (3.22–4.44)	3.67^{b} (3.44–4.10)	3.56^{ab} (3.10–4.23)
Sr 2012	2.81^{ab} (2.62–3.19)	2.72^{a} (2.57–3.08)	2.96^{ab} (2.73–3.64)	2.77^{a} (2.68–3.05)	3.39^{b} (3.29–3.75)	2.78^{ab} (2.58–3.14)	2.80^{ab} (2.59–3.20)	2.55^{a} (2.42–2.89)	2.67^{a} (2.53–2.95)
Tl 2011	0.01^{a} (0.010–0.013)	0.02^{adf} (0.014–0.019)	0.01^{ae} (0.0098–0.0125)	0.02^{adef} (0.015–0.018)	0.05^{c} (0.047–0.055)	0.02^{bf} (0.019–0.027)	0.03^{b} (0.002–0.030)	0.02^{bdf} (0.018–0.025)	0.02^{bf} (0.020–0.030)
Tl 2012	0.01^{af} (0.010–0.015)	0.01^{a} (0.011–0.014)	0.01^{e} (0.007–0.009)	0.02^{adf} (0.014–0.017)	0.03^{c} (0.030–0.035)	0.02^{bf} (0.014–0.018)	0.02^{bd} (0.017–0.024)	0.02^{bd} (0.015–0.020)	0.02^{ab} (0.014–0.018)
Zn 2011	67.0 (64.2–70.8)	65.5 (62.6–69.5)	64.4 (61.2–68.8)	65.5 (63.1–69.3)	62.9 (61.2–66.0)	67.3 (62.9–72.6)	64.6 (60.9–70.9)	64.1 (61.0–68.8)	67.7 (61.8–75.2)
Zn 2012	69.7 (66.2–75.4)	64.7 (62.6–67.9)	60.1 (58.1–63.8)	65.1 (63.3–68.4)	62.9 (61.3–66.2)	64.6 (61.0–70.6)	61.0 (58.1–65.7)	62.1 (59.9–65.4)	62.3 (60.2–65.3)

Table 1 (continued)

Element	R1	R2	R3	MD	SS	D1	D2	D3	D4
N^a 2011	25	27	21	37	56	12	29	28	12
N^a 2012	25	39	42	56	61	23	29	32	31

Concentrations of As, Cd, Cr, and V were also quantified but were below the detection limit in over half of the samples from all of the colonies in both years and were not considered further. Colonies that share the same superscript did not differ significantly from each other in that year of the study for that element while colonies that do not share a letter differ significantly from each other at $p \leq 0.05$. Concentrations of Cu and Zn did not differ significantly among colonies

[a] Sample size

many that are associated with reproductive impairment in birds (Rowe et al. 2002; NRC 2006; Ohlendorf 2011). In the 2.5 years between the spill and initiation of our study, most of the fly ash was removed from the river, but approximately 400,000 m^3 remained in the system (TVA 2011b). Thus, birds and other wildlife may be exposed to residual concentrations of some elements, particularly As, Se, and Tl, which are elevated above normal background levels (Beck et al. 2014), but in most cases below those typically associated with adverse reproductive effects (reviewed in Ohlendorf and Heinz 2011; Shore et al. 2011). Because element exposure is relatively modest following remediation of the site but will likely remain above background for the near future, it is important to determine if variation in other environmental conditions, such as unfavorable weather, could exacerbate their effects.

In this study, we examined the effects of exposure to modestly elevated concentrations of elements, local weather conditions, and their interaction on offspring growth, and measures of reproductive success in tree swallows (*Tachycineta bicolor*). We first determined if tree swallows were exposed to elevated concentrations of elements near the fly ash spill site and if those elements were maternally and trophically transferred to offspring during egg production and nestling provisioning, respectively. We then determined if element exposure, temperature, rainfall, and female age influenced reproductive parameters. We predicted that exposure to modestly elevated element concentrations, low temperatures, and heavy rainfall would be associated with reduced hatching and fledging success and offspring growth. We further predicted that under poor weather conditions (low temperatures and heavy rain), we would detect greater reductions in reproductive success in swallows exposed to higher concentrations of elements (i.e., additive effects) compared to optimal conditions (mild weather and no impact from the spill).

Methods

Study species

Tree swallows are extensively used in ecotoxicology studies because they are secondary cavity nesters (Robertson et al. 2011), and both sexes typically forage within 300–500 m of their box during the breeding season (Dunn and Hannon 1992; Quinney and Ankney

1985). Thus, strategic placement of nest boxes in contaminated and reference areas ensures that swallows are exposed to local contaminants through the diet (Beck et al. 2013). They are aerial insectivores and feed extensively on emerging aquatic insects in riparian areas (Custer et al. 2010; Custer 2011; Beck et al. 2013). Maternal transfer and dietary exposure to low concentrations of a number of elements including Cu, iron (Fe), Hg, Se, and Zn did not affect hatching success or nestling survival in tree swallows (Custer et al. 2006, 2008). However, exposure to elevated concentrations of Hg, particularly coupled with hot or dry weather, can reduce fledging success (Brasso and Cristol 2008; Hallinger and Cristol 2011).

Temperature has strong effects on fledging success in tree swallows. Cold temperatures and rainfall reduce the availability of flying insects, leading to reduced foraging success during a time of high energetic demands for adults and developing young (Winkler et al. 2013; Nooker et al. 2005). Cold temperatures and rainfall are associated with reduced growth, poor body condition, and short wing lengths (McCarty and Winkler 1999; Nooker et al. 2005; Dawson 2008), and cold temperatures can lead to pronounced reductions in fledging success in comparison to warmer weather (Winkler et al. 2013).

Field methods

We studied tree swallows in Roane (35.9° N, 84.5° W) and Loudon (35.8° N, 84.3° W) Counties, TN, USA, from March to July 2011 and 2012. Our study site encompassed an element contamination gradient that ranged from background exposure at reference colonies to modestly elevated exposure near the site of the ash spill and in areas where ash was not removed during remediation efforts (Fig. 1). We placed nest boxes in two colonies along the Emory River (spill site (SS) and downstream 1 (D1)), two colonies along the Clinch River (downstream 2 (D2) and downstream 3 (D3)), and one colony downstream on the Tennessee River (downstream 4 (D4)). We had three reference colonies, two located approximately 30.5 km east of Kingston at Ft. Loudoun Dam (reference 1, R1) and at Tellico Dam (reference 2, R2). Reference 3 (R3) was located upstream on the Tennessee River from the confluence with the Clinch River, at Long Island. We also placed boxes at Melton Hill Dam (MD) on the Clinch River which served a role analogous to a positive control because preliminary data gathered prior to this study indicated that tree swallows are exposed to ash-related elements such as Se at this colony (ARCADIS 2011). The source(s) of this contamination is unclear but could include the Bull Run Fossil Plant (TVA 2011a; Stantec 2009), a former coal ash storage pond associated with the Y-12 Security Complex (Cook et al. 1999), and/or other nonpoint sources (USDA 2009).

We placed or maintained nest boxes in each area in late February or early March, when tree swallows were arriving and prospecting for nest sites. All of the boxes were located within 70 m of the shore to facilitate foraging on emerging aquatic insects. We spaced nest boxes 15 m apart when in a single row, or 20 m apart with a staggered alignment when there were two or more rows. We checked nest boxes every 4 days beginning in late March for signs of nesting activity so that we could accurately record clutch initiation dates. We recorded the final clutch size, number of eggs that hatched, and the number of young that survived to day 17.

We captured adults using mist nets or trapped them in the nest box while incubating or provisioning young. Adults were sexed by the presence of a brood patch (females) or cloacal protuberance (males) or, if these were absent, by measuring the wing length, with wings shorter than 113 mm being indicative of females and wings longer than 122 mm being indicative of males (Stutchbury and Robertson 1987). Females were aged as second year (SY) or after second year (ASY) based on plumage coloration; SY females were primarily brown and ASY females were iridescent blue. Adults were banded with a combination of one metal band and one colored leg band placed on opposite legs to help us distinguish individuals breeding in neighboring boxes and between males and females. We obtained small ($\leq$120 μL) blood samples from all adults by puncturing the brachial vein after cleansing the area with 90 % ethanol. Whole blood was frozen at −20 °C for element analysis (see below). From each adult, we measured left and right tarsus length (each tarsus was measured twice), wing chord, and body mass. When nestlings were 13 days old, we obtained morphological measurements and a blood sample (as described for adults) and banded them with a metal leg band. All bird banding was conducted under US Geological Survey Bird Banding Lab permit 23513 and approved by the Virginia Tech IACUC committee under protocol 11-043-FIW and 12-072-FIW.

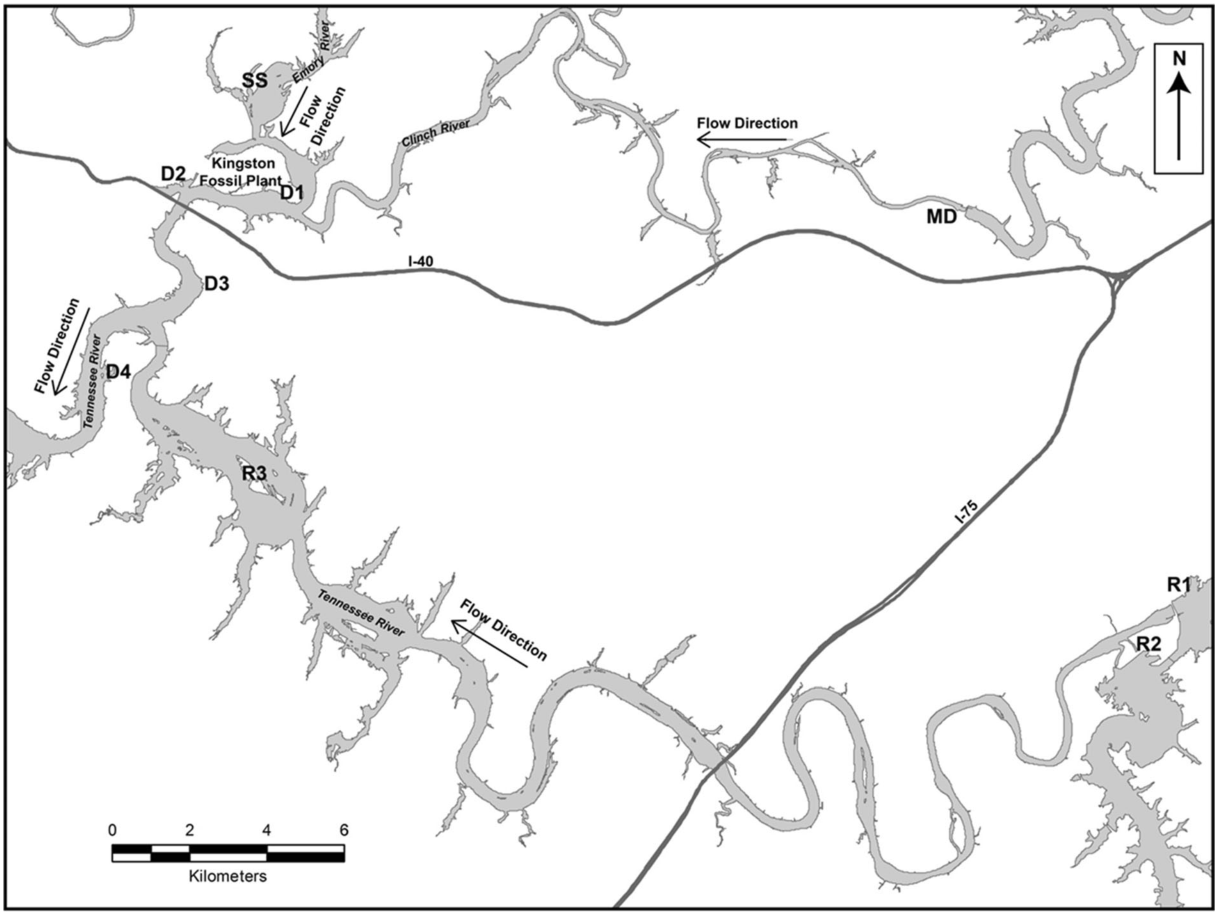


Fig. 1 Tree swallow colonies located near Kingston, TN. The study area consisted of two highly impacted colonies located on the Emory River. One was located at the site of the spill (spill site, SS, N=94) and the second at the confluence of the Clinch and Emory River (downstream 1, D1, N=31). Moderately impacted colonies were located on the Clinch River at downstream 2 (D2, N=31) and downstream 3 (D3, N=43) and a low impacted colony was located downstream on the Tennessee River (D4, N=51). We used three reference colonies; two were located near Lenoir City, TN 30.5 km east of Kingston. Reference 1 (R1, N=46) was located at Ft. Loudoun Dam on the Tennessee River and reference 2 (R2, N=53) at Tellico Dam on the Little Tennessee River. Reference 3 was located on Long Island (R3, N=53) on the Tennessee River upstream from the confluence with the Clinch River. We also placed boxes at Melton Hill Dam (MD, N=68) on the Clinch River which served a role analogous to a positive control

Weather conditions

We obtained meteorological data from two small weather stations located near the SS on the Emory River and near MD on the Clinch River (Fig. 2). We used weather data from the Emory River station for the colonies SS, D1-D4, and R3 and used the Clinch River data for MD, R1, and R2. Because cold temperatures and rainfall can reduce the availability of flying insects (McCarty 2001; Winkler et al. 2013), we calculated the average ambient temperature and total rainfall for each nest over four stages of breeding: 5 days prior to clutch initiation (prelaying), laying through the end of incubation (laying plus incubation), from hatch to nestling age 13 (for nestling growth variables measured at day 13), and from hatch to nestling age 17 (for fledging success, evaluated as survival to day 17).

We also examined the effects of unseasonably cold and challenging weather conditions along with element exposure on hatching and fledging success. Maximum daily temperatures below 18.5 °C reduce the availability of flying insects and three or more consecutive days with highs below this temperature reduces fledging success in tree swallows (Winkler et al. 2013). We used these criteria to identify periods of challenging weather at our study site (Supplementary Table 1). We identified two periods in 2011 and three in 2012 where temperatures met these requirements; however, only in 2011

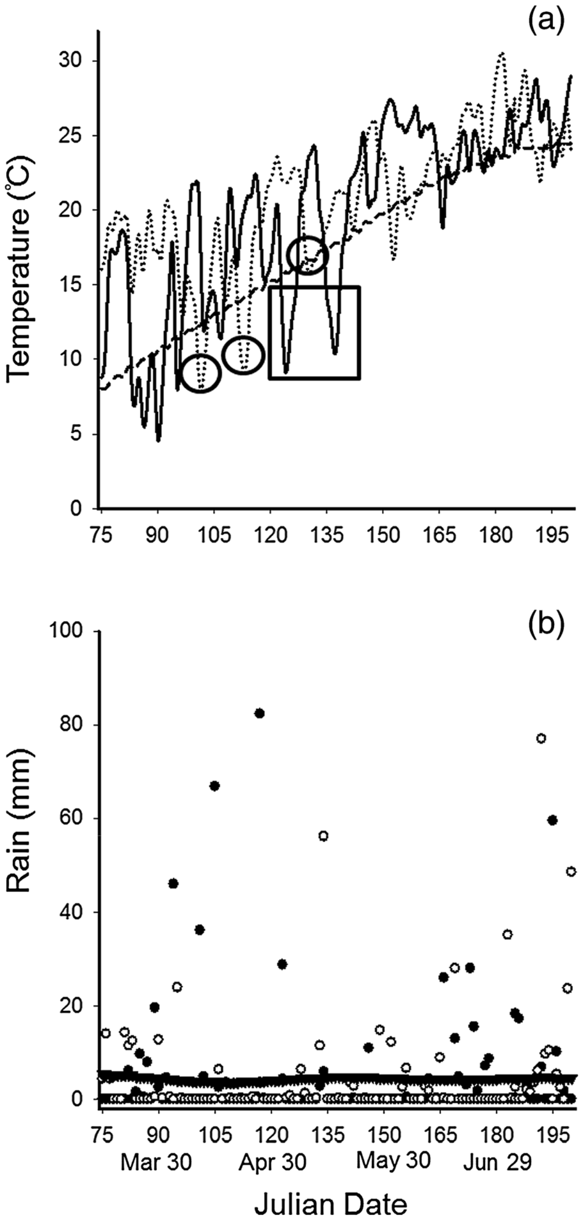


Fig. 2 Average daily temperature (**a**) and total rainfall (**b**) from March 1st through July 18th in Kingston, TN. We present weather data collected at the SS for both years because weather data from the two stations were quite similar. Temperature (**a**) *solid line* 2011, *dotted line* 2012, *dashed line* 30-year average. In **a**, the *black square* indicates the two cold periods that occurred in 2011 and the *three circles* indicate the cold periods that occurred in 2012. Total rainfall (**b**) *solid circle* 2011, *open circle* 2012, *filled triangle* 30-year average

were conditions unseasonably cold based on 30-year average temperatures at Kingston, TN (Supplementary Table 1). The 30-year average high temperature in Kingston, TN, from May 3rd to 7th is approximately 24.0 °C, and from May 12th to May 19th, it is approximately 26.7 °C. From May 3rd to 7th in 2011, the average high temperature dropped to 19.6 °C, and from May 15th to 19th, the average high temperature was only 13.3 °C. Because nests that contained nestlings during the May 15th–19th cold period in 2011 also experienced cold conditions during incubation from May 3rd to 7th, we treated these as a single event and primarily used May 15th–19th nest conditions to categorize nest fates. We categorized nests as affected or unaffected by the unseasonably cold weather at the egg or nestling stage. Nests were considered affected at the nestling stage if the box contained young hatched on or before May 15th (no young were present May 3rd–7th) and one or more nestling(s) were subsequently found dead in the box from May 15th to May 20th. We also considered nests affected during the egg stage if ≥50 % of the eggs failed to hatch in clutches scheduled to hatch May 7th–May 23rd. Nests were considered unaffected by the cold period if all of the nestlings present in the brood on May 15th survived through to May 20th or if more than half of the clutch hatched.

Maternal transfer of elements

We assessed maternal transfer of elements to eggs by randomly collecting a single egg from each clutch within 2 days of clutch completion. Eggs were placed in plastic bags, labeled with a unique sample id, and protected in plastic containers lined with bubble wrap. Samples were placed in a cooler until transported back to the lab, where eggs were weighed to the nearest 0.001 g. Eggs were frozen and stored at −20 °C until being prepared for element analysis.

Sample preparation and element analysis

Egg samples were prepared for element analysis at Virginia Tech. Eggs were slightly thawed, and a single incision was made in the shell, and all shell fragments were removed. The still frozen yolk and albumin were transferred to a 5-mL plastic container and weighed to the nearest 0.1 mg. Frozen egg contents were dried to asymptotic mass in a freeze dryer. After drying, egg contents were homogenized by stirring vigorously with a Teflon spatula that was cleaned between samples with metal-free detergent (Citranox®) and Millipore water and dried with a Kim Wipe. We transferred 50–100 mg of homogenized egg to a preweighed Eppendorf tube, and samples were stored in a desiccator until being shipped for element analysis. Blood samples required no preparation.

Samples were shipped overnight on dry ice to the Trace Element Analysis Core at Dartmouth College. Concentrations of elements present in blood and egg samples were quantified using inductively coupled plasma mass spectrometry (ICP-MS). Concentrations of As, barium (Ba), Cd, chromium (Cr), Cu, Fe, manganese (Mn), Hg, Se, strontium (Sr), thallium (Tl), vanadium (V), and Zn were quantified for each sample. Samples were digested by open vessel digestion with 0.5-mL 9:1 HNO_3/HCl (Optima, Fisher Scientific, St Louis MO) using microwave heating at 105 °C for 45 min. After cooling, 0.1 mL H_2O_2 was added to the samples, and they were taken through a second heating step. The samples were then diluted to 10 mL with deionized water. The digested samples were analyzed for element concentrations by collision cell ICP-MS (7700x, Agilent, Santa Clara, CA). Concentrations of As, Ba, Cd, Cr, Cu, Fe, Mn, Sr, Tl, V, and Zn, (He collision mode), Se (reaction mode), and Hg (normal mode) were quantified in each sample. Digestion quality control measures included digestion blanks, fortified blanks, and reference materials (NIST 2976, mussel tissue) at a frequency of 1 each per 20 samples. For eggs, digestion and analytical sample duplicates and spikes were performed at a frequency of 1 each per 20 samples, but there was insufficient blood to allow for digestion of duplicates or spikes. Additional quality control consisted of reporting limit checks, interference checks, and initial and continuing calibration checks and blanks.

Detection limits for each sample varied because the mass of each sample used in the analysis varied (Supplementary Table 2). If the element concentration was below the detection limit, we assigned that sample a concentration of half of the detection limit for statistical comparisons. Arsenic, Cd, Cr, and V concentrations in eggs and As, Cd, Cr, Hg, Tl, and V concentrations in blood samples were below the detection limit in over half of the samples from each colony and were not considered further. Average relative % difference between duplicates for eight elements over five analyses was 12±2 %. Average % recovery for 13 elements in spiked samples over five analyses was 97±21 %. For egg digestion duplicates, average relative % difference between duplicates for 9 elements over 24 analyses was 14±4 %. Average % recovery for eight elements in matrix spiked samples over 17 analyses was 108±13 %. Average % recovery for Mn, Fe, Cu, Zn, As, Se, Sr, Cd, and Hg was 100±13 % for five separate digestions of NIST 2976, but Cr recovery averaged 48 %, presumably because the Cr was in a form that is not solubilized by the open vessel acid digestion used here. Other elements were not certified in the NIST standard.

Data analysis

We were specifically interested in the effects of elements associated with the fly ash spill on tree swallow reproduction. Therefore, we included elements that were found in significantly higher concentrations at the SS compared to the three reference colonies in at least 1 year of the study in our analyses of reproductive effects. To determine this, we used separate MANOVAs to compare log-transformed egg and blood element concentrations among colonies followed by univariate ANOVAs and Tukey post hoc tests to determine if the SS had significantly elevated element concentrations. When multiple elements were associated with the spill, we performed principal components analysis (PCA) on log-transformed element concentrations to capture relative variation in element concentrations while reducing the dimensionality of the data set. This approach was necessary because of issues with multicollinearity among elements associated with fly ash that prohibited the inclusion of multiple elements in statistical models. Retaining the elements in mixtures in the analyses is preferred because it reduces the number of statistical comparisons, and many elements have interactions among them (Garcia-Barrera et al. 2012; Zwolak and Zaporowska 2012; Marmiroli and Maestri 2008). After running the PCA, we compared PC scores among colonies using an ANOVA to determine if exposure to the mixture of elements changed between years and among colonies.

Preliminary analyses indicated that clutch initiation date was highly, positively correlated with average temperature throughout the nesting cycle (both $r^2 \geq 0.46$, $df=578$, both $p \leq 0.001$). This confounding relationship prevented us from including clutch initiation date in models because our focus was on the effects of ambient temperature and element exposure on reproductive parameters and nestling development. Because prior work indicated that young females lay smaller clutches and have reduced hatching and fledging success early in the season compared to ASY females (Stutchbury and Robertson 1988), we included female age (second year or after second year) in all models. To determine how element exposure and weather conditions affected reproductive parameters, we used generalized linear models with appropriate error distributions and link functions. We evaluated the fit of each model using Akaike's information criteria (AIC) adjusted for small sample sizes (AICc) (Akaike 1973). Models included year, female age, weather conditions relevant for the reproductive stage, element PC scores or concentrations, and interactions between weather conditions and element exposure. First, we examined the effects of prelaying (5 days prior to clutch initiation) weather conditions and the other independent variables on clutch initiation date, clutch size, and egg mass. We included clutch size as a covariate in models examining egg mass because we detected a significant positive relationship between these two variables in preliminary analyses ($r^2=0.13$, $df=584$, $p<0.001$). To avoid pseudoreplication, we only evaluated the mass of a single egg in each clutch (the one we collected for element analysis). We calculated hatching success as the proportion of eggs that hatched in the nest after accounting for the single egg removed for element analysis. Hatching success models included weather conditions from the prelaying period through the day nestlings hatched. For analyses of nestling growth, we randomly selected a single nestling from each clutch to avoid issues with pseudoreplication and quantified blood element concentrations for that individual. To determine if maternally transferred elements had longer-term effects on offspring development, we ran models that included egg elements, prehatch weather conditions, and the other independent variables on nestling wing length, residual mass, and reproductive success. We calculated reproductive success as the number of young present at day 17 out of the number of eggs laid after adjusting for our collection of a fresh egg because this analysis focused on the influence of conditions from laying to fledging on the number of young produced. For evaluating conditions during the nestling period only, we used weather conditions from the day the first egg hatched through day 13 for wing length and residual mass models and used weather conditions from hatch to day 17 in fledging success models. In these models, we calculated fledging success as the proportion of young present in the nest at day 17 out of the number of young that hatched because we were solely focused on the influence of environmental conditions posthatch. We used the residuals from the regression of nestling body mass on average tarsus length as a measure of residual body mass (mass controlling for structural size). While the use of residuals as a measure of body condition is controversial (Green 2001), studies have shown that residuals do correlate well with lipid reserves (Ardia 2005; Schulte-Hostedde et al. 2005) and thus can be representative of body condition. The number of young present in the nest box was unrelated to wing length and residual body mass (both $p \geq 0.74$) and thus was not included in our models. In cases where independent variables during incubation and the nestling stage influenced the same dependent variable, we used partial correlations to try to tease apart the relative influence of prehatch and posthatch conditions on offspring. To focus on the unseasonably cold weather in 2011, we used a likelihood ratio test to determine if the number of nests affected by challenging weather differed among colonies.

We calculated the Akaike weight for each generalized linear model and summed these from largest to smallest to identify the 90 % confidence set of models (Burnham and Anderson 2002). The 90 % confidence set should include all of the models that have some meaningful support and permits the calculation of model averaged parameter estimates and standard errors (Burnham and Anderson 2002; Anderson 2008). Parameter estimates indicate the extent and direction of change in the dependent variable given a one unit change in that parameter while all other parameters are held constant (Liao 1994). We also calculated parameter weights for each term that appeared in the 90 % confidence set by summing the model weights for all of the models in the 90 % confidence set that included that term. Parameter weights above 0.70 indicate a relatively strong relationship with the dependent variable. Further, the occurrence of model terms in a greater number of models in the 90 % confidence set is indicative of their relative explanatory power (Burnham and Anderson 2002). Sample sizes differed between egg and nestling analyses because of predation, nest abandonment, and incomplete sampling of eggs or young. All statistical tests were two-tailed and alpha=0.05. All analyses were performed with PASW 18 (Predictive Analytics Software version 18).

Results

Egg element concentrations and PCA among colonies

We quantified egg element concentrations in a single egg from 247 nests in 2011 and 338 nests in 2012 for a total of 585 nests. We detected significantly elevated concentrations of Hg, Se, Sr, and Tl in eggs from the SS compared to all three reference colonies in at least 1 year of the study (Table 1). Post hoc tests revealed that Hg, Se, and Tl concentrations were elevated at the SS above concentrations found at reference colonies in both years (all $p<0.001$), while Sr concentrations declined in the second year to concentrations that did not differ significantly from those at two of the reference colonies (both $p\geq0.23$, Table 1). Within the SS, concentrations of Se, Sr, and Tl all declined significantly between years (all $p \leq 0.001$) while egg Hg concentrations increased significantly between years ($p=0.001$). Egg concentrations of Ba, Cu, Fe, Mn, and Zn were not significantly different between the SS and the three reference colonies and were not considered further (Table 1). We included Hg, Se, Sr, and Tl concentrations in a PCA that produced a single principal component that explained a total of 56.0 % of the variance in egg element concentrations and received strong, positive loadings for all four elements (Supplementary Table 3). When we compared PC scores among colonies, we found that year ($F_{(1,\ 567)}=129.9$, $p<0.001$) and colony ($F_{(8,\ 567)}=159.0$, $p<0.001$) significantly influenced PC scores, and the interaction between year and colony was nearly significant (Fig. 3, $F_{(8,\ 567)}=1.89$, $p=0.06$). At the SS in 2011, Egg_{PC} scores were significantly greater than at any other colony and in either year of the study (all $p\leq0.001$). Egg_{PC} scores declined significantly at the SS between 2011 and 2012 ($p<0.001$), but in 2012, the SS continued to have significantly greater Egg_{PC} scores than all of the other colonies (all $p\leq0.001$).

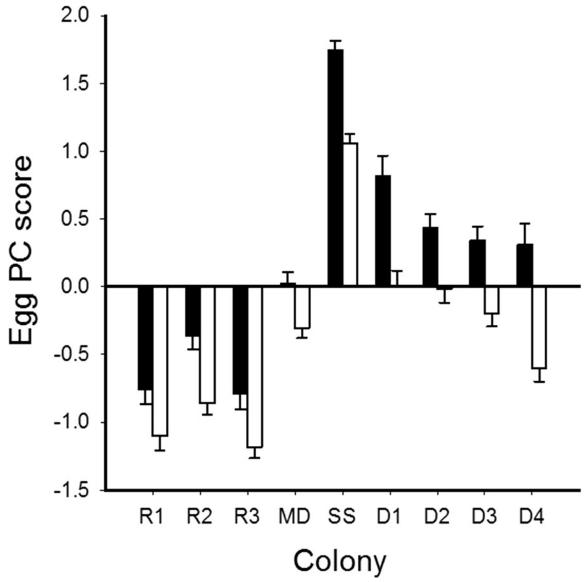


Fig. 3 Egg PC scores at tree swallow colonies impacted by a recently remediated fly ash spill and at nearby reference sites. In 2011 (*filled bars*), the SS had significantly greater PC1 scores, and hence greater maternal transfer of Hg, Se, Sr, and Tl than any other colony. In 2012 (*clear bars*), the SS still had significantly greater maternal transfer of contaminants to eggs than any other colony in that year, but PC scores decreased significantly at this colony between 2011 and 2012

Effects of prehatch weather and maternal transfer of elements on swallows

For clutch initiation date, the 90 % confidence set consisted of seven models, with year, female age, and prelaying temperature appearing in all seven models and receiving the highest parameter weights (Supplementary Table 4). The top two models received over 55 % of the model weights and only differed from the other five in their inclusion of rain. There was a positive association between clutch initiation date and temperature (Table 2). In 2012, clutch initiation dates were earlier than in 2011 and ASY females began breeding earlier than SY females (Table 3).

For clutch size, the 90 % confidence set consisted of 31 models, but the individual model weights were quite low and the intercept-only model appeared in the 90 % confidence set suggesting that these models had weak explanatory power. Year, female age, prelaying temperature, prelaying rainfall, and Egg_{PC} scores appeared in over half of the top models (Supplementary Table 5). Female age and prelaying temperature received the highest parameter weights (Table 2), and model averaged parameter estimates indicated that both variables were negatively related to clutch size (Table 2). We found that SY females laid smaller clutches than ASY females and slightly larger clutches were laid in 2011 than those in 2012 (Table 3).

The 90 % confidence set for egg mass consisted of 28 models (Supplementary Table 6). The top model included clutch size, female age, prelaying temperature and rainfall, and the temperature × rainfall interaction term. Rainfall appeared in 27 of the 28 models while

Table 2 Model averaged parameter estimates and parameter weights from the 90 % confidence set of models examining the relationship between year, female age, ambient temperature, rainfall, element exposure (Egg_{PC} score), and interactions between element exposure and weather on clutch initiation date, egg mass, clutch size, and hatching success in tree swallows

Variable	Parameter	Parameter estimate	Standard error	Parameter weight
Clutch initiation date	Year	**−3.127**	**0.617**	**1.000**
	Age	**3.198**	**0.629**	**1.000**
	Temp	**2.125**	**0.094**	**1.000**
	Rain	−0.417	0.461	0.542
	Egg_{PC} [a]	0.121	0.222	0.344
	Temp × Egg_{PC}	−0.001	0.004	0.046
	Rain × Egg_{PC}	−0.023	0.037	0.058
	Temp × rain	−0.005	0.016	0.100
Clutch size	Year	0.013	0.010	0.469
	Age	**−0.042**	**0.019**	**0.847**
	Temp	**−0.004**	**0.002**	**0.717**
	Rain	3.2×10^{-4}	0.005	0.311
	Egg_{PC}	−0.001	0.007	0.303
	Temp × Egg_{PC}	6.18×10^{-5}	0.0002	0.051
	Rain × Egg_{PC}	4.09×10^{-5}	0.0001	0.007
	Temp × rain	-1.5×10^{-5}	0.0002	0.041
Egg mass	Clutch size	**0.121**	**0.079**	**1.00**
	Year	−0.002	0.033	0.324
	Age	**−0.014**	**0.002**	**0.814**
	Temp	**0.002**	**0.006**	**0.900**
	Rain	**0.012**	**0.001**	**0.991**
	Egg_{PC}	0.0004	0.007	0.380
	Temp × Egg_{PC}	0.0001	0.003	0.114
	Rain × Egg_{PC}	3.06×10^{-5}	0.0001	0.083
	Temp × Rain	**0.004**	**0.0005**	**0.819**
Hatching success	Year	−0.004	0.004	0.369
	Age	**−0.041**	**0.012**	**1.000**
	Temp	−0.001	0.001	0.488
	Rain	0.002	0.003	0.392
	Egg_{PC}	−0.001	0.004	0.360
	Temp × Egg_{PC}	0.0003	0.0002	0.086
	Rain × Egg_{PC}	−0.0003	0.0002	0.035
	Temp × Rain	1.71×10^{-5}	5.68×10^{-5}	0.034

Clutch size was also included as a factor in egg mass models. Bold terms appeared in the top two models and in more than half of models in the 90 % confidence set and had parameter weights in excess of 0.70 indicating that they are related to the dependent variable

[a] Principal component (PC) score for egg elements received high positive factor loading for Hg, Se, Sr, and Tl

Temp temperature

temperature appeared in 21 of the models, and their interaction term appeared in 17 models. Clutch size was included in all of the models because of its significant relationship with egg mass and thus received the highest parameter weight (Table 2). Female age, prelaying temperature, prelaying rainfall, and their interaction term also received high parameter weights. However, the model averaged parameter estimates for

Table 3 Mean and standard errors of reproductive parameters between years and female age classes

	Year				Female Age			
	2011	*n*	2012	*n*	SY	*n*	ASY	*n*
Clutch initiation date	126.4±1.16	247	122.9±0.99	338	133.8±1.49	138	121.5±0.83	447
Clutch size	5.22±0.05	247	5.12±0.05	338	4.75±0.07	138	5.29±0.04	447
Egg mass[a]	1.80±0.01	247	1.80±0.01	338	1.77±0.01	138	1.80±0.01	447
Hatching success	0.85±0.02	237	0.88±0.01	297	0.80±0.02	127	0.88±0.02	407
Wing length	48.0±0.46	224	51.6±0.42	269	49.3±0.56	149	50.2±0.38	344
Residual mass	−0.26±0.17	224	0.36±0.15	269	−0.38±0.21	149	0.28±0.14	344
Reproductive success	0.68±0.02	180	0.76±0.02	251	0.69±0.03	93	0.74±0.02	338
Fledging success	0.82±0.03	180	0.83±0.02	251	0.80±0.03	93	0.83±0.02	338

[a] LS means are reported for egg mass because clutch size was included as a covariate in those models

these variables were relatively small suggesting that they have a weak relationship with egg mass.

For hatching success, the 90 % confidence set consisted of 24 models (Supplementary Table 7). The best model contained only female age, and this variable appeared in all of the models in the 90 % confidence set and thus received a high parameter weight (Table 2). SY females had slightly lower hatching success than ASY females, particularly in 2012 (Table 3). Year, temperature, rainfall, and Egg_{PC} appeared in more than half of the models, but their occurrence in these models is likely due to their co-occurrence with female age because they each received low parameter weights and model averaged parameter estimates (Table 2).

We examined the influence of weather conditions experienced during incubation and egg element concentrations on nestling growth and reproductive success as well. For wing length, the 90 % confidence set of models consisted of nine models, and all of these models included year, rainfall and temperature during incubation, and the interaction between rainfall and temperature (Supplementary Table 8), and all of these terms received high parameter weights (Table 4). An additional seven models also included Egg_{PC} scores, and five included female age while the remaining models differed in their inclusion of the interaction between Egg_{PC}scores and temperature or rain. Nestling wing length was greater in 2012 than that in 2011, and older females had nestlings with longer wings than younger females (Table 3). Across both years, cold temperatures and greater rainfall were associated with shorter wing lengths while warm temperatures and heavy rainfall or cold temperatures and no rainfall were associated with longer wing lengths (Fig. 4a). These effects were particularly pronounced in 2011 (Fig. 4b), but in 2012, ambient weather during incubation had little effect on nestling wing length (Fig. 4c).

For residual body mass, the 90 % confidence set consisted of 30 models, and the top model included year and female age (Supplementary Table 9). Female age appeared in 29 of the 30 models while year appeared in 20 of the 30 models, and these two terms received the highest parameter weights (Table 4). Both weather variables and Egg_{PC} appeared in over 19 models, but these variables had moderate parameter weights and low model averaged parameter estimates and likely little influence on residual body mass (Table 6). Nestlings reared by SY females had lower residual body mass than those reared by ASY females, and nestlings reared in 2011 had lower residual body mass than those reared in 2012 (Table 5).

For reproductive success, the 90 % confidence set consisted of 38 models; rainfall during incubation appeared in 31 of these and appeared in the top model along with year (Supplementary Table 10). Rainfall during incubation received a high parameter weight (Table 4), but year and the remaining terms appeared in fewer than 22 of the 38 models (Supplementary Table 10) and did not receive high parameter weights.

Nestling blood element concentrations among colonies

We quantified element concentrations from a single nestling in 493 nests: 224 nestlings in 2011 and 269 nestlings in 2012. We compared concentrations of elements in nestling blood and found that only Se

Table 4 Model averaged parameter estimates from the 90 % confidence set of models examining the relationship between year, female age, ambient temperature during incubation, rainfall during incubation, egg element exposure, and interactions between element exposure and weather on nestling size and reproductive success in tree swallows

Variable	Parameter	Parameter estimate	Standard error	Parameter weight
Wing	Year	**−1.19**	**0.326**	**1.000**
	Age	−0.33	0.274	0.595
	Inc temp	**0.16**	**0.064**	**1.000**
	Inc rain	**−0.08**	**0.222**	**1.000**
	Egg_{PC}[c]	−0.03	0.158	0.515
	Inc temp × Egg_{PC}	0.02	0.015	0.239
	Inc rain × Egg_{PC}	−0.03	0.036	0.150
	Inc temp × Inc rain	**0.25**	**0.044**	**1.000**
Residual body mass	Year	**−0.22**	**0.109**	**0.823**
	Age	**−0.34**	**0.127**	**0.983**
	Inc temp	0.02	0.015	0.634
	Inc rain	0.03	0.047	0.553
	Egg_{PC}	−0.05	0.060	0.505
	Inc temp × Egg_{PC}	−0.01	0.004	0.172
	Inc rain × Egg_{PC}	0.02	0.015	0.166
	Inc temp × Inc rain	0.01	0.006	0.362
	Inc temp × Inc rain × Egg_{PC}	−0.0002	0.0002	0.012
Reproductive success	Year	−0.019	0.010	0.598
	Age	−0.010	0.008	0.299
	Inc temp	0.002	0.002	0.536
	Inc rain	**−0.018**	**0.009**	**0.868**
	Egg_{PC}	−0.002	0.005	0.317
	Inc temp × Egg_{PC}	4.19×10^{-05}	0.000	0.030
	Inc rain × Egg_{PC}	-1.43×10^{-04}	0.001	0.049
	Inc temp × Inc rain	0.002	0.001	0.408

Bold terms appeared in the top two models and in more than half of models in the 90 % confidence set and had parameter weights in excess of 0.70 indicating that they are related to the dependent variable

Inc incubation, *Temp* temperature

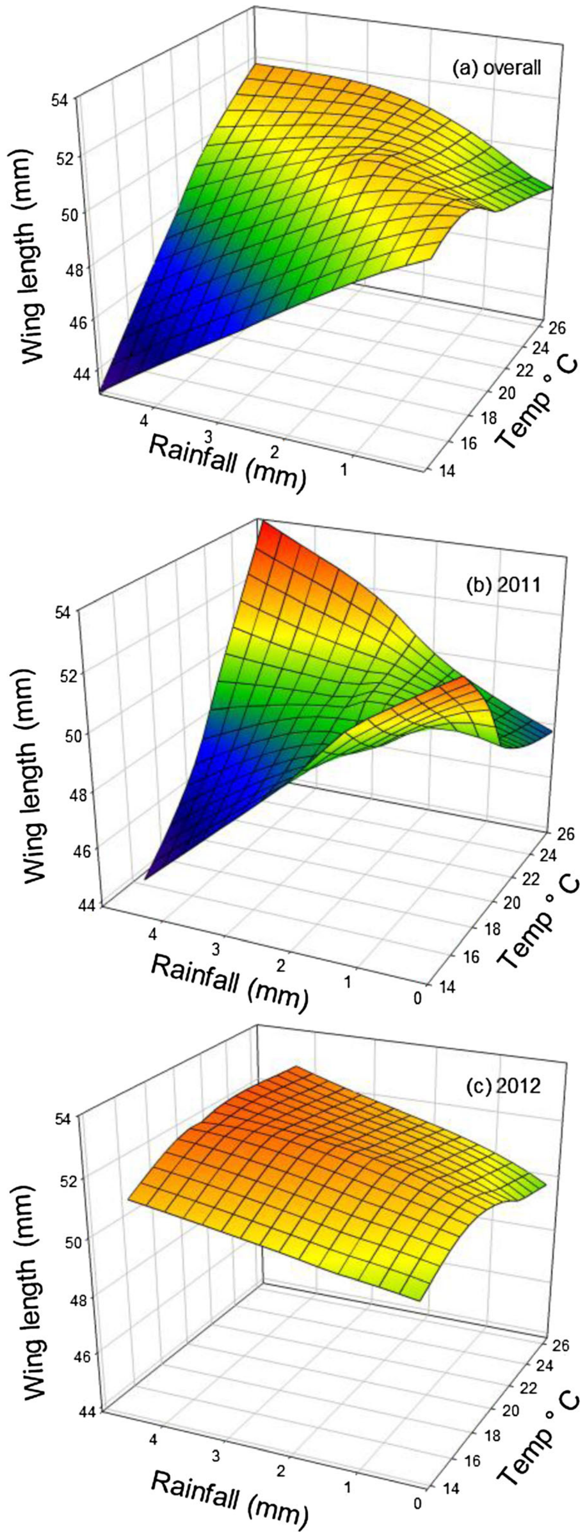
[c] Principal component (PC) score for egg elements received high positive factor loading for Hg, Se, Sr, and Tl

concentrations were significantly elevated at the SS compared to the reference colonies (Table 5, Fig. 5, $F_{(8,\ 480)}$=23.9, p<0.001). Concentrations of Ba, Cu, Fe, Mn, Sr, and Zn at the SS were similar to the three reference colonies and were not considered further (Table 5). Nestlings at the SS had significantly greater blood Se concentrations than nestlings in the three reference colonies in both years (Fig. 5, all p<0.001). In 2011, concentrations of Se at the SS were significantly greater than those at D1-4 (all $p\leq0.03$), and in 2012 remained significantly greater than D2 and D3 (both $p\leq$ 0.002). Se concentrations did not differ significantly between years ($F_{(1,\ 480)}$=1.9, p=0.17), and Se concentrations did not decrease significantly between 2011 and 2012 at the SS (p=1.0). The year by colony interaction was statistically significant ($F_{(8,\ 480)}$=9.4, p<0.001) and is largely attributable to the decrease in Se concentrations that occurred at MD between 2011 and 2012.

Effects of dietary elements and weather on nestling size and fledging success

The 90 % confidence set of models for wing length consisted of eight models; year, temperature, rainfall,

Fig. 4 The relationship between weather conditions during incubation and wing length in nestling tree swallows. Overall (**a**) and in 2011 (**b**) greater rainfall and colder temperatures during incubation were associated with shorter wing lengths in nestlings while warmer temperatures and greater rainfall were associated with longer wing lengths. In 2012 (**c**), there was a subtle decrease in wing length at either low or high temperatures and no rainfall, but the relationship was not as pronounced as in 2011



blood Se concentration, and the temperature × Se interaction appeared in every model (Supplementary Table 11) and received high parameter weights and model averaged parameter estimates (Table 6). Female age and the temperature × rain interaction appeared in half of the top models and the rain × Se interaction in five of the top models (Supplementary Table 11) but only female age received a moderate parameter weight (Table 6). Nestlings had shorter wings in 2011 than those in 2012 (Table 3). With both years of data combined, we found that nestlings grew longer wings at higher temperatures and greater blood Se concentrations (Fig. 6a). We also examined this interaction separately in each year and found that in 2011, the longest wing lengths were associated with high temperatures and high blood Se concentrations (Fig. 6b). However, in 2012, nestlings with greater blood Se concentrations grew longer wings, irrespective of the temperature (Fig. 6c).

We attempted to determine the relative importance of prehatch and posthatch weather conditions on nestling wing length by focusing on a single weather variable while controlling for the other weather variables and blood Se concentrations in partial correlations. We found that the influence of weather conditions on nestling wing length varied between years. We first focused on temperature during incubation; in 2011, we found a negative relationship between ambient temperature during incubation and wing length (r=−0.17, df=219, p=0.01), while in 2012, we found a weak positive relationship (r=0.12, df=264, p=0.05). In 2011, rainfall during incubation was unrelated to wing length (r=0.03, df=219, p=0.72), but in 2012, we found a weak positive relationship between rainfall during incubation and wing length (r=0.15, df=264, p=0.01). Ambient temperature during the nestling period had a strong positive association with wing length in 2011 (r=0.47, df=219, p<0.001), while in 2012, there was a weak negative relationship (r=−0.15, df=264, p=0.02).

For residual body mass, the 90 % confidence set consisted of 18 models; year, temperature, and rainfall appeared in all of the models (Supplementary Table 12) and had the highest parameter weights (Table 6). Female age appeared in ten models and also had a high

Table 5 Geometric means and 95 % confidence intervals for nestling blood element concentrations (μg/g wet weight) among tree swallow colonies

Element	R1	R2	R3	MD	SS	D1	D2	D3	D4
Ba 2011	0.66 (0.61–0.72)	0.72 (0.58–0.99)	0.63 (0.56–0.74)	0.76 (0.71–0.90)	0.78 (0.73–0.96)	0.71 (0.64–0.82)	0.75 (0.67–0.92)	0.63 (0.59–0.72)	0.74 (0.58–0.97)
2012	0.69 (0.61–0.78)	0.73 (0.60–1.13)	0.64 (0.55–0.84)	0.61 (0.59–0.64)	0.67 (0.65–0.73)	0.67 (0.63–0.74)	0.62 (0.57–0.70)	0.63 (0.59–0.74)	0.83 (0.66–1.33)
Cu 2011	0.27^{a} (0.26–0.29)	0.31^{a} (0.30–0.33)	0.29^{a} (0.27–0.32)	0.29^{a} (0.28–0.31)	0.33^{a} (0.31–0.37)	0.31^{a} (0.29–0.33)	0.31^{a} (0.30–0.34)	0.27^{a} (0.26–0.29)	0.32^{a} (0.26–0.40)
2012	0.32^{a} (0.28–0.37)	0.37^{a} (0.31–0.50)	0.31^{ab} (0.26–0.42)	0.32^{a} (0.31–0.34)	0.30^{ab} (0.29–0.33)	0.30^{ab} (0.28–0.32)	0.29^{a} (0.27–0.31)	0.34^{a} (0.30–0.42)	0.46^{b} (0.29–1.15)
Fe 2011	351.5^{ab} (334.8–372.1)	404.6^{b} (370.4–453.5)	342.5^{ab} (317.7–383.9)	354.5^{ab} (338.9–382.1)	351.9^{ab} (339.2–380.2)	365.1^{ab} (339.8–404.2)	328.8^{ab} (307.1–366.4)	300.0^{a} (284.8–323.9)	390.6^{ab} (272.1–558.4)
2012	363.5^{a} (339.5–402.4)	431.3^{a} (358.2–588.5)	407.1^{a} (332.0–560.2)	389.6^{a} (379.2–406.3)	356.4^{a} (345.8–375.1)	351.1^{a} (329.0–383.5)	348.8^{a} (332.1–370.4)	391.8^{a} (366.4–444.5)	566.2^{b} (464.3–839.9)
Mn 2011	0.04^{a} (0.03–0.06)	0.04^{a} (0.04–0.05)	0.04^{a} (0.03–0.06)	0.04^{a} (0.03–0.07)	0.04^{a} (0.04–0.05)	0.04^{a} (0.04–0.06)	0.04^{a} (0.04–0.05)	0.04^{a} (0.03–0.05)	0.03^{a} (0.03–0.05)
2012	0.05^{ab} (0.04–0.07)	0.05^{a} (0.04–0.08)	0.05^{a} (0.04–0.07)	0.06^{a} (0.05–0.07)	0.03^{bc} (0.03–0.04)	0.05^{a} (0.05–0.06)	0.03^{c} (0.02–0.04)	0.04^{abc} (0.04–0.05)	0.06^{a} (0.04–0.11)
Se 2011	0.83^{a} (0.73–1.02)	0.82^{ab} (0.61–1.28)	0.71^{ab} (0.60–0.96)	1.90^{c} (1.87–2.84)	1.68^{c} (1.61–1.87)	0.98^{a} (0.89–1.12)	1.03^{a} (0.93–1.22)	1.09^{a} (0.98–1.31)	0.40^{b} (−0.18–2.42)
2012	0.73^{a} (0.64–0.98)	0.75^{a} (0.62–1.12)	0.75^{a} (0.59–1.18)	0.99^{a} (0.92–1.36)	1.77^{b} (1.72–2.16)	1.41^{b} (1.28–1.66)	1.04^{a} (0.96–1.17)	1.02^{a} (0.91–1.33)	1.21^{ab} (0.96–1.91)
Sr 2011	0.08^{a} (0.08–0.09)	0.08^{ab} (0.06–0.10)	0.09^{ab} (0.08–0.11)	0.08^{ab} (−0.16–0.73)	0.10^{b} (0.10–0.12)	0.10^{ab} (0.05–0.23)	0.08^{ab} (0.07–0.09)	0.07^{a} (0.04–0.15)	0.06^{ab} (0.05–0.09)
2012	0.06^{a} (0.05–0.07)	0.06^{a} (0.05–0.08)	0.06^{a} (0.05–0.09)	0.05^{a} (0.05–0.06)	0.06^{a} (0.06–0.08)	0.06^{a} (0.05–0.07)	0.05^{a} (0.04–0.05)	0.06^{a} (0.05–0.07)	0.06^{a} (0.05–0.10)
Zn 2011	6.40^{a} (6.11–6.75)	6.03^{a} (5.51–6.78)	6.00^{a} (5.71–6.35)	5.94^{a} (5.64–6.44)	6.77^{a} (6.51–7.23)	6.06^{a} (5.61–6.72)	5.66^{a} (5.15–6.98)	6.22^{a} (5.69–7.07)	5.67^{a} (4.92–6.61)
2012	6.33^{a} (6.06–6.67)	7.23^{a} (5.86–10.06)	7.38^{a} (6.11–10.15)	6.33^{a} (6.18–6.53)	6.25^{a} (5.30–8.37)	6.18^{a} (5.91–6.50)	6.16^{a} (5.92–6.46)	6.88^{a} (6.50–7.51)	9.73^{b} (7.64–15.52)
N[a] 2011	18	17	19	40	49	21	26	27	9
2012	21	27	18	50	64	21	22	24	25

Concentrations of As, Cd, Cr, Tl, and V were also quantified but were below the detection limit in over half of the samples in both years and concentrations of Hg were BDL in 2012 and were not considered in analyses. Colonies that share the same superscript did not differ significantly from each other in that year for that element while colonies that do not share a letter differ significantly from each other at $p \leq 0.05$. Concentrations of Ba did not differ significantly among colonies

[a] Sample size

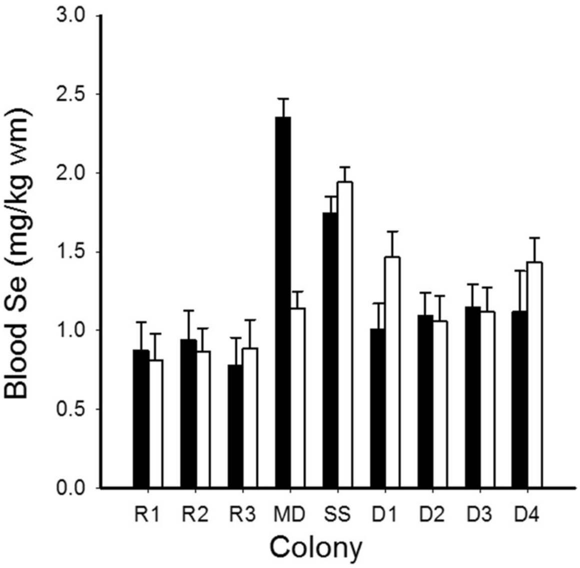


Fig. 5 Nestling blood Se concentrations among colonies impacted by a recently remediated ash spill and at nearby reference sites. In 2011 (*solid bars*), concentration of Se at the SS (site of the fly ash spill) was significantly greater than the three reference colonies and all of the colonies downstream from the spill. In 2011, only MD, the colony also impacted by ash-related contaminants from another source, did not have significantly lower Se concentrations than the SS. In 2012 (*clear bars*), the SS had significantly greater Se concentrations from the three reference colonies, D2, D3, and MD. Concentrations of Se at the SS in 2012 did not differ significantly from those found at the SS in 2011. All statistical analyses were performed on log-transformed Se concentrations, but untransformed data are depicted in the figure for clarity

parameter weight while blood Se concentration appeared in 14 models and received a moderate parameter weight. The results indicated that SY females tended to produce young with lower residual body mass than ASY females and that nestlings had greater residual body mass in 2012 compared to 2011 (Table 3). Model averaged parameter estimates indicated that greater residual body mass was weakly positively associated with greater rainfall and higher blood Se concentrations (Table 6).

For fledging success, we found that the 90 % confidence set consisted of 14 models, with temperature, rainfall, and their interaction appearing in all of the models (Supplementary Table 13) and receiving the highest parameter weights (Table 6). With both years of data combined, fledging success was lowest at cold temperatures with no rainfall and greatest at high temperatures and no rainfall (Fig. 7a). We examined these relationships separately in each year and found that in 2011, fledging success was again greatest at high temperatures and no rainfall but lowest at cold temperatures with greater rainfall (Fig. 7b). However, in 2012, fledging success increased slightly with greater rainfall and was not strongly influenced by temperature (Fig. 7c). Year, female age, and blood Se concentrations also received high parameter weights and appeared in at least nine of the models (Table 6). Fledging success was slightly higher in 2012 than that in 2011 and in ASY females than that in SY females (Table 3), and blood Se concentrations were negatively associated with fledging success (Table 6).

Effects of unseasonably cold weather on hatching and fledging success

Between May 3rd–7th and May 15th–19th 2011, unseasonably cold weather occurred and caused nestling mortality or complete nest failure that killed embryos and/or nestlings in most of the colonies. These weather conditions were stressful for the swallows and were related to reduced hatching and fledging success at our site; 19.2 % (25/130) of the nests that were initiated prior to May15th experienced complete fledging failure (all of the nestlings died, not attributable to predation) in 2011. In contrast, only 4.2 % (9/216) of nests initiated prior to May 15th experienced complete fledging failure in 2012. Across all of the colonies, 37.5 % (106/283) of nests experienced some reproductive losses in association with the cold weather. Around 35.6 % of nests at the egg stage and 40 % of nests with nestlings on May 15th experienced partial or complete hatching failure or loss of young during or in the days immediately following the cold snap. We found significant differences among colonies in the proportion of broods and clutches that suffered hatching and fledging losses associated with the cold snap (Fig. 8, *likelihood ratio*=*37.2*, *df*=24, *p*=0.04). Over 50 % of the nests at R1, D2, and MD experienced reductions in hatching and fledging success around the time of the cold snap (Fig. 8). Because the SS and majority of downstream colonies did not experience greater reductions in hatching and fledging success than reference colonies during the cold snap, we did not find evidence of an interaction between modest element concentrations and inclement weather.

Table 6 Model averaged parameter estimates from the 90 % confidence set of models examining the relationship between year, female age, ambient temperature, rainfall, element exposure, and interactions between element exposure and weather on nestling size and fledging success in tree swallows

Variable	Parameter	Parameter estimate	Standard error	Parameter weight
Wing	Year	**−1.75**	**0.304**	**1.000**
	Age	−0.324	0.267	0.587
	Temp	**0.240**	**0.066**	**1.000**
	Rain	**0.582**	**0.225**	**1.000**
	Se[a]	**7.44**	**1.20**	**1.000**
	Temp[b] × Se	**1.06**	**0.249**	**1.000**
	Rain × Se	0.343	0.571	0.358
	Temp × rain	0.001	0.016	0.262
Residual body mass	Year	**−0.345**	**0.119**	**1.000**
	Age	**−0.202**	**0.108**	**0.773**
	Temp	**−0.074**	**0.025**	**1.000**
	Rain	**0.334**	**0.085**	**1.000**
	Se	0.402	0.368	0.646
	Temp × Se	0.008	0.017	0.176
	Rain × Se	0.038	0.074	0.180
	Temp × rain	0.014	0.011	0.454
Fledging success	Year	**0.172**	**0.082**	**0.859**
	Age	**−0.172**	**0.078**	**0.872**
	Temp	**0.077**	**0.020**	**1.000**
	Rain	**0.221**	**0.059**	**1.000**
	Se	**−0.627**	**0.758**	**0.837**
	Temp × Se	0.129	0.099	0.544
	Rain × Se	−0.955	0.833	0.709
	Temp × rain	**−0.059**	**0.016**	**1.000**
	Temp × Rain × Se	0.026	0.027	0.175

[a] Se nestling blood selenium concentration μg/g wet weight

[b] temp temperature posthatch

Bold terms appeared in the top two models and in more than half of models in the 90 % confidence set and had parameter weights in excess of 0.70 indicating that they are related to the dependent variable

Discussion

Exposure to contaminants and global climate change have the potential to individually and/or interactively affect reproductive success, offspring development, and physiology in birds and other taxa (reviewed in Hooper et al. 2013; Noyes et al. 2009; Moe et al. 2013). As the effects of climate change will likely be more severe in the future (IPCC 2013), it is important to address the current relationships between climate and contaminant exposure as these studies can serve as a baseline for examining future interactions. Using a comprehensive 2-year dataset, we examined the relationship between modest element exposure, weather conditions throughout the breeding season, and their interaction on measures of reproductive success and growth of tree swallows. We determined that exposure to residual element contamination had no negative effect on tree swallow reproduction or nestling growth. We found that inclement weather reduced aspects of growth, hatching success, and fledging success of swallows but did not exacerbate effects of modest exposure to elements from the remediated spill.

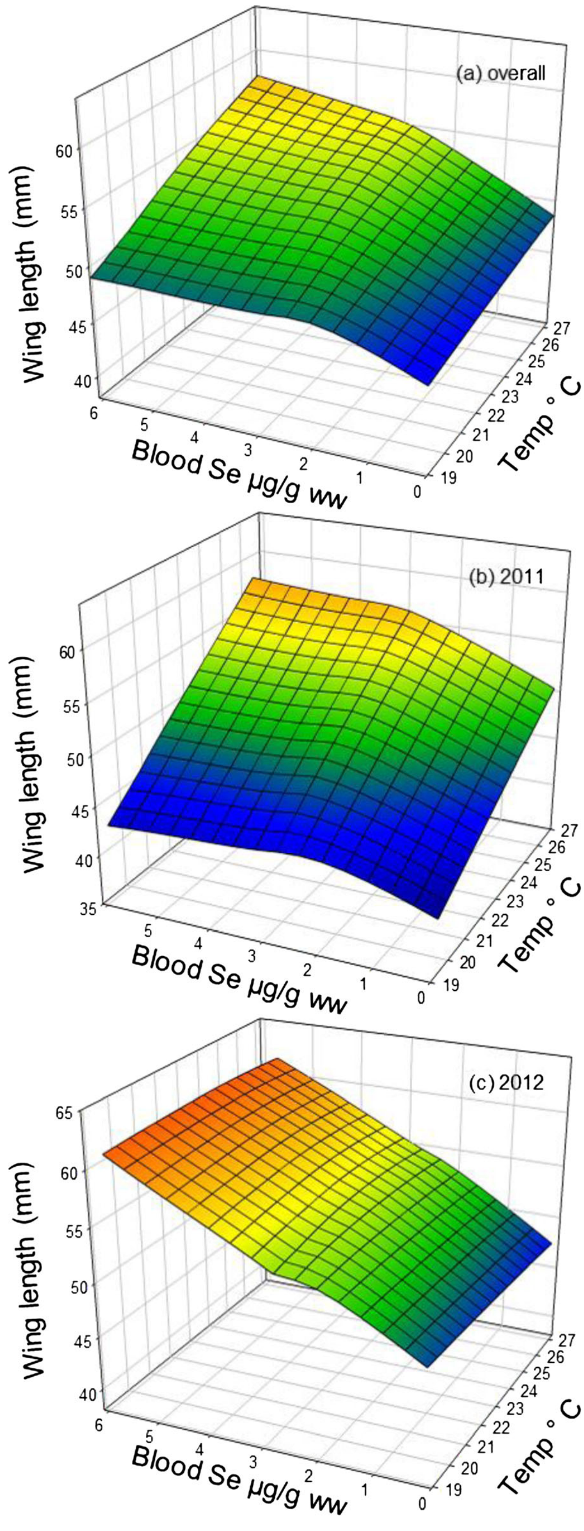
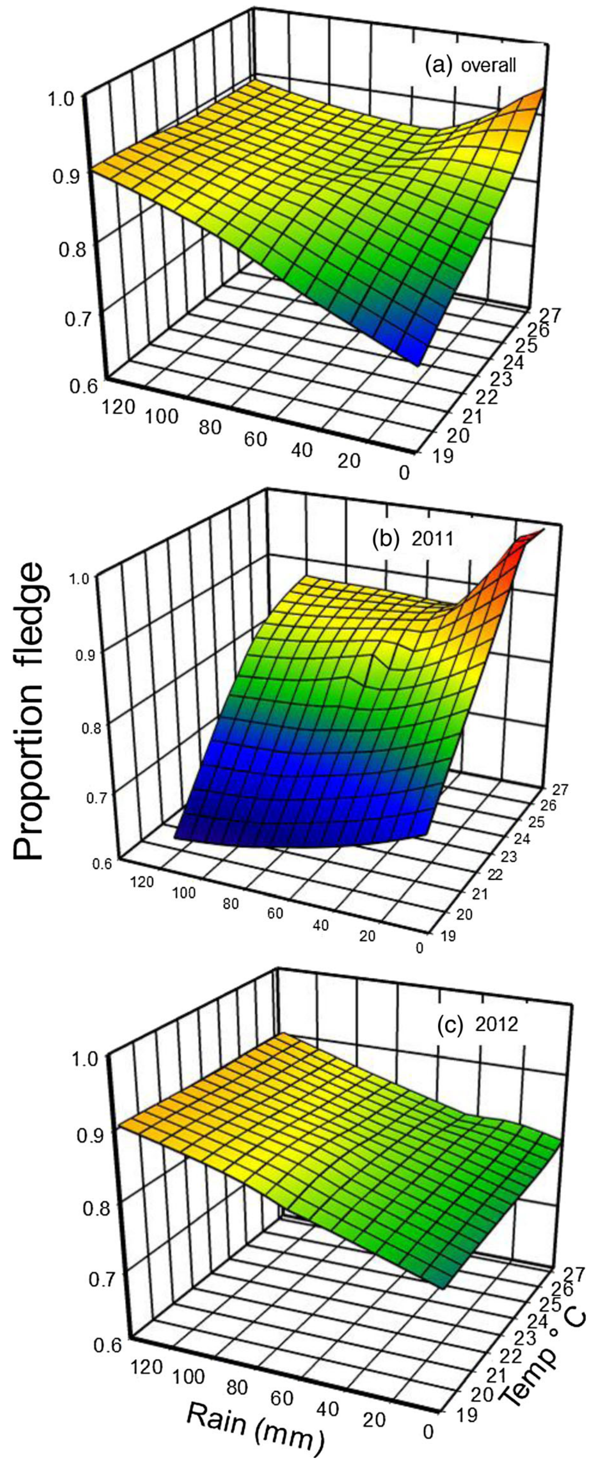


Fig. 6 The relationship between blood Se concentration μg/g wet weight (ww), temperature during the nestling period, and wing length in nestling tree swallows exposed to elements from a remediated coal ash spill and at reference colonies. We found that wing length was influenced by a significant interaction between nestling blood Se concentration and ambient temperature. For both years combined (**a**) and in 2011 (**b**), nestling wing lengths were greatest at higher ambient temperatures and greater concentrations of Se and were shortest at low ambient temperatures and Se concentrations. In 2012 (**c**), greater blood Se concentrations were associated with longer wing lengths, irrespective of ambient temperature during the nestling period

Maternal transfer of elements and egg reproductive parameters

Female tree swallows near the fly ash spill maternally transferred Hg, Se, Sr, and Tl to eggs at concentrations elevated above reference levels, even 2.5 years after the spill and following extensive remediation efforts. However, these concentrations were below those associated with toxic effects in other avian species (Janz et al. 2010; Heinz et al. 2011). Furthermore, Egg_{PC} scores, and egg concentrations of Se, Sr, and Tl, decreased at the SS between 2011 and 2012 although Hg concentrations increased at the SS between years. These results suggest that natural processes such as dilution and offsite transport continue to attenuate exposure postremediation. Consistent with modest maternal transfer of Hg, Se, Sr, and Tl to eggs at the SS and other impacted colonies, we found no evidence of adverse effects of element exposure on clutch initiation date, egg mass, clutch size, or hatching success and no evidence of longer-term effects on nestling growth or reproductive success. Selenium is one of the primary drivers of ecological risk in systems impacted by fly ash, and egg hatchability is the most sensitive indicator of Se toxicity in avian species (Ohlendorf 2003). Egg Se concentrations exceeding 10 μg/g dry weight (dw) are the predicted lower threshold for adverse reproductive effects in birds, though species vary in their sensitivity (Heinz 1996; Janz et al. 2010). The highest mean egg Se concentrations we detected were at the SS and were slightly more than 3 μg/g dw (range at SS, 2011: 2.34–5.19 μg/g dw, 2012: 2.20–7.96 μg/g dw), below concentrations that affect hatching success in most avian species and similar to concentrations necessary for normal development in domestic birds (Puls 1994; Janz et al. 2010). Prior work on tree swallows found no adverse effects of average egg Se concentrations of 1.2–1.7 μg/g dw (Custer et al. 2006) or 2.1 μg/g dw (Custer et al. 2006). These studies also found that average egg Sr concentrations of 4.3–8.2 μg/g dw and Hg concentrations of 0.20–0.25 μg/g

Fig. 7 The relationship between ambient temperature and rainfall during the nestling period and fledging success in tree swallows. Fledging success was influenced by a significant interaction between ambient temperature and rainfall during the nestling period. **a** For both years combined, fledging success was greatest at higher ambient temperatures and lowest at low ambient temperatures and no rainfall. **b** In 2011, a similar pattern was found except that the lowest fledging success occurred at low temperatures and high rainfall. **c** In 2012, greater fledging success was associated with slightly increased rainfall at all temperatures



dw had no adverse effects on tree swallow reproduction (Custer et al. 2006, 2008). A study on tree swallows exposed to very high concentrations of Hg showed females transferred Hg to their eggs (average egg Hg= 0.34 μg/g wet weight (ww), approximately 1.34 μg/g dw), but found no differences in nest initiation date, clutch size, or hatching success between contaminated and reference sites (Brasso and Cristol 2008; Brasso et al. 2010), suggesting that these endpoints may be insensitive to Hg exposure in tree swallows. However, the same study demonstrated that these Hg concentrations can reduce egg size (Brasso and Cristol 2008) while the lower Hg concentrations in our study did not.

Nestling dietary exposure, growth, and fledging success

We found variation among colonies in concentrations of several of the elements in nestling blood, but only concentrations of Se were significantly greater at the SS than at any other colony in both years of the study. Selenium concentrations in nestling blood at the SS did not change from 2011 to 2012, suggesting continued trophic exposure through provisioned emerging aquatic insects at this colony (Beck et al. 2013, 2014), in contrast to the decline in Se concentrations we detected in eggs. Nestling blood Se concentrations at the SS averaged 1.82 μg/g ww over both years (range 2011, 0.86–2.83 μg/g ww; 2012, 0.80–4.84 μg/g ww). Avian blood Se concentrations of 1.0 μg/g ww are considered a lower threshold for potential health concern in birds (reviewed in Ohlendorf and Heinz 2011), and only 4 of the 113 nestlings sampled at the SS had concentrations below this threshold. However, many studies that found a relationship between blood Se concentrations and reproduction or survival detected effects at blood Se concentrations much higher than this threshold and following prolonged periods of exposure (>11 weeks) (Heinz and Fitzgerald 1993; Franson et al. 2007). In adult mallards (*Anas platyrhynchos*), blood Se concentrations of 5–15 μg/g ww affected survival, but some individuals survived the entire experiment with blood Se concentrations of 12 μg/g ww (Heinz and Fitzgerald 1993). In another study, body mass of Se-exposed juvenile

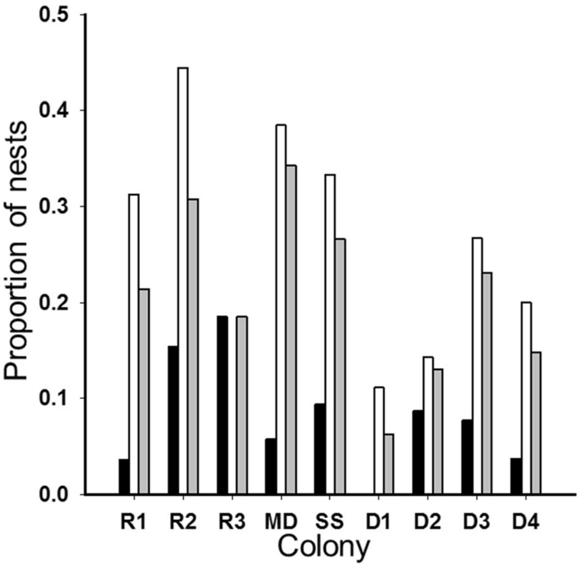


Fig. 8 The influence of unseasonably cold weather on reproductive success in tree swallows in eastern TN in 2011. The proportion of nests that suffered reproductive losses in response to cold weather events differed significantly among colonies and between nesting stages. The proportion of nests experiencing hatching failure (*black bars*) was lowest at D1 while the proportion of nests with young (*clear bars*) that experienced reduced fledging success was lowest at R3 and D1. The total proportion of nests in both stages (*gray bars*) affected by the spill was greatest at R2, MD, and the SS. Nests affected at the egg stage/total nests, nests affected at nestling stage/total number in nestling stage at each colony were R1: 1/28, 5/16; R2: 4/26, 4/9; R3: 5/27, 0/10, MD: 2/35, 10/26; SS: 6/64, 11/33; D1: 0/16, 1/9; D2: 2/23, 1/7; D3: 2/26, 4/15; D4: 1/27, 3/15

common eiders (*Somateria mollissima*) did not differ from controls until blood Se concentrations exceeded 17.5 μg/g ww (Franson et al. 2007). It remains unknown what blood concentrations of Se pose health concerns to tree swallow nestlings. Given that Se concentrations in nestlings near the remediated spill area exceed the lower threshold for concern and did not decline over the 2 years of our study, future studies should continue to monitor dietary Se sources (emerging aquatic insects), resultant exposure, and effects on insectivorous wildlife.

The elevated concentrations of Se we detected in tree swallows at the SS were not associated with residual body mass or fledging success but were related to wing length. In 2012, greater blood Se concentrations were positively associated with wing length irrespective of ambient temperature and were associated with greater wing lengths at warmer temperatures in 2011. These modestly elevated concentrations of Se may have a positive effect on wing growth because of its essential role in nutrition (Puls 1994; Reilly 2006; Rayman 2012), and these increases in wing length could be advantageous for nestlings. In nestling tree swallows, longer wing lengths are associated with the ability to monopolize parental food delivery, earlier fledging (Michaud and Leonard 2000), and a greater probability of survival to adulthood (McCarty 2001) compared to nestlings with shorter wings.

Influence of weather and elements on growth, hatching success, and fledging success

Seasonal weather patterns had little influence on nestling condition but were related to nestling wing length and fledging success in our study population. We found that unseasonably cold temperatures and high rainfall during incubation were negatively related to nestling wing length while warm weather and high rainfall were associated with the longest wing lengths. But, wing length was also influenced by an interaction between ambient temperature and blood Se concentrations during the nestling period. This interaction was particularly evident in 2011, when lower ambient temperatures during the nestling period were associated with shorter wing lengths, while in 2012, temperature during the nestling period had little effect on wing length. We attempted to disentangle the relative importance of incubation and posthatch conditions and found that ambient temperature during the nestling period had the strongest effect on nestling wing length in 2011, when unseasonably cold weather overlapped with nestling growth. Thus, it seems that the combination of cold weather and/or reduced insect availability inhibited wing growth, similar to other studies on tree swallows (Dawson et al. 2005; McCarty and Winkler 1999). While most studies have focused on the influence of posthatch weather conditions on nestling growth in tree swallows, a recent study indicated that egg incubation temperatures are influenced by ambient weather (Coe et al. 2015) and incubation temperature is related to nestling growth, including wing length (Coe et al. unpublished data). Our results suggest that wing growth, which is primarily a measure of feather growth, is a more sensitive indicator of environmental conditions experienced during development than residual body mass. This may be because the development of skeletal features, such as the tarsus, is more constrained by access to specific nutrients, such as calcium (Dawson and Bidwell 2005), and because tarsus length is highly heritable in tree swallows (Wiggins 1990), further reducing the potential effects of weather conditions or element exposure on its development. Wing growth appears to be more plastic and less restricted by access to specific nutrients (Bitton et al. 2006). Allocating resources to wing growth under favorable environmental conditions would likely be selectively advantageous given the benefits of greater wing lengths for tree swallow nestlings (Michaud and Leonard 2000; McCarty 2001).

Variation in average temperature and total rainfall during development also influenced fledging success, and this was particularly the case in 2011 when unseasonably cold weather had adverse consequences for tree swallow hatching and fledging success. We found that high temperatures and no rainfall were associated with the greatest fledging success and this was especially the case in 2011. During the unseasonably cold weather in 2011, 62 of 272 nests experienced some reduction in hatching or fledging success during this cold period. Our results suggest that temperatures dropped to levels that could impede the foraging success of tree swallows, and as a result, adult tree swallows may have resorted to the immediate energy requirements associated with self-maintenance at the expense of allocating energy toward incubation, brooding, and feeding young. We predicted that the combined effects of element exposure and these severe weather conditions would affect egg and nestling survival to a greater extent than either factor on its own. However, we found no evidence to support this prediction. Our results suggest that the modest concentrations of elements remaining after remediation were insufficient to impair the ability of swallows to cope with this environmental challenge.

Conclusions

Our results indicated that several years after the 2008 ash spill, tree swallows were still exposed to modestly elevated concentrations of elements and that parents transferred some of these elements to their young through maternal transfer to eggs and provisioning of insects to nestlings. Selenium concentrations were most notable but were below levels of toxicological concern in eggs and just above levels of possible concern in nestling blood. Low-level exposure after such a large spill event is likely attributable to extensive remediation efforts that occurred in the 2.5 years between the fly ash spill and the start of our study, and ongoing dilution and offsite transport of elements. In support of the idea that attenuation is continuing in the system, many element concentrations decreased in the spill area from 2011 to 2012, except Se in nestling blood and Hg in eggs which remained relatively stable. Most importantly, we found no reductions in hatching or fledging success associated with low-level exposure to elements. However, the long-term effects of chronic exposure to low concentrations of contaminants during early development are largely unknown. Exposure to low element concentrations during development has been shown to have long-term negative effects on reproductive success in adulthood (Baos et al. 2012) indicating that further research in this area is required. We found that a short period of inclement weather during a peak reproductive period was associated with reduced hatching and fledging success at a large proportion of nests across the study area in 2011 but was not accentuated by exposure to elements. However, the combined effects of exposure to higher contaminant concentrations and more extreme weather have affected hatching or fledging success in tree swallows and other species (Gentes et al. 2006; Hallinger and Cristol 2011; Hill et al. 2008; Custer et al. 2003). These interactions will likely become more pronounced as climate change is expected to increase the frequency and severity of extreme weather events (IPCC 2013). This may be particularly important at species range limits where they are already near the edge of their physiological tolerance for temperature and other abiotic factors (Hooper et al. 2013).

Acknowledgments We thank John Hallagan, Matt Hepp, Dean Sedgewick, Mark Hepner, Elizabeth Burton, Jesse Morris, Darin Blood, Juan Botero, Angela Garica, Brittney Coe, Ashley Love, Steve Munoz, Ben Nickely, Elizabeth Smith, and Lisa Trapp for assistance in the field and Jean Favara, Suzie Walls, Wes James, Neil Carriker, and the USDA APHIS Knoxville for providing logistical support. We thank David Hankins for assisting with the maps. Funding for this project was provided by Tennessee Valley Authority grant to WAH and DMH.

References

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In P. N. Petrov & F. Csaki (Eds.), *Second international symposium on information theory* (pp. 267–281). Budapest: Akademiai Kiado.

Anderson, D. R. (2008). *Model based inference in the life sciences*. New York: Springer.

ARCADIS. (2011). *Draft trace element concentrations in tree swallows: 2009-2010*. Kingston: Tennessee Valley Authority.

Ardia, D. R. (2005). Super size me: an experimental test of the factors affecting lipid content and the ability of residual body mass to predict lipid stores in nestling European Starlings. *Functional Ecology, 19*(3), 414–420.

Baos, R., Jovani, R., Serrano, D., Tella, J. L., & Hiraldo, F. (2012). Developmental exposure to a toxic spill compromises long-term reproductive performance in a wild, long-lived bird: the white stork (*Ciconia ciconia*). *PLoS ONE, 7*(4), e34716. doi:10.1371/journal.pone.0034716.

Barrett, M. A., Brown, J. L., Junge, R. E., & Yoder, A. D. (2013). Climate change, predictive modeling and lemur health: assessing impacts of changing climate on health and conservation in Madagascar. *Biological Conservation, 157*(1), 409–422.

Beck, M. L., Hopkins, W. A., & Jackson, B. P. (2013). Spatial and temporal variation in the diet of tree swallows: implications for trace element exposure following habitat remediation. *Archives of Environmental Contamination and Toxicology, 65*(3), 575–587.

Beck, M. L., Hopkins, W. A., & Jackson, B. P. (2014). Variation in riparian consumer diet composition and differential bioaccumulation by prey influence the risk of exposure to elements from a recently remediated fly ash spill. *Environmental Toxicology and Chemistry, 33*(11), 2595–2608.

Bergeron, C. M., Hopkins, W. A., Todd, B. D., Hepner, M. J., & Unrine, J. M. (2011). Interactive effects of maternal and dietary mercury exposure have latent and lethal consequences for amphibian larvae. *Environmental Science & Technology, 45*(8), 3781–3787.

Berglund, A. M. M., Ingvarsson, P. K., Danielsson, H., & Nyholm, N. E. I. (2010). Lead exposure and biological effects in pied flycatchers (*Ficedula hypoleuca*) before and after the closure of a lead mine in northern Sweden. *Environmental Pollution, 158*(5), 1368–1375.

Bitton, P. P., Dawson, R. D., & O'Brien, E. L. (2006). Influence of intraclutch egg-mass variation and hatching asynchrony on relative offspring performance within broods of an altricial bird. *Canadian Journal of Zoology-Revue Canadienne De Zoologie, 84*(12), 1721–1726.

Brasso, R. L., Abdel Latif, M. K., & Cristol, D. A. (2010). Relationship between laying sequence and mercury concentration in Tree Swallow eggs. *Environmental Toxicology and Chemistry, 29*(5), 1155–1159.

Brasso, R. L., & Cristol, D. A. (2008). Effects of mercury exposure on the reproductive success of tree swallows (*Tachycineta bicolor*). *Ecotoxicology, 17*(2), 133–141.

Brown, C. R., & Brown, M. B. (1986). Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). *Ecology, 67*(5), 1206–1218.

Brown, G. P., & Shine, R. (2007). Rain, prey and predators: climatically driven shifts in frog abundance modify reproductive allometry in a tropical snake. *Oecologia, 154*(2), 361–368.

Bryan, A. L., Hopkins, W. A., Baionno, J. E., & Jackson, B. P. (2003). Maternal transfer of contaminants to eggs of Common Grackles (*Quiscalus quiscala*) nesting on coal fly ash basins. *Archives of Environmental Contamination and Toxicology, 45*(2), 273–277.

Burger, J. R., & Gochfield, M. (1997). Risk, mercury levels, and birds: relating adverse laboratory effects to field biomonitoring. *Environmental Research, 75*(2), 160–172.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer-Verlag.

Coe, B. H., Beck, M. L., Chin, S. Y., Jachowski, C. M. B., & Hopkins, W. A. (2015). Local variation in climate influences parental care and resultant embryonic developmental conditions in a passerine bird. *Journal of Avian Biology*. doi:10.1111/jav.00581.

Cook, R. B., Suter, G. W., & Sain, E. R. (1999). Ecological risk assessment in a large river-reservoir: 1. Introduction and background. *Environmental Toxicology and Chemistry, 18*(4), 581–588.

Cunningham, S. J., Martin, R. O., Hojem, C. L., & Hockey, P. A. R. (2013). Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: A study of common fiscals. *PLoS ONE, 8*(9), e74613. doi:10.1371/journal.pone.0074613.

Custer, C. A., Custer, T. W., Dummer, P. A., & Munney, K. L. (2003). Exposure and effects of chemical contaminants on tree swallows nesting along the Houatonic River, Berkshire County, Massachusetts, USA 1998-2000. *Environmental Toxicology and Chemistry, 22*(7), 1605–1621.

Custer, C. M. (2011). Swallows as sentinel species for contaminant exposure and effect studies. In J. Elliott, C. Bishop, & C. Morrissey (Eds.), *Wildlife ecotoxicology: Forensic approaches* (pp. 45–91). New York: Springer.

Custer, C. M., Custer, T. W., Warburton, D., Hoffman, D. J., Bickham, J. W., & Matson, C. W. (2006). Trace element concentrations and bioindicator response in tree swallows from northwestern Minnesota. *Environmental Monitoring and Assessment, 118*(1), 247–266.

Custer, C. M., Gray, B. R., & Custer, T. W. (2010). Effects of egg order on organic and inorganic element concentrations and egg characteristics in tree swallows, *Tachycineta bicolor. Environmental Toxicology and Chemistry, 29*(4), 909–921.

Custer, T. W., Custer, C. A., Johnson, K. M., & Hoffman, D. J. (2008). Mercury and other element exposure to tree swallows (*Tachycineta bicolor*) nesting on Lostwood National Wildlife Refuge, North Dakota. *Environmental Pollution, 155*(2), 217–226.

Dawson, R. D. (2008). Timing of breeding and environmental factors as determinants of reproductive performance of tree swallows. *Canadian Journal of Zoology-Revue Canadienne De Zoologie, 86*(8), 843–850.

Dawson, R. D., & Bidwell, M. T. (2005). Dietary calcium limits size and growth of nestling tree swallows in a non-acidified landscape. *Journal of Avian Biology, 36*(2), 127–134.

Dawson, R. D., Lawrie, C. C., & O'Brien, E. L. (2005). The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia, 144*(3), 499–507.

Dunn, P. O., & Hannon, S. J. (1992). Effects of food abundance and male parental care on reproductive success and monogamy in tree swallows. *Auk, 109*(3), 488–499.

Eeva, T., Ahola, M., & Lehikoinen, E. (2009). Breeding performance of blue tits (*Cyanistes caeruleus*) and great tits (*Parus *major*) in a heavy metal polluted area. *Environmental Pollution, 157*(11), 3126–3131.

Eeva, T., & Lehikninen, E. (1995). Egg shell quality, clutch size, and hatching success of the great tit (*Parus major*) and the pied flycatcher (*Ficedula hypoleuca*) in an air pollution gradient. *Oecologia, 102*(3), 312–323.

Eeva, T., & Lehikninen, E. (1996). Growth and mortality of nestling great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) in a heavy metal pollution gradient. *Oecologia, 108*(4), 631–639.

Fischer, B. B., Pomati, F., & Eggen, R. I. L. (2013). The toxicity of chemical pollutants in dynamic natural systems: the challenge of integrating environmental factors and biological complexity. *Science of the Total Environment, 449*, 253–259.

Franson, J. C., Hoffman, D. J., Wells-Berlin, A., Perry, M. C., Shearn-Bochsler, V., Finley, D. L., et al. (2007). Effects of dietary selenium on tissue concentrations, pathology, oxidative stress, and immune function in common eiders (*Somateria mollissima*). *Journal of Toxicology and Environmental Health Part A, 70*(9–10), 861–874.

Garcia-Barrera, T., Gomez-Ariza, J. L., Gonzalez-Fernandez, M., Moreno, F., Garcia-Sevillano, M. A., & Gomez-Jacinto, V. (2012). Biological responses related to agonistic, antagonistic and synergistic interactions of chemical species. *Analytical and Bioanalytical Chemistry, 403*(8), 2237–2253.

Gentes, M.-L., Waldner, C., Papp, Z., & Smits, J. E. G. (2006). Effects of oil sands tailings compounds and harsh weather on mortality rates, growth and detoxification efforts in nestling tree swallows (*Tachycineta bicolor*). *Environmental Pollution, 142*(1), 24–33.

Gooderham, K., & Schulte-Hostedde, A. (2011). Macroparasitism influences reproductive success in red squirrels (*Tamiasciurus hudsonicus*). *Behavioral Ecology, 22*(6), 1195–1200.

Gouin, T., Armitage, J. M., Cousins, I. T., Muir, D. C. G., Ng, C. A., Reid, L., et al. (2013). Influence of global climate change on chemical fate and bioaccumulation: the role of multimedia models. *Environmental Toxicology and Chemistry, 32*(1), 20–31.

Green, A. J. (2001). Mass/length residuals: measures of body condition or generators of spurious results? *Ecology, 82*(5), 1473–1483.

Hallinger, K. K., & Cristol, D. A. (2011). The role of weather in mediating the effect of mercury exposure on reproductive success in tree swallows. *Ecotoxicology, 20*(6), 1368–1377.

Harding, L. E. (2008). Non-linear uptake and hormesis effects of selenium in red-winged blackbirds (*Agelaius phoeniceus*). *Science of the Total Environment, 389*(2–3), 350–366.

Heinz, G. H. (1996). Selenium in birds. In W. N. Beyer, G. H. Heinz, & A. W. Redmon-Norwood (Eds.), *Environmental contaminants in wildlife: Interpreting tissue concentrations* (pp. 447–458). Boca Raton: CRC Lewis.

Heinz, G. H., & Fitzgerald, M. A. (1993). Overwinter survival of mallards fed selenium. *Archives of Environmental Contamination and Toxicology, 25*(1), 90–94.

Heinz, G. H., & Hoffman, D. J. (2003). Predicting mercury in mallard ducklings from mercury in chorioallantoic membranes. *Bulletin of Environmental Contamination and Toxicology, 70*(6), 1242–1246.

Heinz, G. H., Hoffman, D. J., Klimstra, J. D., Stebbins, K. R., Kondrad, S. L., & Erwin, C. A. (2011). Teratogenic effects of injected methylmercury on avian embryos. *Environmental Toxicology and Chemistry, 30*(7), 1593–1598.

Hill, E. F., Henny, C. J., & Grove, R. A. (2008). Mercury and drought along the lower Carson River, Nevada: II. Snowy egret and black-crowned night-heron reproduction on Lahontan Reservoir, 1997-2006. *Ecotoxicology, 17*(2), 117–131.

Hinam, H. L., & Clair, C. C. S. (2008). High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of Northern saw-whet owls. *Biological Conservation, 141*(2), 524–535.

Holmstrup, M., Bindesbol, A. M., Oostingh, G. J., Duschl, A., Scheil, V., Kohler, H. R., et al. (2010). Interactions between effects of environmental chemicals and natural stressors: a review. *Science of the Total Environment, 408*(18), 3746–3762.

Hooper, M. J., Ankley, G. T., Cristol, D. A., Maryoung, L. A., Noyes, P. D., & Pinkerton, K. E. (2013). Interactions between chemical and climate stressors: a role for mechanistic toxicology in assessing climate change risks. *Environmental Toxicology and Chemistry, 32*(1), 32–48.

Hopkins, W. A., DuRant, S. E., Staub, B. P., Rowe, C. L., & Jackson, B. P. (2006). Reproduction, embryonic development, and maternal transfer of contaminants in the amphibian *Gastrophryne carolinensis*. *Environmental Health Perspectives, 114*(5), 661–666.

IPCC. (2013). Climate change. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, & J. Boschung, et al. (Eds.), *The physical science basis. Contribution of Working Group I to the fifth assessment report of the intergovernmental panel on climate change* (p. 1535). Cambridge: Cambridge University.

Janssens, E., Dauwe, T., Pinxten, R., Bervoets, L., Blust, R., & Eens, M. (2003). Effects of heavy metal exposure on the condition and health of nestlings of the great tit (*Parus major*), a small songbird species. *Environmental Pollution, 126*(2), 267–274.

Janz, D. M., DeForest, D. K., Brooks, M. L., Chapman, P. M., Gilron, G., Hoff, D., et al. (2010). Selenium toxicity to aquatic organisms. In P. M. Chapman, W. J. Adams, M. L. Brooks, C. G. Delos, S. N. Luoma, & W. A. Maher, et al. (Eds.), *Ecological assessment of selenium in the aquatic environment* (pp. 141–231). New York: CRC Press.

Liao, T. F. (1994). Generalized linear models and the interpretation of parameters. In *Interpreting probability models logit, probit, and other generalized linear models Quantitative applications in the social sciences* (pp. 4–11). Thousand Oaks: SAGE Publications Inc.

Marmiroli, N., & Maestri, E. (2008). Health implications of trace elements in the environment and the food chain. In M. N. V. Prasad (Ed.), *Trace elements as contaminants and nutrients* (pp. 23–49). Hoboken: Wiley.

McCarty, J. P. (2001). Variation in growth of nestling tree swallows across multiple temporal and spatial scales. *Auk, 118*(1), 176–190.

McCarty, J. P., & Winkler, D. W. (1999). Relative importance of environmental variables in determining the growth of nestling Tree Swallows *Tachycineta bicolor*. *Ibis, 141*(2), 286–296.

McDonald, P. G., Olsen, P. D., & Cockburn, A. (2004). Weather dictates reproductive success and survival in the Australian brown falcon *Falco berigora. Journal of Animal Ecology, 73*(4), 683–692.

Michaud, T., & Leonard, M. (2000). The role of development, parental behavior, and nestmate competition in fledging of nestling Tree Swallows. *Auk, 117*(4), 996–1002.

Moe, S. J., De Schamphelaere, K., Clements, W. H., Sorensen, M. T., Van den Brink, P. J., & Liess, M. (2013). Combined and interactive effects of global climate change and toxicants on populations and communities. *Environmental Toxicology and Chemistry, 32*(1), 49–61.

Møller, A. P. (2013). Biological consequences of global change for birds. *Integrative Zoology, 8*(2), 136–144.

Nooker, J. K., Dunn, P. O., & Whittingham, L. A. (2005). Effects of food abundance, weather, and female condition on reproduction in tree swallows (*Tachycineta bicolor*). *Auk, 122*(4), 1225–1238.

Noyes, P. D., McElwee, M. K., Miller, H. D., Clark, B. W., Van Tiem, L. A., Walcott, K. C., et al. (2009). The toxicology of climate change: environmental contaminants in a warming world. *Environment International, 35*(6), 971–986.

NRC. (2006). *Managing coal combustion residues in mines*. Washington, D.C.: National Research Council, National Academies Press.

Nyholm, N. E. I., & Myhrberg, H. E. (1977). Severe eggshell defects and impaired reproductive capacity in small passerines in Swedish Lapland. *Oikos, 29*(2), 336–341.

Nystrom, P., Hansson, J., Mansson, J., Sundstedt, M., Reslow, C., & Brostrom, A. (2007). A documented amphibian decline over 40 years: possible causes and implications for species recovery. *Biological Conservation, 138*(3–4), 399–411.

Ohlendorf, H. M. (2003). Ecotoxicology of selenium. In D. J. Hoffman, B. A. Rattner, G. A. J. Burton, & J. J. Cairns (Eds.), *Handbook of ecotoxicology* (2nd ed., pp. 465–500). Boca Raton, Fl: CRC.

Ohlendorf, H. M. (2011). Selenium, salty water, and deformed birds. In J. E. Eliott, C. A. Morrissey, & C. A. Bishop (Eds.), *Wildlife ecotoxicology: forensic approaches* (pp. 325–357). New York: Springer.

Ohlendorf, H. M., & Heinz, G. H. (2011). Selenium in birds. In W. N. Beyer & J. P. Meador (Eds.), *Environmental contaminants in biota* (pp. 669–701). Boca Raton: CRC Press.

Pipoly, I., Bokony, V., Seress, G., Szabo, K., & Liker, A. (2013). Effects of extreme weather on reproductive success in a temperate-breeding songbird. *PLoS ONE, 8*((11), e80033. doi:10.1371/journal.pone.0080033.

Plard, F., Gaillard, J. M., Coulson, T., Hewison, A. J. M., Delorme, D., Warnant, C., et al. (2014). Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS Biology, 12*(4), e1001828. doi:10.1371/journal.pbio.1001828.

Puls, R. (1994). *Mineral levels in animal health* (2nd ed.). Clearbrook: Sherpa International.

Quinney, T. E., & Ankney, C. D. (1985). Prey size selection by tree swallows. *Auk, 102*(2), 245–250.

Rayman, M. P. (2012). Selenium and human health. *Lancet, 379*(9822), 1256–1268.

Reilly, C. (2006). *Selenium in food and health*. New York: Springer.

Robertson, R. J., Stutchbury, B. J., Cohen, R. R., Winkler, D. W., Hallinger, K. K., & Ardia, D. R. (2011). Tree Swallow. http://bna.birds.cornell.edu/bna/species/011/articles/introduction. Accessed 10 Apr 2012.

Rowe, C. L., Hopkins, W. A., & Congdon, J. D. (2002). Ecotoxicological implications of aquatic disposal of coal combustion residues in the United States: a review. *Environmental Monitoring and Assessment, 80*(3), 207–276.

Saether, B. E., Sutherland, W. J., & Engen, S. (2004). Climate influences on avian population dynamics. In A. P. Moller, W. Fielder, & P. Berthold (Eds.), *Birds and Climate Change* (Vol. 35, pp. 185-209, Advances in Ecological Research).

Salafsky, N., Salzer, D., Stattersfield, A. J., Hilton-Taylor, C., Neugarten, R., Butchart, S. H. M., et al. (2008). A standard lexicon for biodiversity conservation: unified classifications of threats and actions. *Conservation Biology, 22*(4), 897–911.

Savage, W. K., Quimby, F. W., & DeCaprio, A. P. (2002). Lethal and sublethal effects of polychlorinated biphenyls on *Rana sylvatica* tadpoles. *Environmental Toxicology and Chemistry, 21*(1), 168–174.

Schulte-Hostedde, A. I., Zinner, B., Millar, J. S., & Hickling, G. J. (2005). Restitution of mass-size residuals: validating body condition indices. *Ecology, 86*(1), 155–163.

Shore, R. F., Pereira, M. G., Walker, L. A., & Thompson, D. R. (2011). Mercury in nonmarine birds and mammals. In W. N. Beyer & J. P. Meador (Eds.), *Environmental contmaninants in biota* (pp. 609–626). Boca Raton, Fl: CRC Press.

Stantec. (2009). *TVA disposal facility assessment phase 1 plant summary Bull Run Fossil Plant (BRF)*. Nashville: Tennessee Valley Authority and Stantec, 76 p.

Stutchbury, B. J., & Robertson, R. J. (1987). Two methods of sexing adult tree swallows before they begin breeding. *Journal of Field Ornithology, 58*(2), 236–242.

Stutchbury, B. J., & Robertson, R. J. (1988). Within-season and age-related patterns of reproductive-performance in female tree swallows (*Tachycineta bicolor*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie, 66*(4), 827–834.

TVA. (2009). *Corrective action plan for the TVA Kingston fossil plant ash release. (Vol. March 2, 2009, pp. 73)*. Kingston: Tennessee Valley Authority.

TVA (2011a). Inspection report: TVA's groundwater monitoring at coal combustion products disposal areas. (Vol. 2009-12991, pp. 29). Knoxville, TN: Office of Inspector General, Tennessee Valley Authority.

TVA. (2011b). *TVA Kingston fossil fuel plant release site on-scene coordinator report for the time-critical removal action May 11, 2009 through December 2010. (pp. 222)*. Harriman, TN: Tennessee Valley Authority.

USDA (2009). Lower Clinch River rapid watershed assessment. (pp. 19). Clinton, TN: United States Department of Agriculture and the Natural Resources Conservation Service.

Weech, S. A., Scheuhammer, A. M., & Wayland, M. E. (2012). Selenium accumulation and reproduction in birds breeding downstream of a uranium mill in northern Saskatchewan, Canada. *Ecotoxicology, 21*(1), 280–288.

Wiggins, D. A. (1990). Food availability, growth, and heritability of body size in nestling tree swallows (*Tachycineta bicolor*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie, 68*(6), 1292–1296.

Winkler, D. W., Luo, M. K., & Rakhimberdiev, E. (2013). Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). *Oecologia, 173*(1), 129–138.

Zanette, L., Clinchy, M., & Smith, J. N. M. (2006). Combined food and predator effects on songbird nest survival and annual reproductive success: results from a bi-factorial experiment. *Oecologia, 147*(4), 632–640.

Zwolak, I., & Zaporowska, H. (2012). Selenium interactions and toxicity: a review Selenium interactions and toxicity. *Cell Biology and Toxicology, 28*(1), 31–46.