scientific reports

OPEN

# Depressed nestling growth during exposure to smoke from distant wildfires

Cara A. Krieg

**Human and animal populations increasingly encounter smoke pollution as climate change enhances the frequency and intensity of wildfires. Most work on smoke effects in animals has studied populations close to fires, populations experiencing small, prescribed burns, or animals in the lab. In June of 2023, smoke from distant Canadian wildfires quickly elevated particulate matter ($PM_{2.5}$) pollution in a wild house wren (*Troglodytes aedon*) population for three days before returning to baseline levels. Compared to previous years, nestlings experiencing three days of elevated $PM_{2.5}$ within the first 6 days of life weighed less on days 6 and 10 after hatching and had shorter tarsometatarsus bones, a sign of smaller skeletal size. In contrast, nestlings that hatched before or after this event did not differ in size from previous years. Although sublethal, these effects may have important consequences for survival and reproduction. As wildfire activity increases, more wildlife populations are at risk of smoke-related fitness consequences, even those distant from the blaze.**

**Keywords** Wildfire smoke, $PM_{2.5}$, Smoke pollution, Nestling growth, House wren, Troglodytes aedon

The global risk of wildland fire is increasing as climate change raises global temperatures and alters precipitation regimes[1–3]. These climate effects are expected to increase not only the frequency but also the intensity of fires[3,4]. The last several decades have seen accelerating rates of 'mega-fires', fires that are more dangerous, more destructive, and more difficult to fight[5,6].

Wildfires pose threats to wildlife populations both near and far from the blaze. Populations close to the fire face increased injury, illness, and mortality, destroyed or altered habitat, and potential loss of food sources[7,8]. Fire dramatically lowers air quality in the surrounding area, resulting in health impacts. Animals living close to fires show elevated levels of carbon monoxide poisoning, neurological deficits, oxidative stress, immune suppression, and other respiratory and cardiovascular alterations as the result of smoke exposure[8,9]. Wildfires also produce large amounts of small, lightweight, airborne particulates ≤ 2.5 µm in aerodynamic diameter ($PM_{2.5}$) that are easily transported long distances[10]. Large wildfires can therefore increase particulate pollution for populations hundreds of miles from the initial fire as these particles are carried on the wind.

Elevated $PM_{2.5}$ concentrations from wildfires cause negative health effects for humans and animals. Human populations experiencing elevated smoke or $PM_{2.5}$ from wildfires have increased all-cause mortality, increased rates of respiratory illness, and increased cardiovascular events[11–13]. Between 1997–2006, landscape fire smoke contributed to an estimated 339,000 premature deaths annually[14]. These effects found in humans mirror those documented in animals[8,9]. Compared to equivalent concentrations of $PM_{2.5}$ generated from urban or industrial sources, smoke pollution from wildfires is more toxic[15,16] due to the higher concentration of polar organic compounds and trace metals that increase its oxidative potential[17,18]. Furthermore, the chemical composition of this smoke transforms with time as it interacts with other components in the atmosphere, posing health risks to populations distant from the initial fire[19].

Despite the short-term risks to individual health and the long-term risks to population growth, few studies have examined the effects of wildfire smoke on free-living wildlife populations far from fire sources. Controlled smoke-exposure experiments using laboratory or captive animals have demonstrated that animals suffer many of same negative health effects as seen in humans[8,9]. However, these studies are poor proxies for the effects in free-living populations where smoke exposure is likely mediated by microhabitat features or behavioral responses[7,8]. A limited number of studies have explored the effects of wildfire smoke on wild insect, mammal, and bird populations (reviewed in[8]). Many of these studies have investigated the impacts of prescribed fire used for habitat management in which fires are small, easily controlled, and short in duration. To date, few studies have directly explored the effects of smoke from large, uncontrolled wildfires. Of those that exist, some

Department of Biology, The University of Scranton, 800 Linden Street, Scranton, PA 18510, USA. email: cara.krieg@scranton.edu

have examined populations living in the burned landscapes that likely experience confounding direct effects from fire[20,21]. A handful of these studies have documented behavioral changes following exposure to smoke pollution from distant fires. These studies have found decreased detection rates of certain species when using citizen-science efforts[22], camera traps[23], or acoustic monitoring[24] during periods of elevated wildfire $PM_{2.5}$. It is unknown whether these changes result from mortality or flexible behavioral responses. Other studies have documented more direct connections between smoke and behavior in wild populations. For example, gibbons (*Hylobates albibarbis*) sing less[25] and Bornean orangutans (*Pongo pygmaeus wurmbii*) move less[26] during periods of heavy smoke.

Even rarer still are studies that link these smoke effects to fitness consequences in wild populations. A very small number of studies have linked wildfire smoke to increased chances of wildlife mortality. For example, migratory birds in the northwestern USA during the 2020 wildfire season halted their progress or altered their route when encountering smoke plumes, ultimately extending their migration duration and raising the chance of mortality[27]. A modeling approach investigating the cause of mass migratory bird die-offs implicated wildfire proximity and air quality in these deaths[28]. Smoke effects can also be sublethal. For example, Bornean orangutans experiencing elevated wildfire $PM_{2.5}$ had negative energy balance unrelated to caloric intake[26]. How these sublethal effects of wildfire smoke translate to offspring production and quality is unknown in nearly all wild populations, despite the importance of these measures for population viability. As the increasing size and frequency of wildfires increases the amount of particulate pollution that can spread long distances[10], these sublethal effects may become an important conservation concern, even in those ecosystems that do not regularly experience fire.

Canada experienced one of its worst wildfire seasons on record during the summer of 2023[29]. Nearly 8 million hectares burned between January 1st and June 28th[29]. In early June 2023, plumes of smoke from fires in Ontario and Quebec dramatically reduced air quality for much of the Eastern United States. From June 6th to June 8th, the daily air quality index (AQI) in Lackawanna County in Northeast Pennsylvania rose to levels considered unhealthy for human populations primarily as the result of increased particulate matter ($PM_{2.5}$) from these wildfires[30] (Fig. 1). $PM_{2.5}$ concentrations then returned to baseline seasonal levels for the next three weeks.

This pollution pulse coincided with the house wren (*Troglodytes aedon*) breeding season. House wrens are small (10–12 g), native, insectivorous songbirds that nest in tree cavities. Using data from a wild breeding population in Lackawanna County, PA, I compared 11 nests that experienced three days of elevated $PM_{2.5}$ in the first six days after hatching and 17 nests that experienced no $PM_{2.5}$ elevation in 2023 to nests that hatched at the same times during the season in 2021 and 2022 (smoke period: 15 nests; no smoke period: 19 nests). I asked whether this short-term exposure to elevated $PM_{2.5}$ concentrations negatively impacted house wren nestling growth. If wildfire smoke has direct or indirect effects on early house wren growth, I predicted that nestlings that experienced three days of elevated $PM_{2.5}$ in the first 6 days after hatching in 2023 would be smaller than nestlings that hatched during the same time of the year during no-smoke years. Because nestling size is linked to the probability of surviving to the next breeding season in house wrens[31], any changes in size may have important fitness consequences.

## Results

Smoke plumes from Canadian wildfires increased the average daily particulate matter ($PM_{2.5}$) concentration and increased the average daily air quality index (AQI) for nestlings that experienced three days of elevated smoke in the first six days of life (Table 1). This elevated particulate matter pollution was correlated with changes in house wren nestling size. House wren nestlings that experienced three days of elevated $PM_{2.5}$ concentrations in the first six days after hatching weighed less on day 6 after hatching when compared to nestlings that hatched at the same time in the season in previous years (Table 2; Fig. 2a). These differences persisted later in development. These same nestlings were still smaller than nestlings from control years on day 10 after hatching (Table 2; Fig. 2b). These nestlings also had shorter tarsometatarsus (tarsus) bones on day 10 (Table 2; Fig. 2c). In contrast, nestling body mass and tarsus length did not differ between the smoke year and control years for nestlings that hatched at other times in the season (Table 2). While there was a significant interaction between year (smoke vs. no smoke) and hatching relative to the smoke pulse (smoke period vs. no-smoke period), there was no overall effect of year on nestling size for any measurement (Table 2). The size of nestlings that hatched during the smoke year was not statistically different from the size of nestlings in no smoke years after controlling for the significant interaction term (Table 2).

Nestlings that hatched during this smoke event were notably different in size relative to typical nestlings and adults. The average day 6 mass from nests experiencing three days of smoke pollution was 0.75 g less than those that hatched at the same time in control years (smoke nest average ± s.d.: 6.11 ± 0.76 g; control year nest average ± s.d.: 6.86 ± 0.74 g). These nestlings were only 89% the size of control nestlings. By day 10, these smoke nestlings had partially recovered. However, they were still an average of 0.60 g smaller than their control counterparts (smoke nest average ± s.d.: 9.64 ± 0.48 g; control year nest average ± s.d.: 10.24 ± 0.45 g). Compared to the adult males that were captured during these study years, nestlings that hatched during this smoke period in the control years were 94.14% of the adult mass on day 10 compared to smoke nestlings who were only 88.6% of this adult mass. Smoke nestlings also differed in overall skeletal size. Tarsometatarsus bone length in smoke nestlings was on average 0.62 mm shorter, an average of 93.73% the average adult length, relative to comparable control nestlings that reached 96.95% the average adult length (smoke nest average ± s.d.: 18.01 ± 0.35 mm; control year nest average ± s.d.: 18.63 ± 0.34 mm).

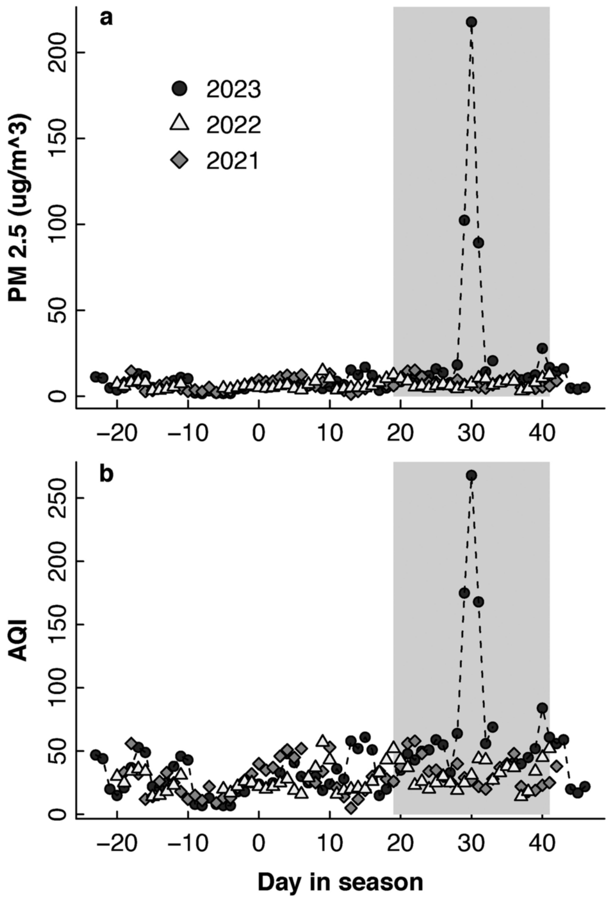


**Fig. 1**. Daily average concentration of airborne particulates ≤ 2.5 µm in aerodynamic diameter ($PM_{2.5}$ (µg/m$^3$)) (**a**) and air quality index (AQI) (**b**) in Lackawanna County, Pennsylvania in 2023 (dark circles), 2022 (light triangles), and 2021 (medium gray diamonds). Data are shown from the day house wrens first arrived at the study site that year through the final nestling day 6 considered in this study. Nests in this study hatched during the days shaded by the gray rectangle. The US EPA considers AQI levels between 0–50 good, 51–100 moderate, 101–150 unhealthy for sensitive groups, 151–200 unhealthy, and 201–300 very unhealthy. Data were obtained from the US EPA air quality monitoring system database [30].

| Treatment group | Daily average $PM_{2.5}$ range (µg/m$^3$) | Average daily $PM_{2.5}$ (µg/m$^3$) | Daily average AQI range[1] | Average daily AQI |
|---|---|---|---|---|
| 3-day smoke period, smoke year[2] | 8.0–217.7 | 60.6 | 33–268 | 111.0 |
| 3-day smoke period, control years[3] | 4.5–10.6 | 7.1 | 19–44 | 29.8 |
| No smoke period, smoke year[4] | 4.1–27.9 | 12.2 | 17–84 | 47.1 |
| No smoke period, control years[5] | 3.3–15.2 | 8.0 | 14–58 | 33.3 |

**Table 1**. Range and average of daily average particulate matter concentration ($PM_{2.5}$) and air quality index (AQI) the six days after hatching for all nests in each treatment group. Data are from the US EPA [30]. [1]U.S. EPA AQI classifications: good: 0–50; moderate: 51–100; unhealthy for sensitive groups: 101–150; unhealthy: 151–200; very unhealthy: 201–300. [2]Data are presented for 6/3/2023 through 6/11/2023. Air quality information for each day is included in these calculations once here and in subsequent categories. All nests in this category experienced the first six days after hatching during this time. [3]6/7/2022 through 6/15/2022 in 2022. 6/11/2021 through 6/19/2021 in 2021. [4]5/27/2023 through 6/3/2023 and 6/9/2023 through 6/23/2023. [5]5/31/2022 through 6/9/2022, 6/13/2022 through 6/22/2022, 6/4/2021 through 6/13/2021, and 6/20/2021 through 6/27/2021.

## Discussion

House wren nestlings that experienced three days of elevated wildfire $PM_{2.5}$ in the first six days after hatching had depressed mass and skeletal size relative to nestlings that did not experience smoke pollution. Nestlings that hatched immediately before or after this pulse did not differ in size from nestlings in previous years, suggesting this is not merely an effect of study year. Although wildfire smoke will pose an increasing risk to animal

| Independent variable | Dependent variable | | |
|---|---|---|---|
| | Day 6 mass | Day 10 mass | Tarsus length |
| Year (smoke vs. no smoke) | | | |
| Residuals degrees of freedom | 58 | 56 | 55 |
| F value | 0.36 | 1.38 | 0.21 |
| *p*-value | 0.55 | 0.25 | 0.65 |
| Hatched during smoke period (yes vs. no) | | | |
| F value | 6.98 | 3.41 | 3.67 |
| *p*-value | **0.01** | 0.07 | 0.06 |
| Year x smoke period interaction | | | |
| F value | 4.54 | 6.41 | 6.78 |
| *p*-value | **0.04** | **0.01** | **0.01** |
| Post-hoc contrast: Šidák corrected *p*-values | | | |
| Smoke vs. no-smoke year, smoke period | **0.05** | **0.05** | **0.01** |
| Smoke vs. no-smoke year, no smoke period | 0.80 | 0.43 | 0.88 |

**Table 2**. Results from two-way ANOVAs on the effects of year, hatch time relative to smoke pollution spike, and their interaction on nestling day 6 mass (g), day 10 mass (g), and tarsometatarsus (tarsus) length (mm). Bolded values indicate statistically significant differences.

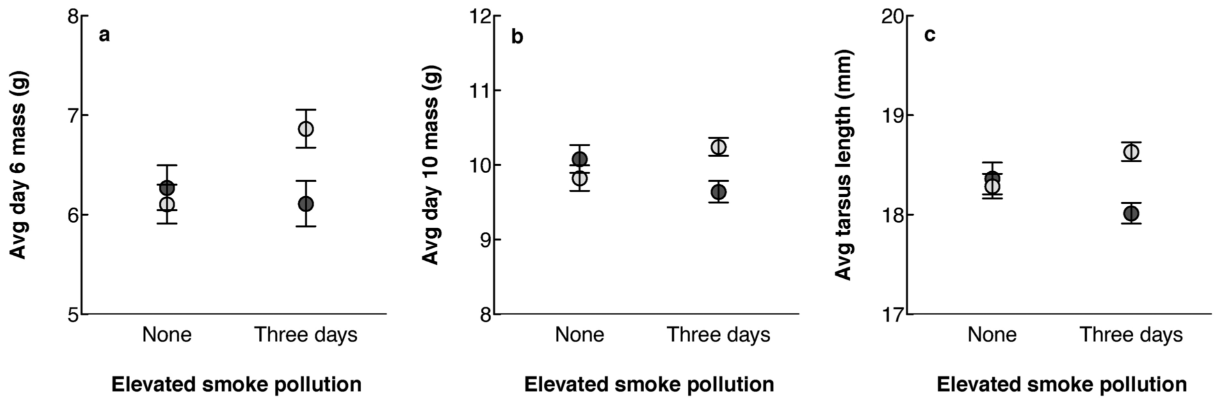


**Fig. 2**. Average ± standard error of the mean day 6 mass (**a**), day 10 mass (**b**), and tarsometatarsus (tarsus) length (**c**) of house wren nestlings that experienced three days of elevated wildfire smoke pollution compared to within and between year controls. Nestlings from 2023 (dark points) that experienced this smoke in the first 6 days after hatching (11 nests) were smaller than nestlings from control years (light points) that hatched at the same time in the season (15 nests). Nestlings that hatched before or after this spike did not differ between years (2023: 17 nests, 2021–2022: 19 nests). Axes limits are set to the largest and smallest nest average for each measurement.

populations in the coming decades, relatively few studies have examined the effects of smoke alone on free-living wildlife populations[8]. This is the first study to document an association between wildfire smoke from distant fires and changes in offspring development in a wild, avian species. Bird respiratory systems are highly sensitive to air pollution due to their morphological adaptations that improve respiratory efficiency[32]. This makes birds a useful indicator species for detecting early ecosystem effects of air pollution[33]. These results have important conservation implications for vulnerable populations exposed to wildfire smoke.

Particulate matter may have depressed house wren nestling growth in this study in several ways. Particulates can have direct physiological effects as they accumulate in the respiratory system. Aerosolized particulates less than 3 μm in diameter infiltrate deep into the avian lung with the depth of infiltration increasing when birds are exposed to particulates for multiple hours[34,35]. Inhaled particulate matter can weaken immune function, increase the inflammatory response, and elevate oxidative stress in both humans and animals[8,11,12]. Some of these effects can persist between developmental stages. For example, captive rhesus macaque (*Macaca mulatta*) infants exposed to wildfire smoke from distant fires in the first three months of life showed reduced immune function and lung capacity that persisted into adolescence[36]. Oxidative stress may mediate a trade-off between self-maintenance and growth[37,38]. A 2016 metanalysis found that increased oxidative stress produces a constraint on growth, leading to slower growth rates when oxidative stress is elevated[37]. Furthermore, genetic pathways responsible for oxidative damage repair and stress resistance also produce antagonistic effects on development, metabolism, and the completion of the cell cycle (reviewed in[38]). Elevated oxidative stress may be especially problematic early in development as organisms are thought to already have higher baseline levels of oxidative stress resulting from increased metabolic activity at that stage[38]. House wren nestlings experiencing elevated particulate matter early in development may devote more resources to antioxidant production or damage repair, reducing the resources available for growth.

Additionally, smoke may have altered the health and behavior of house wren parents, resulting in reduced food provisioning to offspring during the elevated smoke period. Elevated smoke or $PM_{2.5}$ concentrations produces behavioral changes in other species of birds. Tule geese (*Anser albifrons elgasi*) encountering thick smoke plumes during the 2020 migration season stopped flying or altered their flight paths[27]. Rock doves (*Columba livia*) exposed to phosphoric acids aerosols in the lab reduced spontaneous activity[39]. Similar declines in behavior following smoke exposure have been found in gibbons (*Hylobates albibarbis*)[25], Bornean orangutans (*Pongo pygmaeus wurmbii*)[26], painted lady butterflies (*Vanessa cardui L.*)[40], and Cape honeybees (*Apis mellifera capensis*)[41]. If house wren parents foraged less often during the smoke period, this may have slowed offspring growth. It is also possible that house wren parents suffered detrimental effects from smoke, even if their nests hatched after the smoke spike. Although there was no difference in size between these later hatching nests and those with the same timing in no-smoke years, it is possible this smoke event had additional impacts on nestling survival or performance that would only be evident on a longer time scale.

Depressed nestling growth may have also resulted from alterations in the food chain during the smoke period. Particulate pollution can reduce insect populations either directly or indirectly through its effect on their food sources[42]. In one study, squinting bush brown butterfly larva (*Bicyclus anynana*) exposed to elevated $PM_{2.5}$ from incense burning in the lab had increased mortality, delayed development, and suppressed pupal weight compared to controls[43]. Larvae that were raised in normal air but fed on vegetation grown under smoke conditions still showed delayed development and depressed pupal weight[43]. Elevated $PM_{2.5}$ concentrations can also lead to increased mortality in fruit flies (*Drosophila melanogaster*)[44] and decreased flight speed and duration in painted lady butterflies (*Vanessa cardui L.*)[40]. Therefore, the smoke event in this study may have altered prey abundance, quality, or behavior, reducing the food available for house wren nestlings.

Finally, smoke pollution may have depressed house wren nestling growth through its effects on temperature. Wildfire smoke plumes reduce daytime surface air temperatures by scattering or absorbing short-wave solar radiation[45]. Average day time air temperatures during the three-day smoke period in this study were notably cooler than the days preceeding this spike (three days smoke: average temperature ± s.d. = 14.06 ± 3.17 C; week before smoke: average temperature ± s.d. = 19.67 ± 2.57 C). This reduction in day-time temperatures may have had direct consequences for house wren nestlings. House wren broods with 4–6 nestlings in the nest can independently thermoregulate between days 3–5 after hatching[46]. Prior to this time, the female broods the young to maintain their temperature[47]. Lower ambient temperatures require females to spend more time brooding and less time foraging, potentially reducing food provisioning to the offspring. After reaching thermoregulatory independence, nestling metabolic rate increases with decreasing temperature, requiring more food from parents during cooler temperatures[48]. If parents were unable to match this increased demand, nestling growth may have slowed. Decreased daytime temperatures may also indirectly impact nestlings as insect prey is less active during these cold snaps[49,50].

Further work is needed to determine the mechanism driving the changes in nestling development during the smoke period. In this study, nests from the smoke year were compared to nests from the same time in the season in no-smoke years in order to control for the potential confounding effects of parental quality, seasonal fluctuations in prey type and abundance, and typical weather patterns. However, this is still an observational study. It is possible that an additional, unaccounted for variable unrelated to the direct or indirect effects of smoke differed between the smoke year and no-smoke years during the smoke period and was actually responsible for these differences. Replicate work in other populations during other smoke events and controlled experimental manipulations would help to untangle these possibilities.

Although sublethal, the changes to growth documented here likely have fitness consequences for the house wrens in this study. House wren nestlings show logistic growth early in development with the most rapid period of growth happening between days 3–8 after hatching[51,52]. During this time, nestlings grow an average of 0.52 g a day[51]. Thus, nestlings experiencing three days of elevated smoke during early development were more than a day behind in growth relative to their control counterparts. The magnitude of this effect is similar to the effect of sibling competition within a house wren nest. Work in other house wren populations has found that approximately half of house wren nests have eggs that hatch within one day (defined as synchronous hatching), whereas the other nests have eggs that hatch over a 2–4 day period (defined as asynchronous hatching)[53,54]. Compared to larger, asynchronous first-hatched siblings, late-hatching house wren nestlings are only 89% the size of their siblings on day 7 after hatching[52]. In some cases, slow-growing nestlings can gain weight after day 10–12 and catch up to their larger siblings[52]. Nestlings that cannot catch up in time risk starvation if their nestmates leave the nest (fledge) before they are able[47]. If the entire clutch is behind in development, they fledge later[55] and thus face extended risk of discovery by nest predators. House wren mass at fledging is an important predictor of house wren reproductive success. House wren nestlings in the top 25% of size-adjusted body mass are more than twice as likely to return from migration and breed in the subsequent years than nestlings in the bottom 25%[31].

Tarsometatarsus (tarsus) length may also have fitness consequences. This measure is a common proxy for overall body size in ornithology[56]. House wren tarsus length is relatively stable following day 11 after hatching[52]. Unlike mass and feather length, tarsus length does not change after fledging[52]. The fitness effects of tarsus length have not been directly examined in house wrens. However, tarsus length has a relationship with survival and reproduction in other passerine songbirds. In one study, house martin (*Delichon urbica*) nestlings found dead in the nest had shorter tarsi than their surviving siblings[57]. In another, pied flycatcher (*Ficedula hypoleuca*) nestlings with very short tarsi were less likely to survive between fledging and breeding[58]. Tarsus length is also correlated with male and/or female reproductive success in pied flycatchers[58,59], the red bishop (*Euplectes orix*)[60], and the blue tit (*Parus caeuleus*)[61]. While these changes in growth during just three days of elevated smoke pollution are subtle, they are likely to influence individual survival and reproductive success. Had this particulate exposure been longer, consequences for the population may have been more extreme.

Particulate pollution from wildfires poses an important threat to wildlife populations due to its ability to travel long distances. Animals living in fire-prone landscapes have experienced selection on the ability to detect and appropriately respond to approaching wildfires[62]. Populations living in landscapes where fire is rare or landscapes where fire characteristics (e.g. timing, intensity) have recently changed are at the biggest risk of extinction because they are evolutionarily naïve[62]. Wildfire smoke presents a particular conservation concern because of its ability to travel long distances to populations where fire is rare. These populations are unlikely to have experienced selection for physiological or behavioral responses that could mitigate the effects of wildfire smoke. This is especially likely when these smoke events are spatially or temporally unpredictable or short in duration, as the event in this study. This study suggests that a smoke event as short as three days may impact offspring development and, potentially, long-term survival and reproduction. Whether and how conservation managers can mitigate these effects depends on the mechanisms responsible. For example, providing supplemental dietary antioxidants to red-winged blackbirds (*Agelaius phoeniceus*) increases growth rate and reduces oxidative damage for the smallest nestlings in highly asynchronous nests[63]. Supplemental antioxidants could potentially mitigate the effects found in this study if they result from oxidative stress but may do nothing if they result from decreased temperatures or altered parental behavior. More work is therefore needed on the mechanism responsible for these developmental changes and which populations may be especially vulnerable to these developmental alterations. As climate change increases global particulate pollution from wildfires[64], more wildlife populations will be at risk in the future.

## Methods

### Study site and study species

House wrens visiting the study site have been tracked in detail since the summer of 2019. House wrens breeding in northeast Pennsylvania return from winter migration between mid-April and mid-May each year. Birds arrive at the study location and begin defending territory boundaries over the course of 4–5 weeks. Each year, the majority of birds arriving in these earliest waves are older birds that have previously bred at the study location. The date of the first egg laid varies as much as 3 weeks between nests in the first reproductive attempt in my study population. Birds that return from migration earlier are more likely to begin egg laying first.

House wren activity was monitored at a population nesting in 64 wooden nest boxes located in suitable forest edge habitat at Lackawanna State Park in Lackawanna County (41.580538, -75.703721). Boxes were placed at least 30 m apart over a region of approximately 0.95 square kilometers. The two most distant boxes were approximately 2.08 km apart. Nests were checked every 1–4 days in the morning or early afternoon for signs of wren activity, nest progress, egg laying, and nestling hatching. Nests were checked daily prior to two critical events: (1) the day of the first egg and (2) the day of nest hatching. Female house wrens lay one egg a day until the clutch is complete (4–8 eggs, average ± s.d. in this study: 6.22 ± 0.61 eggs). Females incubate the eggs for 10–15 days until they hatch. Day of hatching was defined as the day the first nestling hatched. In 2022 and 2023, 79% of nests had nestlings that all hatched within the first day (synchronous hatching). All remaining nestlings hatched within three days of the first nestling. In other populations, house wren nestlings that hatch more than a day after their siblings are consistently smaller during most of the nestling period[52]. Both males and females feed nestlings until they are big enough to leave the nest 14–20 days after hatching. Many birds at this study site complete two reproductive attempts each season. Only the first reproductive attempt was considered in this study.

House wren nestlings grow most rapidly between days 3–8 after hatching[51,52]. By day 8, some of the more developed nestlings have begun to approach their final mass and skeletal size[51,52]. At this point, rapid mass gain slows down while feather development continues[52]. House wrens reach asymptotic mass between days 9–13 and asymptotic tarsus length between days 9–11[51,52]. Later hatching nestlings that lag behind their siblings in size reach this asymptotic size at later ends of this range[52]. Work in other populations has found that house wren size at day 12 is a strong predictor of their survival and recruitment into the population the following year[31].

All adult wrens breeding at the study site were captured and color banded in order to track individuals within and between seasons. Forty-two males and 37 females were captured in 2021, 46 males and 49 females were captured in 2022, and 40 males and 54 females were captured in 2023. Birds were captured opportunistically throughout the breeding season during the pre-breeding, egg laying, incubation, or nestling periods of the reproductive cycle. Mist nets with and without audio lures were used to capture birds of both sexes. Some females were also trapped on the nest. For each adult, weight was measured to the nearest 0.25 g using a Pesola scale attached to a cotton bag, and the length of the tarsometatarsus leg bone was measured to the nearest 0.01 mm using digital calipers. Mass of adult female house wrens varies dramatically between the egg laying, incubation, and nestling stages[65]. Because adult male mass does not show these systematic fluctuations[65], the average size of 128 adult males in the population was compared to final nestling size in this study.

### Experimental design

Eleven house wren nests in 2023 experienced 3 days of elevated particulate matter ($PM_{2.5}$) concentrations in the first six days after hatching as the result of smoke from large wildland fires burning in Canada. $PM_{2.5}$ and air quality index (AQI) measurements for Lackawanna County were obtained from the U.S. Environmental Protection Agency (EPA) air quality monitoring system database[30]. The monitor used for this study was located in Scranton, Pennsylvania, approximately 22.5 km from the study site. $PM_{2.5}$ at this monitor was measured using a Teledyne Model T640 which takes continuous measurements and uses the US EPA Federal Equivalent

Method[30]. The U.S. EPA defines AQI values between 151–200 as “unhealthy” and 201–300 as “very unhealthy” for human populations. Both $PM_{2.5}$ concentrations and AQI were elevated into these unhealthy ranges on June 6th, 2023 (daily averages: $PM_{2.5}$ 102.4 μg/m$^3$, AQI 175), June 7th, 2023 (daily averages: $PM_{2.5}$ 217.7 μg/m$^3$, AQI 268), and June 8th, 2023 (daily averages: $PM_{2.5}$ 89.3 μg/m$^3$, AQI 168). In contrast, 17 nests in 2023 hatched either before or after this pollution spike and did not experience elevated $PM_{2.5}$ in the first six days. All nestlings in this group experienced daily average AQI values considered “good” (0–50) or “moderate” (51–100) on each of the 6 days after hatching (Table 1). Although precise $PM_{2.5}$ and AQI values at the study location may have varied slightly from those recorded by the monitor, it is highly likely that air quality was decreased at the study location during the three days in question as the sky was discolored and air quality warnings were issued for the entire county. Grouping nests into two categories (three-day smoke period, no smoke period) rather than using $PM_{2.5}$ concentration as a continuous predictor variable helps mitigate the sampling error that could be introduced by any differences between $PM_{2.5}$ concentration at the monitor location compared to the study site.

These nests from 2023 were compared to nests from 2021 and 2022 that hatched on the same day in the season. The day the first egg was laid at the study site for that year was set as day 1 in the season. Day in the season was used instead of Julian date for two reasons. First, weather patterns vary from year to year, leading to differences in Julian date timing of vegetation growth, insect abundance fluctuations, and migration arrival. Second, house wrens arriving from migration in earlier waves differ from later arrivals in ways that could impact nestling growth (e.g. age, experience, etc.). Fifteen nests from these control years hatched on dates that would have resulted in three days of smoke exposure in 2023. Nineteen nests from the control years hatched on dates considered ‘no smoke exposure’ in 2023. In both cases, all nestlings experienced low $PM_{2.5}$ concentrations and AQI levels in the “good” to “moderate” range on each of the 6 days after hatching (Table 1). All years included nests that hatched up until day 41. After this point, some birds were beginning their second reproductive attempt for the season. Only the first reproductive attempt was considered to avoid pseudoreplication and potential confounding effects of raising additional broods of nestlings.

Nests that had a one or two day overlap with the 3-day smoke period in the first 6 days after hatching were not included in this analysis for two reasons. First, $PM_{2.5}$ concentrations began increasing during the afternoon of June 6th and decreasing during the afternoon of June 8th. Because nests hatch throughout the day, a nest experiencing one or two days of the $PM_{2.5}$ spike could have experienced a very different dose of $PM_{2.5}$ than a nest hatching just a few hours earlier or later. Including only nests that experienced all three days of elevation in the first 6 days after hatching ensures each nest experienced comparable levels of $PM_{2.5}$. Second, the number of nests with one or two days in the smoke period was unbalanced between years (one day: 6 nests smoke year, 3 nests control years; two days: 3 nests smoke year, 12 nests control years). Including only nests with either three days or zero days in the smoke period during the first 6 days of life produced a more balanced designed that fit the assumptions of the statistical analyses. Including these nests as a separate category does not change the results presented here.

## Nestling measurements

To assess the effects of $PM_{2.5}$ on nestling growth, nests were measured at two points in development. Nestlings were measured on day 6 after hatching with day 1 defined as the day the first nestling hatched. Day 6 is in the middle of the period of most rapid growth[51,52]. To determine if smoke pollution had lasting effects, the same nests were measured again on day 10 after hatching. Researchers at this study site avoid handling nestlings between days 11–16 after hatching to prevent scaring nestlings into leaving the nest prematurely. Therefore, day 10 measurements provide the final known size. One nest in the ‘no smoke exposure’ period of the smoke year and one nest in the ‘smoke exposure’ period in a no-smoke year were destroyed by predators before reaching day 10. Additionally, tarsometatarsus was not measured for one nest in the ‘smoke exposure’ period in a no-smoke year. Overall, 62 nests were included in the day 6 analysis but only 60 were available for the day 10 body mass analysis and 59 for the day 10 tarsus analysis. Each nestling was briefly removed from the nest box and weighed to the nearest 0.05 g (day 6) or 0.25 g (day 10) using a Pesola scale attached to a cotton bag. The length of the tarsometatarsus leg bone was measured to the nearest 0.01 mm using a pair of digital calipers. This is a proxy for overall skeletal size. Measurements for all nestlings in the nest were averaged together to produce a single measurement for further analysis.

## Statistical analysis

The effects of $PM_{2.5}$ exposure on the three dependent variables (average mass on day 6, average mass on day 10, average length of the tarsometatarsus bone on day 10) were evaluated using the following procedure. The effects of year (smoke versus control), hatching time relative to the pollution spike (three days of elevated $PM_{2.5}$ in first six days versus no elevation in first six days) and their interaction were evaluated using a two-way ANOVA (analysis of variance test) with type III sum of squares. Post-hoc contrasts using estimated marginal means and a Šidák correction to correct for multiple comparisons were then used to evaluate the effect of year for each level of hatching time in models with significant interaction terms. One ANOVA was conducted for each dependent variable. A Shapiro–Wilk statistic was used to assess the normality of model residuals, a Levene’s test was used to assess the homogeneity of variance between groups, and Cook’s distance in a residuals versus leverage plot was used to identify potential outliers. All models fit the assumptions of an ANOVA. All tests were two-tailed with an alpha level of 0.05. All tests were conducted in R version 4.1.2 using the packages ‘car’[66], ‘olsrr’[67], and ‘emmeans’[68].

## Ethics statement

All work in this study was conducted in accordance with appropriate federal and state permits (Federal Bird Banding Permit 23,302, Pennsylvania Game Commission special use 45,599 and 52257, Pennsylvania DCNR permit for research and/or collection of state park resources 2019–30 and 2022–14). This work was approved by the University of Scranton Institutional Animal Care and Use Committee (#1–19, 1–22). This study complies with the Ornithological Council's guidelines to the use of wild birds in research and the ARRIVE guidelines. No birds suffered adverse effects during brief capture and measurement.

## Data availability

All data supporting this study are available within this manuscript and associated supplementary information files (Supplementary Data 1).

Received: 21 November 2023; Accepted: 4 March 2025
Published online: 10 March 2025

## References

1. Jolly, W. M. et al. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nat. Commun.* **6**, 7537. https://doi.org/10.1038/ncomms8537 (2015).
2. Abatzoglou, J. T. & Williams, A. P. Impact of anthropogenic climate change on wildfire across western US forests. *PNAS* **113**, 11770–11775 (2016).
3. Abram, N. J. et al. Connections of climate change and variability to large and extreme forest fires in southeast Australia. *Commun. Earth Environ.* **2**, 8. https://doi.org/10.1038/s43247-020-00065-8 (2021).
4. Flannigan, M. et al. Global wildland fire season severity in the 21st century. *For. Ecol. Manag.* **294**, 54–61 (2013).
5. Attiwill, P. & Binkley, D. Exploring the mega-fire reality: a 'Forest Ecology and Management' conference. *For. Ecol. Manag.* **294**, 1–3 (2013).
6. Williams, J. Exploring the onset of high-impact mega-fires through a forest land management prism. *For. Ecol. Manag.* **294**, 4–10 (2013).
7. Engstrom, R. T. First-order fire effects on animals: review and recommendations. *Fire Ecol.* **6**, 115–130 (2010).
8. Sanderfoot, O. V. et al. A review of the effects of wildfire smoke on the health and behavior of wildlife. *Environ. Res. Lett.* **16**, 123003. https://doi.org/10.1088/1748-9326/ac30f6 (2021).
9. Sanderfoot, O. V. & Holloway, T. Air pollution impacts on avian species via inhalation exposure and associated outcomes. *Environ. Res. Lett.* **12**, 083002. https://doi.org/10.1088/1748-9326/aa8051 (2017).
10. Makkonen, U., Hellén, H., Anttila, P. & Ferm, M. Size distribution and chemical composition of airborne particles in south-eastern Finland during different seasons and wildfire episodes in 2006. *Sci. Total Environ.* **408**, 644–651 (2010).
11. Reid, C. E. et al. Critical review of health impacts of wildfire smoke exposure. *Environ. Health Perspect.* **124**, 1334–1343 (2016).
12. Cascio, W. E. Wildland fire smoke and human health. *Sci. Total Environ.* **624**, 586–595 (2018).
13. Chen, G. et al. Mortality risk attributable to wildfire-related $PM_{2.5}$ pollution: a global time series study in 749 locations. *Lancet Planet Health* **5**, e579–e587. https://doi.org/10.1016/S2542-5196(21)00200-X (2021).
14. Johnston, F. H. et al. Estimated global mortality attributable to smoke from landscape fires. *Environ. Health Perspect.* **120**, 695–701 (2012).
15. Wegesser, T. C., Pinkerton, K. E. & Last, J. A. California wildfires of 2008: coarse and fine particulate matter toxicity. *Environ. Health Perspect.* **117**, 893–897 (2009).
16. Aguilera, R., Corringham, T., Gershunov, A. & Benmarhnia, T. Wildfire smoke impacts respiratory health more than fine particles from other sources: observational evidence from Southern California. *Nat. Commun.* **12**, 1493. https://doi.org/10.1038/s41467-021-21708-0 (2021).
17. Karthikeyan, S., Balasubramanian, R. & Iouri, K. Particulate air pollution from bushfires: human exposure and possible health effects. *J. Toxicol. Environ. Health Part A* **69**, 1895–1908 (2006).
18. Verma, V. et al. Physiocochemical and toxicological profiles of particulate matter in Los Angeles during the October 2007 Southern California wildfires. *Environ. Sci. Technol.* **43**, 954–960 (2009).
19. Wong, J. P. S. et al. Effects of atmospheric processing on the oxidative potential of biomass burning organic aerosols. *Environ. Sci. Technol.* **53**, 6747–6756 (2019).
20. Singer, F. J., Schreier, W., Oppenheim, J. & Garton, E. O. Drought, fires, and large mammals. *BioScience* **39**, 716–722 (1989).
21. Cahill, A. J. & Walker, J. S. The effects of forest fire on the nesting success of the Red-knobbed Hornbill *Aceros cassidix*. *Bird Conserv. Int.* **10**, 109–114 (2000).
22. Sanderfoot, O. V. & Gardner, B. Wildfire smoke affects detection of birds in Washington State. *Ornithol. Appl.* **123**, 1–14 (2021).
23. Ayars, J. et al. Camera traps link population-level activity patterns with wildfire smoke events for mammals in Eastern Washington State. *Fire Ecol.* **19**, 49. https://doi.org/10.1186/s42408-023-00207-1 (2023).
24. Lee, B. P. Y., Davies, Z. G. & Struebig, M. J. Smoke pollution disrupted biodiversity during the 2015 El Niño fires in Southeast Asia. *Environ. Res. Lett.* **12**, 094022. https://doi.org/10.1088/1748-9326-aa87ed (2017).
25. Cheyne, S. M. Effects of meteorology, astronomical variables, location and human disturbance on the singing apes: *Hylobates albibarbis*. *Amr. J. Primatol.* **70**, 386–392 (2008).
26. Erb, W. M., Barrow, E. J., Hofner, A. N., Utami-Atmoko, S. S. & Vogel, E. R. Wildfire smoke impacts activity and energetics of wild Bornean orangutans. *Sci. Rep.* **8**, 7606. https://doi.org/10.1038/s41598-018-25847-1 (2018).
27. Overton, C. T. et al. Megafires and thick smoke portend big problems for migratory birds. *Ecol.* **103**, e03552. https://doi.org/10.1002/ecy.3552 (2022).
28. Yang, D., Yang, A., Yang, J., Xu, R. & Qiu, H. Unprecedented migratory bird die-off: a citizen-based analysis on the spatiotemporal patterns of mass mortality events in the Western United States. *GeoHealth.* **5**, e2021GH000395. https://doi.org/10.1029/2021GH000395 (2021).
29. Natural Resources Canada. Canadian wildland fire information system. https://cwfis.cfs.nrcan.gc.ca/home (2023).
30. U.S. Environmental Protection Agency (EPA). Air quality system data mart. https://www.epa.gov/outdoor-air-quality-data (2023).
31. Brown, R. E., Brain, J. D. & Wang, N. The avian respiratory system: a unique model for studies of respiratory toxicosis and for monitoring air quality. *Environ. Health Perspect.* **105**, 188–200 (1997).
32. Newman, J. R. & Schreiber, R. K. Animals as indicators of ecosystem responses to air emissions. *Environ. Manag.* **8**, 309–324 (1984).
33. Tell, L. A. et al. An aerosolized fluorescent microsphere technique for evaluating particle deposition in the avian respiratory tract. *Avian Dis.* **50**, 238–244 (2006).
34. Tell, L. A., Stephens, K., Teague, S. V., Pinkerton, K. E. & Raabe, O. G. Study of nebulization delivery of aerosolized fluorescent microspheres to the avian respiratory tract. *Avian Dis.* **56**, 381–386 (2012).
35. Black, C. et al. Early life wildfire smoke exposure is associated with immune dysregulation and lung function decrements in adolescence. *Am. J. Respir. Cell. Mol. Biol.* **56**, 657–666 (2017).
36. Smith, S. M., Nager, R. G. & Costantini, D. Meta-analysis indicates that oxidative stress is both a constraint on and a cost of growth. *Ecol. Evol.* **6**, 2833–2842 (2016).

37. Metcalfe, N. B. & Alonso-Alvarez, C. Oxidative stress as a life-history constraint: the role of reactive oxygen species in shaping phenotypes from conception to death. *Funct. Ecol.* **24**, 984–996 (2010).
38. Sterner, R. T. Whole body exposures to a phosphoric acids aerosol: I. Spontaneous activity effects in wild rodent and avian species. *J. Toxicol. Environ. Health* **39**, 287–308 (1993).
39. Liu, Y., Wooster, M. J., Grosvenor, M. J., Lim, K. A. S. & Francis, R. A. Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.) *Ecol. Entomol.* **46**, 195–208 (2021).
40. Tribe, G., Tautz, J., Sternberg, K. & Cullinan, J. Firewalls in bee nests- survival value of propolis walls of wild Cape honeybee (*Apis mellifera capensis*). *Sci. Nat.* **104**, 29. https://doi.org/10.1007/s00114-017-1449-5 (2017).
41. Liu, Y. et al. Systematic mapping and review of landscape fire smoke (LFS) exposure impacts on insects. *Environ. Entomol.* **51**, 871–884 (2022).
42. Tan, Y. Q., Dion, E. & Monteiro, A. Haze smoke impacts survival and development of butterflies. *Sci. Rep.* **8**, 15667. https://doi.org/10.1038/s41598-018-34043-0 (2018).
43. Wang, X. et al. Exposure to concentrated ambient $PM_{2.5}$ shortens lifespan and induces inflammation-associated signaling and oxidative stress in Drosophila. *Toxicol. Sci.* **156**, 199–207 (2017).
44. Robock, A. Surface cooling due to forest fire smoke. *J. Geophys. Res.* **96**, 20869–20878 (1991).
45. Dunn, E. H. The relationship between brood size and age of effective homeothermy in nestling house wrens. *Wilson Bull.* **88**, 478–482 (1976).
46. Johnson, L. S. House wren (*Troglodytes aedon*), version 1.0. in *Birds of the World* (ed. Poole, A. F.) https://doi.org/10.2173/bow.houwre.01 (Cornell Lab of Ornithology, 2020).
47. Dykstra, C. R. & Karasov, W. H. Daily energy expenditure by nestling house wrens. *Condor* **95**, 1028–1030 (1993).
48. Taylor, L. R. Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol.* **32**, 99–117 (1963).
49. Winkler, D. W., Luo, M. K. & Rakhimberdiev, E. Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). *Oecologia* **173**, 129–138 (2013).
50. Zach, R. Nestling house wrens: weight and feather growth. *Can. J. Zool.* **60**, 1417–1425 (1982).
51. Lago, K., Johnson, L. S. & Albrecht, D. J. Growth of late-hatched, competitively disadvantaged nestling house wrens relative to their older, larger nestmates. *J. Field Ornithol.* **71**, 676–685 (2000).
52. Harper, R. G., Juliano, S. A. & Thompson, C. F. Avian hatching asynchrony: brood classification based on discriminant function analysis of nestling masses. *Ecol.* **74**, 1191–1196 (1993).
53. Harper, R. G., Juliano, S. A. & Thompson, C. F. Intrapopulation variation in hatching synchrony in house wrens: test of the individual-optimization hypothesis. *The Auk* **111**, 516–524 (1994).
54. Johnson, L. S. J., Rauch, R. L. & Dellone, S. N. The process and causes of fledging in a cavity-nesting passerine bird, the house wren (*Troglodytes aedon*). *Ethol.* **110**, 693–705 (2004).
55. Bowers, E. K., Nietz, D., Thompson, C. F. & Sakaluk, S. K. Parental provisioning in house wrens: effects of varying brood size and consequences for offspring. *Behav. Ecol.* **25**, 1485–1493 (2014).
56. Rising, J. D. & Somers, K. M. The measurement of overall body size in birds. *The Auk* **106**, 666–674 (1989).
57. Christe, P., Møller, A. P. & de Lope, F. Immunocompetence and nestling survival in the house martin: the tasty chick hypothesis. *Oikos* **83**, 175–179 (1998).
58. Alatalo, R. V. & Lundberg, A. Heritability and selection on tarsus length in the pied flycatcher (*Ficedula hypoleuca*). *Evol.* **40**, 574–583 (1986).
59. Potti, J. & Merino, S. Heritability estimates and maternal effects on tarsus length in pied flycatchers. *Ficedula hypoleuca. Oecologia* **100**, 331–338 (1994).
60. Fridel, T. W. P. & Klump, G. M. Extrapair paternity in the red bishop (*Euplectes orix*): is there evidence for the good-genes hypothesis?. *Behav.* **139**, 777–800 (2002).
61. Kempenaers, B., Verheyen, G. R. & Dhondt, A. A. Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behav. Ecol.* **8**, 481–492 (1997).
62. Nimmo, D. G., Carthey, A. J. R., Jolly, C. J. & Blumstein, D. T. Welcome to the pyrocene: animal survival in the age of megafire. *Glob. Change Biol.* **27**, 5684–5693 (2021).
63. Hall, M. E., Blount, J. D., Forbes, S. & Royle, N. J. Does oxidative stress mediate the trade-off between growth and self-maintenance in structured families?. *Funct. Ecol.* **24**, 365–373 (2010).
64. Jacob, D. J. & Winner, D. A. Effect of climate change on air quality. *Atmos. Environ.* **43**, 51–63 (2009).
65. Freed, L. A. Loss of mass in breeding wrens: stress or adaptation?. *Ecol.* **62**, 1179–1186 (1981).
66. Fox, J. & Weisberg, S. *An {R} companion to applied regression, third edition*. (Sage, 2019).
67. Hebbali, A. olsrr: Tool for building OLS regression models. *R package version 0.5.3* (2020).
68. Lenth, R. V. emmeans: Estimated marginal means, aka least-squared means. *R package version 1.8.8* (2023).

## Acknowledgements
I thank Rob Barrese and Lackawanna State Park for support and access to lands. K. Odom, S. Power, J. Turnak, C. Zaic, and E. Kurilla contributed to the field work for this study. This work was supported by internal funds from the University of Scranton.

## Author contributions
C. Krieg is responsible for all contributions in this manuscript.

## Declarations

## Competitng interests
The author has no competing interests to declare.

## Additional information
**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-93101-6.

**Correspondence** and requests for materials should be addressed to C.A.K.

**Reprints and permissions information** is available at www.nature.com/reprints.

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.