

Research



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Rainy springs linked to poor nestling growth in a declining avian aerial insectivore (*Tachycineta bicolor*)

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As species shift their ranges and phenology to cope with climate change, many are left without a ready supply of their preferred food source during critical life stages. Food shortages are often assumed to be driven by reduced total food abundance, but here we propose that climate change may cause short-term food shortages for foraging specialists without affecting overall food availability. We frame this hypothesis around the special case of birds that forage on flying insects for whom effects mediated by their shared food resource have been proposed to cause avian aerial insectivores' decline worldwide. Flying insects are inactive during cold, wet or windy conditions, effectively reducing food availability to zero even if insect abundance remains otherwise unchanged. Using long-term monitoring data from a declining population of tree swallows (*Tachycineta bicolor*), we show that nestlings' body mass declined substantially from 1977 to 2017. In 2017, nestlings had lower body mass if it rained during the preceding 3 days, though females increased provisioning rates, potentially in an attempt to compensate. Adult body mass, particularly that of the males, has also declined over the long-term study. Mean rainfall during the nestling period has increased by 9.3 ± 0.3 mm decade⁻¹, potentially explaining declining nestling body mass and population declines. Therefore, we suggest that reduced food availability, distinct from food abundance, may be an important and previously overlooked consequence of climate change, which could be affecting populations of species that specialize on foraging on flying insects.

1. Introduction

As local weather patterns shift in response to climate change, many species are declining because of decreased food abundance [1]. Commonly, climate change reduces food abundance by creating mismatches between offspring demand and the timing of food abundance peaks, as species at differing trophic levels shift their phenology to different degrees [2]. Such mismatches have been linked to population declines in a number of species [1]. Further, spatial mismatches can be as important as temporal ones [1]. As ranges shift in response to climate change and populations go locally extinct, species at higher trophic levels may face food shortages, particularly in the case of specialists [3]. Although less common in the literature, local extinction of prey species has been documented to lead to their predators' extinction [4].

Avian aerial insectivores, a taxonomically diverse guild of birds that forage for flying insects, may also experience food shortages owing to climate change. These birds are declining worldwide [5–8], with particularly strong declines in northeastern North America [5,6]. Although the causes of decline are as yet unknown, insect shortages are a commonly cited hypothesis [9–11]; however, mean insect abundance during nestling development is not predictive of

nestling body mass or survival in cliff, barn or tree swallows [12]. Instead, we suggest short-term shortages of insect prey may be more important. As the climate changes, northeastern North America is experiencing increased precipitation and more variable weather, with both more warm and cold spring days [13]. When local weather conditions are wetter, colder or windier, aerial insects decrease activity [9,14–16], potentially subjecting avian aerial insectivores, and other species that rely on flying insects, to short-term but drastic reductions in food availability, even though overall food abundance is unaffected. The relative importance of short-term reductions in food availability driven by inclement weather for population dynamics could be dependent on its coincidence with periods of high demand for food by dependent offspring.

When weather conditions are poor, parents may be able to compensate for low food availability by increasing their foraging effort, perhaps at the cost of self-maintenance. Although the effects of weather-related food shortages on parental condition are unknown, the avian parental effort has been experimentally altered. In response to these manipulations, parents of many species increase offspring provisioning rates at the expense of their own body condition [17–19], which could explain declining adult body mass in tree swallows [20]. However, other studies have found that parents do not increase effort to compensate for food shortages to the nestlings, suggesting that parents already provision at maximal levels for their local conditions [21–23].

General declines in aerial insect populations may also be contributing to population declines in aerial insectivores. Although long-term records are uncommon, those available show that overall insect abundance may be declining substantially, even as some generalist taxa increase [24–29]. Widespread insect declines may be linked to agricultural intensification and our increasing reliance on pesticides and monocropping ([30] but see [29]). Intensive agriculture has been linked to declines in farmland birds, including aerial insectivores [31–33]. If widespread insect population declines contributed to avian population declines, then we would expect adults to begin breeding at lower body mass and lose more mass throughout the season and nestlings to grow more slowly. If declining insect abundance alone caused the declines, we would not expect these changes to be linked to short-term weather patterns.

Whether short or long-term, food shortages could contribute to aerial insectivore decline by reducing offspring growth. With less food available, we would expect young to grow more slowly and have higher mortality on cool, wet days. For tree swallows (*Tachycineta bicolor*), a common avian aerial insectivore, nestlings are more likely to die when the daily maximum temperature does not exceed 18.5°C, a critical threshold for flying insects [9]. However, the relative importance of temperature, wind speed and precipitation for nestling growth and survival is still unknown [9]. In many species, poor nestling growth is linked to lower fledging success and survival post-fledging [34,35], when most juvenile mortality occurs [36]. Thus, food shortages have the potential to cause population declines by reducing fledging success and juvenile survival [37].

Here, we use a combination of long-term monitoring data from a box-nesting population of tree swallows (1975–2017) and short-term intensive monitoring (2017) to determine how shifting local weather conditions affect tree swallow

body mass. Using the long-term record, we first determined if nestling body mass had declined, indicating reduced growth rates and poor parental provisioning. We also assessed whether adults lost more body mass during the breeding season in recent years as compared to earlier years in the long-term record, indicating that parents increased foraging effort to provision offspring and/or that food availability had declined to the point where adults were unable to forage enough to meet their own needs. We assessed the relative ability of temperature, wind and rain to predict nestling growth and parental effort during the 2017 breeding season and determined if weather parameters that predicted nestling growth or parental effort had changed across time.

2. Material and methods

(a) Long-term monitoring field methods

We monitored a box-nesting population of tree swallows at the Queen's University Biological Station in southeastern Ontario, Canada (44.521° N, 76.385° W) regularly during the annual breeding season (May to July) from 1975 to 2017. Nest-boxes in this population are arranged in grids to mimic the natural distribution of cavities [38]. From 1983 to 2017, we captured adults during breeding. Adults were sexed based on the presence of a brood patch (female) or cloacal protuberance (male). In most years, we also measured adult body mass and wing chord. From 1977 to 2017, nestlings were ringed at 10–16 days old, at which time their body mass and wing chord were also measured. Across the dataset used in this study, we measured 1437 females, 585 males and 10 232 nestlings.

(b) Field methods monitoring nestling development in 2017

We expected that slowed nestling growth and changing patterns of adult body mass evident in the long-term data might be explained by changing local weather patterns. To elucidate associations between nestling growth and daily weather conditions, we closely tracked the growth of 445 nestlings from 91 nests from 25 April to 25 July 2017. We measured nestling body mass every other day from 2 to 12 days old (i.e. at days 2, 4, 6, 8, 10 and 12, $n = 1723$). We did not measure nestlings on days when it was raining so heavily that we would be unable to keep them dry, resulting in some gaps in the measurement records. At 12 days old, we fitted nestlings with a numbered aluminium Canadian Wildlife Service ring.

We caught adults between day 10 and 12 of incubation using a combination of mist netting (males and females) and hand trapping techniques (females). At this time, we fitted each female with a passive integrated transponder (PIT) tag embedded in a leg band. On day 10 of nestling development, we used radio-frequency identification (RFID) at the entrance to the nest-box to determine parental provisioning rates using the set-up developed in [39]. Provisioning rates (i.e. numbers of visits by the parent to the nest-box) accurately reflect the amount of food nestlings received because tree swallows bring similar amounts of insects each trip [40]. We were unable to deploy RFID readers on rainy days. We were able to measure provisioning rates for 55 females.

We compiled wind speed data from weather stations at the Queen's University Biological Station and all other weather data from Environment Canada's Hartington Court weather station (approx. 30 km from the site) [41]. Variables included

maximum daily temperature, daily rainfall and mean wind speed during hours of active foraging (5.30–20.00).

(c) Analysis of long-term trends in body size

To determine whether nestling body mass declined over the long-term record, we used linear mixed models (LMMs). We tested whether body mass varied with the fixed effects of nestling age at the time of measurement, year and their interaction for 10- to 16-day-old nestlings. The response variable in these analyses was body mass of individual nestlings measured only at one time point, so we inferred growth rate from the relationship between nestling body mass and age. If this relationship had changed over time, that would indicate changes in growth rate. Nestling growth rates may have declined over time if food has become more limited. We included a random intercept for nest identity (ID) to account for similar growth trajectories of nest-mates. To determine if nestling body size had changed, we repeated this analysis using the nestling wing chord as the response variable.

Adult body mass might also be affected if food abundance during the breeding season had declined. We expected adult body mass to decline as offspring developed because both parents expend energy to care for their offspring. Therefore, we determined if adult body mass had changed from 1983 to 2017 using LMMs with body mass as the response variable and number of days since the first egg was laid, year and their interaction as fixed effects. Because males and females have different roles (females incubate the eggs and provision nestlings; males only provision nestlings and do so to a lesser degree than females [42]) and because males were typically caught only after nestlings hatched compared to females which were also caught during incubation, we conducted separate analyses for the two sexes. Body mass might not decline linearly during breeding, so we tested for first through to third-order polynomial relationships between adult mass and days since the first egg was laid. Some birds were measured more than once, either within a year or in multiple years, so we included a random intercept for bird ID. To determine if overall body size had changed through time, we conducted similar LMM with wing chord as the response variable and year as the predictor, conducting separate LMMs for each sex. As moulting occurs immediately after the breeding season, wing chord should be static throughout our measurement period, so we did not include days since the onset of egg laying in these models.

(d) Analysis of the effects of local weather conditions in 2017

To determine nestling growth trajectories in 2017, we conducted a linear model with nestling body mass as the response variable and age as the predictor. As growth is often not linear, we assessed the fit of first through to third-order polynomials and logistic regression, settling on a third-order polynomial as the best fit based on Akaike information criterion corrected for small sample size (AICc) score. Younger nestlings had less variation in mass than older nestlings (electronic supplementary material, figure S1), so we used the 'varFixed' function in the *nlme* package to allow variation in mass to increase with age [43,44]. Residual body mass from this model reflects whether individual nestlings were heavy or light for their age.

To assess relations between weather and nestling growth in 2017, we conducted three LMMs from the *lme4* package [45] with residual mass as the response variable and thermoregulatory strategy (poikilotherm, intermediate, homeotherm), one of three weather variables and their interaction as predictors. Thermoregulatory strategy accounts for age-dependent differences in nestlings' response to cold temperatures and starvation. From 0 to 6 days nestlings are poikilothermic, unable to thermoregulate, and can

enter torpor in cold weather; 7–8-day-old nestlings are intermediate, just beginning to develop homeothermy, while 9+ day-old nestlings are fully homeothermic, requiring a constant food source for thermoregulation [46,47]. Whether nestlings are able to enter torpor in response to starvation and cold (poikilotherm) or require constant food sources to fuel metabolism (homeotherm) may influence nestlings' response to weather conditions. We considered total rainfall, mean windspeed and mean maximum daily temperature during the 3 days prior to the day we measured the nestlings because tree swallow nestling development suffers most when inclement weather lasts for three or more days [48]. To distinguish between body mass changes within and between nestlings, we mean centred residual body mass for each nestling, following [49], and tested for nested random intercepts for nestling ID within nest ID. We then ranked the three top models by AICc and adjusted R^2 to determine which weather variable best predicted residual nestling body mass.

To assess the relationship between local weather conditions and female provisioning behaviour, we calculated hourly provisioning rates for PIT-tagged females in 2017 based on 2 h of RFID readings at the nest, following [39]. We conducted separate linear regressions to assess the effects of local weather conditions on provisioning rate, accounting for brood size. We expected females to provision less often when they had fewer offspring demanding food. For weather variables, we considered maximum temperature and mean windspeed on the day of provisioning measurements, and whether or not it had rained in the 3 days prior (as it never rained during our recordings).

(e) Analysis of long-term weather patterns

Because we found that rainfall in the 3 days prior was most predictive of nestling body mass in 2017, we calculated the total rainfall from hatching to fledging for each nest across the long-term dataset. Then, we calculated annual mean rainfall experienced by developing nestlings from 1975 to 2017 and used a linear regression to assess whether this value had changed over time, including a comparison of models with first through to third-order polynomial relationships.

All analyses were conducted in R, version 3.4.3 (30 November 2017) [50]. Assumptions of normality were verified via histograms, quartile–quartile plots and the Shapiro–Wilks tests. The fit of the global model was verified by plotting residuals against all predictors and response variables, verifying for homoskedasticity and the absence of trends, indicating a well-fitting model. We retained all significant variables (as calculated using the *lmerTest* package for models with random effects [51]). We retained random effects when the variance explained was greater than the standard deviation. We assessed the need for inclusion of first-, second- and third-order polynomials by comparing AICc scores.

3. Results

(a) Long-term trends in body size

Nestling body mass has changed over the long-term study period (figure 1). Nestlings are not gaining body mass as much as they used to (age \times year, $F_{1,3466.2} = 26.6$, $p < 0.001$, $n = 10\,232$). In 1977, when we first began measuring nestlings, we inferred from body mass records that 10-day-old to 16-day-old nestlings were growing at a rate of $0.77 \pm 0.08 \text{ g d}^{-1}$ (approx. 3.5% of adult body mass). By contrast, by 2017, nestlings were not growing at all during this period ($-0.05 \pm 0.09 \text{ g d}^{-1}$). The decline in body mass is not simply owing to nestlings being generally smaller; we inferred that nestling wing chord has grown at the same rate from 1988 to 2017 ($2.5 \pm 0.2 \text{ mm d}^{-1}$; age, $F_{1,1460.6} = 164.1$, $p < 0.001$).

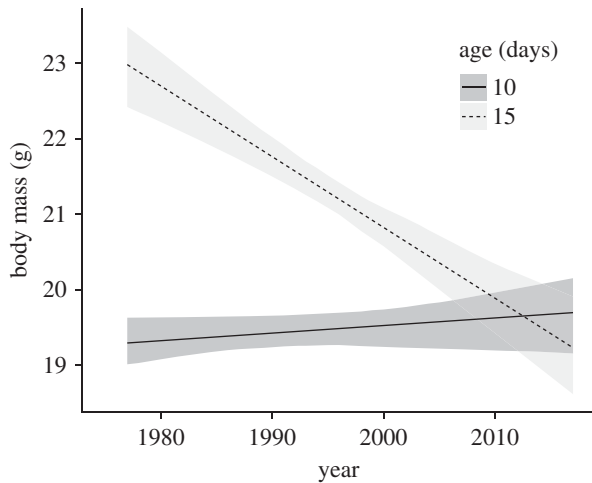


Figure 1. Nestling tree swallows have not gained as much body mass in recent years as they did in the past ($\text{age} \times \text{year}$, $F = 26.56$, $p < 0.001$), illustrated here with data from 10- and 15-day-old nestlings. In 1977, 15-day-old nestlings were considerably heavier than 10-day-old nestlings (23.0 ± 0.3 and 19.3 ± 0.2 g, respectively). By contrast, by 2017, model predictions show 10- and 15-day-old nestlings have similar body mass (19.7 ± 0.3 and 19.2 ± 0.4 g, respectively). The solid line represents model-projected body mass of a 10-day-old nestling from 1975 to 2017. The dashed line represents the projected body mass of a 15-day-old nestling from 1975 to 2017. Shaded areas represent 95% confidence intervals on the projections (dark grey for 10-day-old, light grey for 15-day-old).

It is not just nestlings that are losing body mass. Adult females have always lost body mass throughout the breeding season as they incubate and provision their nestlings. However, in recent years, adult females began breeding at lower body mass and spent more time during incubation recouping body mass before losing body mass again during nestling provisioning, as compared to females earlier in the long-term study (figure 2a; (no. days since first egg) $^2 \times \text{year}$, $F_{2,2885.2} = 31.0$, $p < 0.001$, $n = 3176$). Males were typically not caught prior to incubation so we focused on changes in body mass after hatching, while males were provisioning. Males lost more body mass during nestling provisioning than in the past (figure 2b; no. days since first egg $\times \text{year}$, $F_{1,1141.0} = 5.8$, $p = 0.016$, $n = 1148$). As with nestlings, changing body mass cannot be explained by changes in body size in males or females; wing chord has not declined through time, it even slightly increased in males (females, year, $F_{1,1529.1} = 0.004$, $p = 0.95$; males, 0.3 ± 0.01 mm decade $^{-1}$, year, $F_{1,760.04} = 6.9$, $p = 0.009$, $n_{\text{females}} = 3170$, $n_{\text{males}} = 1477$).

(b) Effects of local weather conditions in 2017

As expected, nestling body mass increased as nestlings got older (age^3 , $F_{3,1719} = 4205.7$, $p < 0.001$, $n = 1723$). Nestling residual body mass was associated with total rainfall, mean windspeed, and mean maximum daily temperature in the 3 days prior to measurement but the strength of the association depended on the thermoregulatory strategy employed by the nestling (rain \times thermoreg., $F_{5,1717} = 22.6$, $p < 0.001$; wind \times thermoreg., $F_{5,1717} = 7.0$, $p < 0.001$; max. temp. \times thermoreg., $F_{5,1717} = 34.1$, $p < 0.001$). When ranked by AICc and R^2 , total rainfall was the best predictor of residual body mass (table 1). Nestlings were lighter for their age when it had rained more in the previous 3 days, particularly

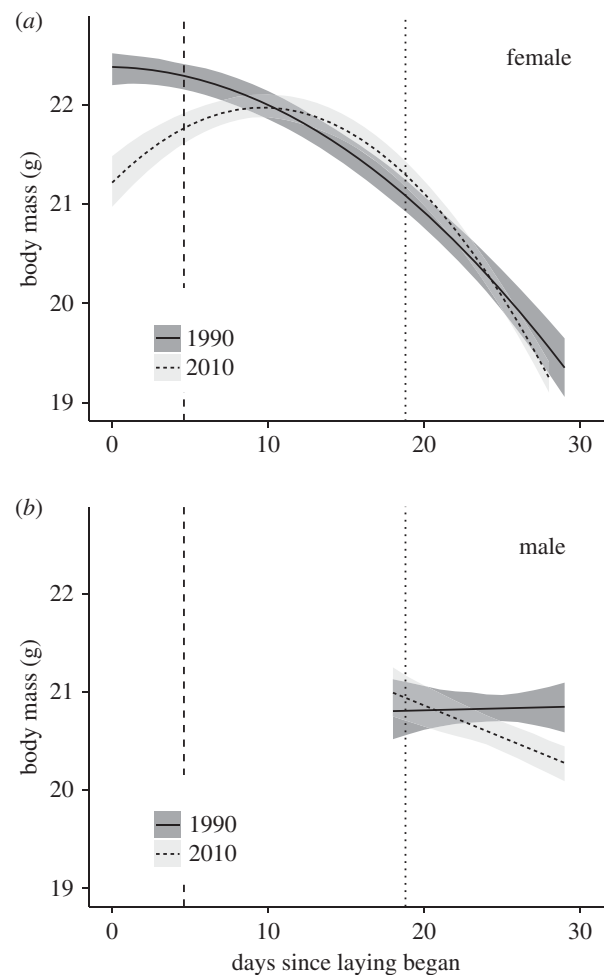


Figure 2. Adult tree swallow body mass fluctuates throughout the breeding season, but these fluctuations have changed from 1983 to 2017, illustrated here with representative data from 1990 and 2010 only, for clarity. (a) For females, body mass has always declined throughout the breeding season. However, in recent years (e.g. 2010), females have started breeding with lower body mass and are spending egg laying and the beginning of incubation gaining mass. (b) In the past (e.g. 1990), male body mass did not change over the breeding period, but in more recent years, males lost body mass during nestling provisioning (e.g. 2010). The solid lines represent model-projected adult mass throughout the breeding season in 1990 and the dashed lines represent adult mass during 2010. Shaded areas represent 95% confidence intervals (dark grey for 1990, light grey for 2010). The vertical dashed line represents the mean start of incubation (4.6 days after the first egg was laid) and the vertical dotted line represents the mean day of hatching (18.8 days after the first egg was laid).

for older, homeothermic nestlings (figure 3; homeotherm $\beta = -0.12 \pm 0.01$ residual mass mm $^{-1}$ rain; intermediate $\beta = -0.07 \pm 0.01$; poikilotherm $\beta = -0.06 \pm 0.01$).

Female provisioning rates were predicted by whether it had rained in the 3 days prior to measurement of behaviour (figure 4a; $F_{1,50} = 5.9$, $p = 0.019$, $n = 53$). If it had rained, female provisioning rate increased by an average of 4 ± 2 visits h $^{-1}$. Female provisioning rate also increased as the number of nestlings in the nest increased (figure 4b; 2.0 ± 0.7 visits h $^{-1}$ nestling $^{-1}$, $F_{1,50} = 7.7$, $p = 0.008$).

(c) Long-term weather patterns

Since 1975, the mean rainfall during nestling development, which was associated both with lower nestling body mass

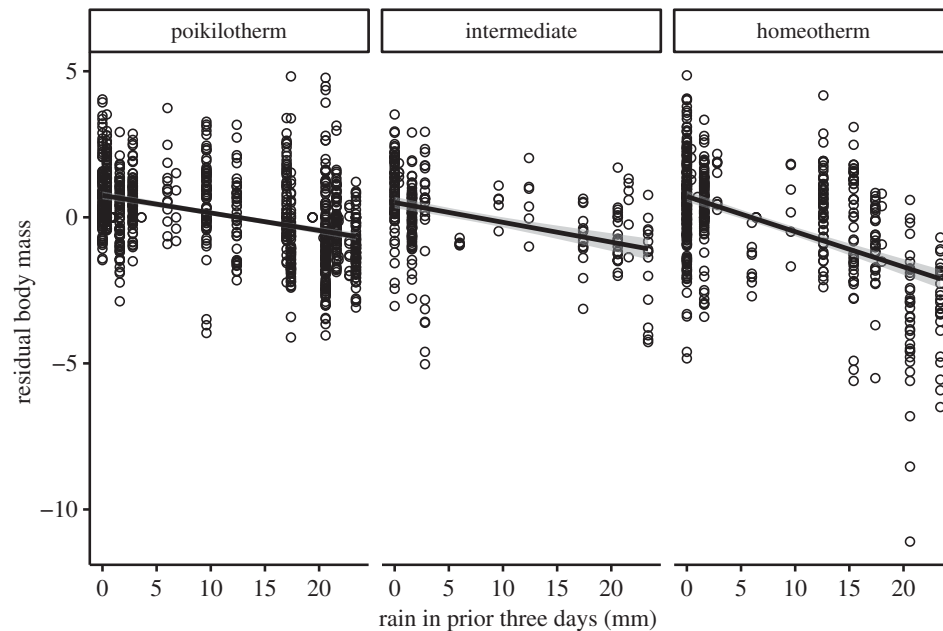


Figure 3. In 2017, nestling tree swallows were lighter for their age (residual body mass, mean centred within nest) when there was more rainfall in the 3 days prior to measurement. This effect was particularly strong in homeothermic nestlings (9–12 days old). Open circles represent measurements of individual nestlings. Black lines represent trendlines with shadings to show 95% confidence intervals.

Table 1. Comparison by AICc of LMMs determining which weather variables best predict residual body mass in tree swallow nestlings at different thermoregulatory stages.

model	LogLik ^a	ΔAICc^b	weight ^c	adjusted R^2
thermoreg ^d \times rain ^e	−3051	0 ^f	1	0.20
thermoreg \times wind ^g	−3142	86.8	0	0.16
thermoreg \times max. temp. ^h	−3094	183.3	0	0.11

^aLog likelihood.

^bDifference in Akaike's information criterion (corrected for small sample size) from the best model (thermoreg₃ \times rain).

^cRelative support for the model as calculated from ΔAICc .

^dThermoregulatory strategy (poikilotherm, intermediate, homeotherm).

^eTotal rainfall in the 3 days prior to measurement.

^f $\text{AICc} = 6115.5$.

^gMean daily windspeed in the 3 days prior to measurement.

^hMean daily maximum temperature in the 3 days prior to measurement.

and increased female provisioning, has increased by 9.3 ± 0.3 mm decade^{−1} (figure 5; $F_{1,39} = 9.2$, $p = 0.004$).

4. Discussion

Climate change has been documented to affect resource availability in numerous systems [1,2,52–54]. Here, we point towards a relatively overlooked alternative mechanism: short-term food shortages caused by climate change's effects on local weather. After periods of rainy weather, when insects are less active [14–16], tree swallow nestlings are more likely to be light for their age (figure 3). Cool temperatures may exacerbate the negative effects of rainfall, through an effect on insect availability and/or nestling metabolic demands. We found that rainfall during nestling development has increased at this study site over the past four decades, following climate change projections for the area [13]. Correspondingly, tree swallow nestlings have become lighter. Therefore, we suggest that nestlings are experiencing a lack of food, not necessarily because of low insect

abundance, but rather because increasingly rainy weather causes short-term insect shortages.

Declining nestling mass is likely to have an important effect on population dynamics. Larger nestlings are more likely to survive to fledging than smaller nestlings in tree swallows [42] and other bird species [55–57]. Across several species, nestlings that fledge with greater body mass better survive the post-fledging period, probably by relying on their larger energy reserves to help them survive periods of low foraging success [35,58]. For this population, during cold snaps and heavy, sustained rainfall, nestling mortality is high but heavier nestlings are slightly more likely to survive [59]. Such selection for heavier nestlings may cause us to underestimate weather conditions' effects on nestling growth and subsequent consequences for fledging success and juvenile survival. Fledging success and juvenile survival strongly influence population dynamics [37] and have declined over time [60], so declining nestling body mass probably contributes to overall declines in this tree swallow population.

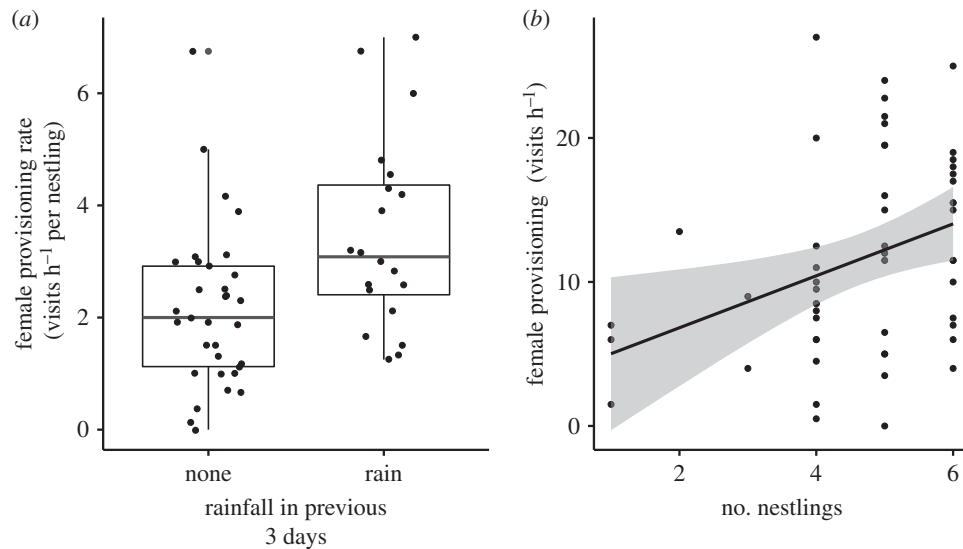


Figure 4. Offspring provisioning rates by female tree swallows were greater when (a) there had been rain in the preceding three days (rain, $F = 6.58$, $p = 0.013$) and (b) there were more nestlings in the nest (2.0 ± 0.7 visits h^{-1} nestling $^{-1}$, $F = 7.75$, $p = 0.008$). All lines represent trendlines with shadings to show the 95% confidence intervals. Boxplot hinges show first and third quartiles, with whiskers extending to the farthest point within 1.5 times the distance of interquartile range, and points spread across the x-axis for readability only. Points represent provisioning rates of unique females (a,b). Note that in (a) only, plotted female provisioning rates are controlled for the number of nestlings in the nest.

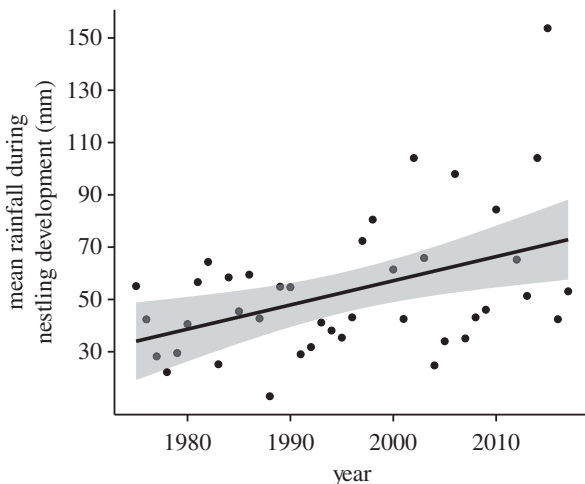


Figure 5. Since 1975, mean rainfall during nestling development has increased by 9.3 ± 0.3 mm decade $^{-1}$ ($F = 9.17$, $p = 0.004$). For each nest, we calculated the total rainfall between hatching and fledging. From there we calculated the mean annual rainfall during nestling development across all nests in the population for each year between 1975 and 2017. The black line represents the trendline and the shaded area represents the 95% confidence interval.

From 1983 to 2017, parental self-maintenance suffered (figure 2). Females are beginning incubation with progressively lower body mass and spending the incubation period foraging to improve their body condition. By the time the brood hatches, females have regained body condition to pre-decline levels and then lose mass throughout nestling development, similarly across the study period. This finding was somewhat surprising, because we found that females increase nestling provisioning and effort following rain events, something that is happening more frequently in recent years. By contrast, males have lost an increasing amount of body mass while provisioning nestlings. Males may be finding it difficult to feed themselves and their offspring adequately during wet weather or feeling the effects of more widespread insect population declines [14,24–26,61].

We present evidence that climate change may affect tree swallow food availability through short-term insect shortages. Although overall declining insect abundance may also be a factor [24–28], we suspect that weather-induced food shortages may be more important. Tree swallows and other avian aerial insectivores show the most notable declines in northeastern North America ([5,7,62] but see [6]), where climate change is causing increasingly rainy spring weather [13]. By contrast, the most intensive agriculture in North America occurs in the midwest, a region where most avian aerial insectivores are not declining [5–7,63]. Additionally, insect availability does not consistently predict breeding success or body mass [12]. If agriculture was responsible for the decline, one might expect the fastest aerial insectivore declines to occur in regions with the most intensive agriculture.

Tree swallows and aerial insectivores are far from the only species for whom climate change may be reducing food availability [1,2,52–54]. From the charismatic polar bear, reduced to hunting for bird eggs rather than seals when the sea ice melts early [54], to the minuscule water flea (*Daphnia*), whose abundances no longer peak in synchrony with their algal food sources [62], species of all trophic levels and ecosystems are experiencing the effects of climate change through food insecurity. Sometimes, food insecurity is caused by declining populations or altered accessibility of prey items, as in the case of the polar bear, where melting sea ice has both prevented the seal population from reproducing successfully [64] and hindered bears' ability to hunt [54]. Sometimes, as in the case of *Daphnia* [62] and several other taxa [53,65–67], food insecurity is owing to mismatches in phenology, where all species in the food web are still present, but the timing of peak demand by consumers no longer matches the timing of peak abundance of prey. Like these many other species, avian aerial insectivores seem to be experiencing food insecurity. For any species that are foraging specialists relying on flying insects, variable weather will generate periods when prey are inaccessible, with increasingly variable weather conditions probably increasing short-term food insecurity. The importance of weather variability on food security is well known in agriculture and

of great concern to humanitarians working to feed the growing human population (reviewed in [68]), but much work remains to fully understand the effects of weather variability on food security in the ecological context of population dynamics. Therefore, we suggest that consideration of food availability, as distinct from food abundance, may be important for predicting long-term effects of climate change.

Ethics. All work was approved by the Queen's University Animal Care Committee, as well as the Canadian Wildlife Service.

Data accessibility. Raw data and R code are archived in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.7m41jd8> [69].

Authors' contributions. R.J.R. (1975–2007) and F.B. (2008–2017) managed and contributed to the monitoring of the study population. A.R.C. and F.B. conceived of the study. A.R.C. compiled the long-term data. K.E. and A.R.C. conducted the 2017 fieldwork. Á.Z.L. analysed the RFID data and calculated provisioning rates. A.R.C. completed

the statistical analyses. A.R.C. wrote the initial manuscript, with help from F.B. All authors edited the manuscript.

Competing interests. We declare we have no competing interests.

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References

- Cahill AE *et al.* 2012 How does climate change cause extinction? *Proc. R. Soc. B* **280**, 20121890. (doi:10.1098/rspb.2012.1890)
- Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F. 2002 Ecological responses to recent climate change. *Nature* **414**, 389–395. (doi:10.1038/416389a)
- Dunne JA, Williams RJ, Martinez ND. 2002 Network structure and biodiversity loss in food webs: robustness increase with connectance. *Ecol. Lett.* **5**, 558–567. (doi:10.1046/j.1461-0248.2002.00354.x)
- Durance I, Ormerod SJ. 2010 Evidence for the role of climate in the local extinction of a cool-water trichod. *J. North Am. Benthol. Soc.* **29**, 1367–1378. (doi:10.1899/09-159.1)
- Nebel S, Mills A, McCracken JD, Taylor PD. 2010 Declines of aerial insectivores in North America follow a geographic gradient. *Avian Conserv. Ecol.* **5**, 1. (doi:10.5751/ACE-00391-050201)
- Michel NL, Smith AC, Clark RG, Morrissey CA, Hobson KA. 2016 Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. *Ecography (Cop.)* **39**, 774–786. (doi:10.1111/ecog.01798)
- Smith AC, Hudson MAR, Downes CM, Francis CM. 2015 Change points in the population trends of aerial-insectivorous birds in North America: synchronized in time across species and regions. *PLoS One* **10**, 1–23. (doi:10.1371/journal.pone.0130768)
- Inger R, Gregory R, Duffy JP, Stott I, Voříšek P, Gaston KJ. 2015 Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecol. Lett.* **18**, 28–36. (doi:10.1111/ele.12387)
- Winkler DW, Luo MK, Rakhimberdiev E. 2013 Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). *Oecologia* **173**, 129–138. (doi:10.1007/s00442-013-2605-z)
- English PA, Green DJ, Nocera JJ. 2018 Stable isotopes from museum specimens may provide evidence of long-term change in the trophic ecology of a migratory aerial insectivore. *Front. Ecol. Evol.* **6**, 14. (doi:10.3389/fevo.2018.00014)
- English PA, Nocera JJ, Pond BA, Green DJ. 2017 Habitat and food supply across multiple spatial scales influence the distribution and abundance of a nocturnal aerial insectivore. *Landsc. Ecol.* **32**, 343–359. (doi:10.1007/s10980-016-0454-y)
- Imley TL, Mann HAR, Leonard ML. 2017 No effect of insect abundance on nestling survival or mass for three aerial insectivores. *Avian Conserv. Ecol.* **12**, 19. (doi:10.5751/ACE-01092-120219)
- Kunkel KE, Stevens LE, Stevens SE, Sun L, Janssen E, Wuebbles D, Rennells J, DeGaetano A, Dobson JG. 2013 Regional climate trends and scenarios for the U.S. National Climate Assessment. Part 1. Climate of the northeast U.S., pp. 1–87. Washington, DC: NOAA.
- Grüebler MU, Morand M, Naef-Daenzer B. 2007 A predictive model of the density of airborne insects in agricultural environments. *Agric. Ecosyst. Environ.* **123**, 75–80. (doi:10.1016/j.agee.2007.05.001)
- Taylor LR. 1963 Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol.* **32**, 99–117. (doi:10.2307/2520)
- Williams CB. 1951 Changes in insect populations in the field in relation to preceding weather conditions. *Proc. R. Soc. B* **138**, 130–156. (doi:10.1086/303379)
- Dijkstra C, Bult A, Bijlsma S, Daan S, Meijer T, Zijlstra M. 1990 Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *J. Anim. Ecol.* **59**, 269–285. (doi:10.2307/5172)
- Lendvai ÁZ, Akcay C, Stanback M, Haussmann MF, Moore IT, Bonier F. 2017 Male parental investment reflects the level of partner contributions and brood value in tree swallows. *bioRxiv*, 216119. (doi:10.1101/216119)
- Pérez JH *et al.* 2016 Nestling growth rates in relation to food abundance and weather in the Arctic. *Auk* **133**, 261–272. (doi:10.1642/AUK-15-111.1)
- Rioux Paquette S, Pelletier F, Garant D, Belisle M. 2014 Severe recent decrease of adult body mass in a declining insectivorous bird population. *Proc. R. Soc. B* **281**, 20140649. (doi:10.1098/rspb.2014.0649)
- Moreno J, Merino S, Potti J, de León A, Rodríguez R. 1999 Maternal energy expenditure does not change with flight costs or food availability in the pied flycatcher (*Ficedula hypoleuca*): costs and benefits for nestlings. *Behav. Ecol. Sociobiol.* **46**, 244–251. (doi:10.1007/s002650050616)
- Winkler DW, Allen PE. 1995 Effects of handicapping on female condition and reproduction in tree swallows (*Tachycineta bicolor*). *Auk* **112**, 737–747.
- Pérez JH, Ardia DR, Chad EK, Clotfelter ED. 2008 Experimental heating reveals nest temperature affects nestling condition in tree swallows (*Tachycineta bicolor*). *Biol. Lett.* **4**, 468–471. (doi:10.1098/rsbl.2008.0266)
- Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF, Griswold TL. 2011 Patterns of widespread decline in North American bumble bees. *Proc. Natl Acad. Sci. USA* **108**, 662–667. (doi:10.1073/pnas.1014743108)
- Shortall CR, Moore A, Smith E, Hall MJ, Woiwod IP, Harrington R. 2009 Long-term changes in the abundance of flying insects. *Insect Conserv. Divers.* **2**, 251–260. (doi:10.1111/j.1752-4598.2009.00062.x)
- Hallmann CA *et al.* 2017 More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* **12**, e0185809. (doi:10.1371/journal.pone.0185809)
- Conrad KF, Warren MS, Fox R, Parsons MS, Woiwod IP. 2006 Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* **132**, 279–291. (doi:10.1016/j.biocon.2006.04.020)
- Thomas JA. 2005 Monitoring change in the abundance and distribution of insects using butterflies

- and other indicator groups. *Phil. Trans. R. Soc. B* **360**, 339–357. (doi:10.1098/rstb.2004.1585)
29. Hallmann CA, Foppen RPB, van Turnhout CAM, de Kroon H, Jongejans E. 2014 Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* **511**, 341–343. (doi:10.1038/nature13531)
 30. Rioux Paquette S, Garant D, Pelletier F, Bélisle M. 2013 Seasonal patterns in tree swallow prey (Diptera) abundance are affected by agricultural intensification. *Ecol. Appl.* **23**, 122–133. (doi:10.1890/12-0068.1)
 31. Donal PF, Gree RE, Heath MF. 2001 Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. B* **268**, 25–29. (doi:10.1098/rspb.2000.1325)
 32. Jerrentrup JS, Dauber J, Strohbach MW, Mecke S, Mitschke A, Ludwig J, Klimek S. 2017 Impact of recent changes in agricultural land use on farmland bird trends. *Agric. Ecosyst. Environ.* **239**, 334–341. (doi:10.1016/j.agee.2017.01.041)
 33. Stanton RL, Morrissey CA, Clark RG. 2018 Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. *Agric. Ecosyst. Environ.* **254**, 244–254. (doi:10.1016/j.agee.2017.11.028)
 34. Cleasby IR, Nakagawa S, Gillespie DOS, Burke T. 2010 The influence of sex and body size on nestling survival and recruitment in the house sparrow. *Biol. J. Linn. Soc.* **101**, 680–688. (doi:10.1111/j.1095-8312.2010.01515.x)
 35. Tinbergen JM, Boerlijst MC. 1990 Nestling weight and survival in individual great tits (*Parus major*). *J. Anim. Ecol.* **59**, 1113–1127. (doi:10.1080/01425690801966386)
 36. Gruebler MU, Korner-Niervergelt F, Naef-Daenzer B. 2014 Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. *Ecol. Evol.* **4**, 756–765. (doi:10.1002/ece3.984)
 37. Cox AR, Robertson RJ, Fedy BC, Rendell WB, Bonier F. 2018 Demographic drivers of local population decline in tree swallows (*Tachycineta bicolor*). *Condor* **120**, 842–851.
 38. Robertson RJ, Rendell WB. 1990 A comparison of the breeding ecology of a secondary cavity nesting bird, the tree swallow (*Tachycineta bicolor*), in nest boxes and natural cavities. *Can. J. Zool.* **68**, 1046–1052. (doi:10.1139/z90-152)
 39. Lendvai ÁZ, Akçay Ç, Ouyang JQ, Dakin R, Domalik AD, St. John PS, Stanback M, Moore IT, Bonier F. 2015 Analysis of the optimal duration of behavioral observations based on an automated continuous monitoring system in tree swallows (*Tachycineta bicolor*): is one hour good enough? *PLoS One* **10**, 1–11. (doi:10.1371/journal.pone.0141194)
 40. McCarty JP. 2002 The number of visits to the nest by parents is an accurate measure of food delivered to nestlings in tree swallows. *J. F. Ornithol.* **73**, 9–14. (doi:10.1648/0273-8570(2002)073)
 41. Environment Canada. 2018 National climate data and information archive. See climate.weather.gc.ca/historical_data/search_historic_data_e.html.
 42. Whittingham LA, Dunn PO, Clotfelter ED. 2003 Parental allocation of food to nestling tree swallows: the influence of nestling behaviour, sex and paternity. *Anim. Behav.* **65**, 1203–1210. (doi:10.1006/anbe.2003.2178)
 43. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2017 nlme: linear and nonlinear mixed effects models. See <https://CRAN.R-project.org/package=nlme>.
 44. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.
 45. Bates D, Maechler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
 46. Marsh RL. 1980 Development of temperature regulation in nestling tree swallows. *Condor* **82**, 461–463. (doi:10.2307/1367576)
 47. Dunn EH. 1975 The timing of endothermy in the development of altricial birds. *Am. Ornithol. Soc.* **77**, 288–293.
 48. McCarty JP, Winkler DW. 1999 Relative importance of environmental variables in determining the growth of nestling tree swallows *Tachycineta bicolor*. *Ibis (Lond. 1859)* **141**, 286–296. (doi:10.1111/j.1474-919X.1999.tb07551.x)
 49. van de Pol M, Wright J. 2009 A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim. Behav.* **77**, 753–758. (doi:10.1016/j.anbehav.2008.11.006)
 50. R Core Team. 2018 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
 51. Kuznetsova A, Brockhoff PB, Christensen RHB. 2017 lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26. (doi:10.18637/jss.v082.i13)
 52. Curran PJ, Obeidat K, Losardo D. 2010 Twelve frequently asked questions about growth curve modeling. *J. Cogn. Dev.* **11**, 121–136. (doi:10.1080/15248371003699969.Twelve)
 53. Post E, Forchhammer MC. 2008 Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Phil. Trans. R. Soc. B* **363**, 2369–2375. (doi:10.1098/rstb.2007.2207)
 54. Iverson SA, Gilchrist HG, Smith PA, Gaston AJ, Forbes MR. 2014 Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian Arctic. *Proc. R. Soc. B* **281**, 20133128. (doi:10.1098/rspb.2013.3128)
 55. Smith HG, Bruun M. 1998 The effect of egg size and habitat on starling nestling growth and survival. *Oecologia* **115**, 59–63. (doi:10.1007/s004420050491)
 56. Krebs EA. 1999 Last but not least: nestling growth and survival in asynchronously hatching crimson rosellas. *J. Anim. Ecol.* **68**, 266–281. (doi:10.1046/j.1365-2656.1999.00284.x)
 57. Magrath RD. 1991 Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *J. Anim. Ecol.* **60**, 335. (doi:10.2307/5464)
 58. Naef-Daenzer B, Widmer F, Nuber M. 2001 Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *J. Anim. Ecol.* **70**, 730–738. (doi:10.1046/j.0021-8790.2001.00533.x)
 59. Ouyang JQ, Lendvai Á, Dakin R, Domalik AD, Fasanello VJ, Vassallo BG, Haussmann MF, Moore IT, Bonier F. 2015 Weathering the storm: parental effort and experimental manipulation of stress hormones predict brood survival. *BMC Evol. Biol.* **15**, 219. (doi:10.1186/s12862-015-0497-8)
 60. Cox AR. 2018 Population decline in an avian aerial insectivore (*Tachycineta bicolor*) linked to climate change. MSc thesis, Queen's University, Kingston, Ontario, Canada.
 61. Cane JH, Tepedino VJ. 2001 Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conserv. Ecol.* **5**, 1. (doi:10.2307/26271794)
 62. Edwards M, Richardson AJ. 2004 Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881–884. (doi:10.1038/nature02808)
 63. Shutler D et al. 2012 Spatiotemporal patterns in nest box occupancy by tree swallows across North America. *Avian Conserv. Ecol.* **7**, 3. (doi:10.5751/ACE-00517-070103)
 64. Kovacs KM, Lydersen C, Overland JE, Moore SE. 2011 Impacts of changing sea-ice conditions on Arctic marine mammals. *Mar. Biodivers.* **41**, 181–194. (doi:10.1007/s12526-010-0061-0)
 65. McKinnon L, Picotin M, Bolduc É, Juillet C, Bêty J. 2012 Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Can. J. Zool.* **90**, 961–971. (doi:10.1139/z2012-064)
 66. Saino N et al. 2011 Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proc. R. Soc. B* **278**, 835–842. (doi:10.1098/rspb.2010.1778)
 67. Singer MC, Parmesan C. 2010 Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Phil. Trans. R. Soc. B* **365**, 3161–3176. (doi:10.1098/rstb.2010.0144)
 68. Kotir JH. 2011 Climate change and variability in Sub-Saharan Africa: a review of current and future trends and impacts on agriculture and food security. *Environ. Dev. Sustain.* **13**, 587–605. (doi:10.1007/s10668-010-9278-0)
 69. Cox AR, Robertson RJ, Lendvai ÁZ, Everitt K, Bonier F. 2019 Data from: Rainy springs Linked to poor nestling growth in a declining avian aerial insectivore (*Tachycineta bicolor*). Dryad Digital Repository. (<https://doi.org/10.5061/dryad.7m41jd8>)