Ornithology, 2025, 142, 1–14
https://doi.org/10.1093/ornithology/ukaf007
Advance access publication 25 March 2025
Research Article

Ornithology
OXFORD

Egg translocation across a local range boundary reduces hatch rates in a trailing-edge population of a migratory songbird, *Setophaga caerulescens* (Black-throated Blue Warbler)

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ABSTRACT

The abiotic range limitation hypothesis states that species distributions are shaped by physiological constraints imposed by temperature and precipitation. To test this hypothesis, we assessed the impacts of climate on hatch rates by reciprocally translocating complete clutches of both *Setophaga caerulescens* (Black-throated Blue Warbler) and *S. citrina* (Hooded Warblers) across a local range boundary of *S. caerulescens* in the southern Appalachian Mountains. The *S. caerulescens* population occurs at the trailing edge of its breeding range, whereas the *S. citrina* population occurs near the core of its range. The hatching probability of *S. caerulescens* eggs declined from 0.93 ± 0.02 to 0.60 ± 0.07 when moved to *S. citrina* nests in warmer conditions. Translocation, however, had little effect on hatching probability of *S. citrina* eggs when moved to *S. caerulescens* nests in cooler environments. Thirteen reciprocal clutch translocations were performed; 17 clutches were moved as controls; and 49 nests were not manipulated. We monitored species-specific incubation behavior, measured microclimate conditions inside and outside nests using hygrochron iButtons, and examined the effects of temperature and humidity on nestling growth rates. Higher ambient temperatures had a greater effect on hatching probability than did humidity, but we were unable to determine if reduced hatching was caused by changes in temperature, humidity, or their interaction. We suggest that, in warmer conditions, *S. caerulescens* eggs in *S. citrina* nests may have been unable to cool sufficiently to avoid excessive water loss due to higher ambient temperatures but not a difference in relative humidity. Our finding that hatch rates of *S. caerulescens* declined when translocated to warmer conditions supports the hypothesis that distributions of trailing-edge populations are limited in part by climate effects on reproductive rates.

Keywords: egg translocation, hatch rates, migratory songbird, nest temperature, range limits, *Setophaga caerulescens*, *Setophaga citrina*, trailing-edge populations

How to Cite

Merker, S. A., T. S. Sillett, B. G. Freeman, R. J. Cooper, and R. B. Chandler (2025). Egg translocation across a local range boundary reduces hatch rates in a trailing-edge population of a migratory songbird, *Setophaga caerulescens* (Black-throated Blue Warbler). Ornithology 142:ukaf007.

LAY SUMMARY

- Trailing-edge populations are populations at the receding margin of a species' shifting geographic range and are considered to be at high risk of extinction from changing climate conditions.
- Increasing temperatures may reduce hatch rates and alter nestling growth in trailing-edge songbird populations.
- To test whether warmer conditions affected hatch rates of trailing-edge songbird eggs, we moved entire clutches of *Setophaga caerulescens* (Black-throated Blue Warbler) and eggs into low-elevation nests of the closely related *S. citrina* (Hooded Warbler). We also moved *S. citrina* eggs into the high-elevation nests of *S. caerulescens*.
- *Setophaga caerulescens* eggs hatched at a lower rate when moved to lower elevations where climate conditions were warmer. *Setophaga citrina* eggs were unaffected by being moved into *S. caerulescens* nests in cooler conditions at high elevations.
- Translocated nestling growth was mostly unaffected by being nestlings being raised in different conditions, but some *S. citrina* nestlings responded by growing larger wings and tarsi.
- Results of our experiment support the hypothesis that climate conditions set range limits of trailing-edge populations by impacting avian reproductive rates. The mechanism by which temperature or humidity reduced hatch rates of the trailing-edge population remains uncertain.

Submission Date: June 11, 2024. Editorial Acceptance Date: March 12, 2025

La translocación de huevos a través del límite de un rango de distribución local reduce las tasas de eclosión en una población en el margen de distribución de un ave migratoria, *Setophaga caerulescens*

RESUMEN

La hipótesis de limitación abiótica de la distribución establece que la distribución de las especies está determinada por restricciones fisiológicas impuestas por la temperatura y la precipitación. Para probar esta hipótesis, evaluamos los impactos del clima en las tasas de eclosión mediante la translocación recíproca de nidadas completas de *Setophaga caerulescens* y *S. citrina* a través del límite de un rango de distribución local de *S. caerulescens* en el sur de los montes Apalaches. La población de *S. caerulescens* se encuentra en el margen de su área de reproducción, mientras que la población de *S. citrina* se encuentra cerca del núcleo de su distribución. La probabilidad de eclosión de los huevos de *S. caerulescens* disminuyó de 0.93 ± 0.02 a 0.60 ± 0.07 cuando fueron trasladados a nidos de *S. citrina* en condiciones más cálidas. Sin embargo, la translocación tuvo poco efecto en la probabilidad de eclosión de los huevos de *S. citrina* cuando fueron trasladados a nidos de *S. caerulescens* en ambientes más fríos. Se realizaron trece translocaciones recíprocas de nidadas; diecisiete nidadas fueron trasladadas como controles; y cuarenta y nueve nidos no fueron manipulados. Monitoreamos el comportamiento de incubación específico de cada especie, medimos las condiciones microclimáticas dentro y fuera de los nidos utilizando el iButton hygrochron y examinamos los efectos de la temperatura y la humedad en las tasas de crecimiento de los polluelos. Las temperaturas ambientales más altas tuvieron un efecto mayor en la probabilidad de eclosión que la humedad, pero no pudimos determinar si la reducción en la eclosión fue causada por cambios en la temperatura, la humedad o su interacción. Sugerimos que, en condiciones más cálidas, los huevos de *S. caerulescens* en nidos de *S. citrina* pueden no haber sido capaces de enfriarse lo suficiente para evitar una pérdida excesiva de agua debido a temperaturas ambientales más altas, pero no a una diferencia en la humedad relativa. Nuestro hallazgo de que las tasas de eclosión de *S. caerulescens* disminuyeron cuando fueron translocados a condiciones más cálidas respalda la hipótesis de que la distribución de las poblaciones en el margen de su área de distribución está limitada en parte por los efectos del clima en las tasas reproductivas.

Palabras clave: ave canora migratoria, límite del rango de distribución, población en el margen de distribución, tasas de eclosión, temperatura del nido, translocación de huevos, *Setophaga caerulescens*, *Setophaga citrina*

INTRODUCTION

Many populations near low-latitude and low-elevation range boundaries are declining in response to climate change (Parmesan and Yohe 2003, Parmesan 2006, Chen et al. 2011, Freeman et al. 2018, Williams and Blois 2018, Gaya and Chandler 2025). Loss of these trailing-edge populations could reduce species-level genetic diversity and impact ecosystem function (Hampe and Petit 2005, Hardie and Hutchings 2010). Understanding how climate change affects trailing-edge populations requires information about the factors limiting their distributions. The biotic interaction hypothesis posits that processes such as competition and predation limit species distributions near low-latitude, low-elevation range margins where species richness is greatest (Dobzhansky 1950, MacArthur 1972, Jankowski et al. 2010, Jankowski et al. 2013, Freeman and Montgomery 2016, Freeman et al. 2022). The abiotic range limitation hypothesis states that distributions of trailing-edge populations are shaped by physiological thresholds sensitive to changes in temperature and precipitation (Hampe and Petit 2005, Hickling et al. 2006, Cahill et al. 2014, Rubenstein et al. 2020, Merker and Chandler 2021). In birds, changes in temperature and precipitation could impact peripheral populations through direct effects on egg physiology and hatch rates, but few studies have investigated this form of abiotic range limitation.

Although evidence supports the role of temperature in setting species range limits, the ecological processes associated with temperature-mediated range shifts remain unclear (MacArthur 1972, Jankowski et al. 2013). High temperatures can negatively affect reproduction and development in many taxa, potentially influencing species distributions (Hansen 2009, DuRant et al. 2013, Mendonca et al. 2018). Egg hatch rates may be negatively affected by temperature extremes (Webb 1987), but responses depend on egg structure and parental care strategies (McClintock et al. 2014, Coe et al. 2015). For example, hatch rates of *Rallus elegans* (King Rail) decreased when exposed to extreme ambient temperatures that could not be mitigated by parental clutch shading (Clauser and McRae 2017). Rising temperatures could therefore cause trailing-edge populations to shift to higher latitudes or elevations as they track physiologically optimal conditions necessary for reproduction (La Sorte and Jetz 2010). Such changes have been observed in the Peruvian Andes where high-elevation birds shifted their distributions and, in some cases, became extirpated due to warming temperatures (Freeman et al. 2018). Thus, understanding the physiological response of eggs to novel environments is essential to understanding the effects of climate change on trailing-edge populations.

Bird eggs are considered ectothermic (Hiebert and Noveral 2007) and should remain within a relatively narrow temperature range during incubation to properly develop and hatch (White and Kinney 1974, Webb 1987, Conway and Martin 2000a, Lundblad and Conway 2021). The "optimal microclimate" hypothesis predicts that optimal temperature conditions for eggs are the same for most bird species, regardless of ambient conditions (White and Kinney 1974, Webb 1987, Sturkie, 2012). To ensure eggs remain within this optimal temperature range, birds adjust incubation behavior in response to variation in ambient temperature (Webb 1987, Sturkie 2012, Walters et al. 2016). The trade-off between incubation and off-nest bouts is managed by adjusting the amount of time off the nest and the frequency of off-nest excursions in response to ambient conditions (Webb 1987, Smith et al. 2018). Although time on the nest generally increases as ambient temperature increases, due to reduced metabolic demand (Davis et al. 1984, Walters et al. 2016), it is unknown if behavioral responses to changing ambient conditions can mitigate population-level negative impacts of warmer temperatures. Failure to behaviorally mitigate changing climate conditions could result in reduced productivity from egg failure and ultimately lead to range contraction or extirpation at the trailing edge. While temperature is strongly supported as a limiting factor, other abiotic factors may impact species distributions at the trailing edge.

Humidity can limit species distributions, but it has received far less attention than temperature, especially in studies of vertebrates (Baldauf et al., Shirazi et al. 1996, Bohning-Gaese and Lemoine 2004, Sales et al. 2016). Humidity can directly influence bird populations, for example, through its impact on egg development (Walsberg 1980, 1983, Gillespie et al. 2000, Hedhly et al. 2009, Jaworski and Hilszczanski 2013). Habitat-specific variation in eggshell pore density is vital for proper gas exchange between the environment and the embryo (Rahn et al. 1979). *Haemorhous mexicanus* (House Finch) in their human-introduced range laid eggs with thicker shells and fewer pores than in their natural range where humidity is lower (Stein and Badyaev 2011). This surprising result suggests that birds can manipulate eggshell thickness and porosity to mitigate ambient climate conditions. In addition, when *H. mexicanus* eggs were translocated between native (Montana, USA) and introduced ranges (Alabama, USA), embryo survival decreased despite inner nest temperatures remaining in the range necessary for embryo development at each location (Stein and Badyaev 2011). These results suggest that humidity is important in determining avian range limits because birds cannot manipulate nest humidity as easily as nest temperature (Rahn et al. 1977, Martin et al., 2007, Stein and Badyaev 2011, Portugal et al. 2014, Smith et al. 2018). Thus, a deeper understanding of how egg hatch rates are affected by local climate conditions is needed, especially near range boundaries where species may be near physiological thresholds.

Although unsuitable climate conditions can result in egg failure, nestlings may also experience deleterious effects of unsuitable climate conditions, including reduced survival and altered growth rates (Rodríguez and Barba 2016, Ospina et al. 2018). However, the effect of climate on nestling growth is complex and variable (McCarty and Winkler 1999, Dawson et al. 2005). For example, both extreme low temperatures and high average temperatures can affect nestling mass gain (Murphy 1985, Larson et al 2015). Additionally, nestling mass of *Tachycineta bicolor* (Tree Swallow) was found to increase when temperature in nest cavities was artificially inflated, but only at a site where population density was relatively low (Dawson et al. 2005, Pérez et al. 2008). Nestlings that hatch in suboptimal climate conditions may experience altered growth rates leading to declines in survival and reproductive success (Sauve et al. 2021).

We used a reciprocal egg translocation experiment to test the hypothesis that the effects of temperature and humidity on egg development limit the trailing-edge range boundary of a trailing-edge population of a migratory passerine, *Setophaga caerulescens* (Black-throated Blue Warbler), which, in our study area in the southern Appalachian Mountains, is restricted to high elevations (Lewis et al. 2022), where temperatures are cooler and precipitation is higher than at low-elevations. Because precipitation increases with elevation, we predicted that relative humidity at nest sites would also be higher and, conversely, we expected that nest locations at lower elevations would have lower relative humidity. We moved *S. caerulescens* eggs across the species' local range boundary, swapping *S. caerulescens* eggs with eggs of an ecologically similar congener, *S. citrina* (Hooded Warbler), that occurs primarily in warmer and potentially less humid conditions at low elevations in our study area. We predicted that eggs experimentally moved to nests outside the local range of *S. caerulescens* would have lower hatch rates than control eggs. We further predicted that *S. citrina* hatch rates would not be affected by translocation because the species occurs near the core of its range in our study area and thus is unlikely to be near its physiological limits. Although most bird species maintain eggs within narrow temperature ranges, we expected negative effects of translocation on eggs of the trailing-edge population because of warmer and potentially less humid ambient climate conditions experienced when females were not incubating. Because female incubation behavior can change in response to changing ambient climate conditions, we expected females to increase duration of incubation bouts, as in other species, as temperatures increased due to reduced energetic needs in warmer temperatures. Finally, for translocated eggs that hatched, we hypothesized that nestlings raised outside of their native range would experience altered growth rates (Boyle et al. 2016). Specifically, we predicted that the trailing-edge population would experience greater growth rates when raised in warmer and potentially less humid conditions, due to lower energy expenditure on thermoregulation (Davis et al. 1984, Walters et al. 2016). Conversely, we predicted that nestlings in the range core population would grow slower in cooler and potentially more humid conditions because more energy would be used for thermoregulation.

METHODS

Study Site

Fieldwork was conducted in the Nantahala National Forest in southwestern North Carolina, USA (Figure 1). We selected this region of the southern Appalachian Mountains because it has a high diversity of species with trailing-edge populations, including >20 species of birds (Merker and Chandler 2020). Many of these trailing-edge populations have closely related congeners, at the core of their range, that occur at all elevations, typically with the highest densities at lower elevations. The site is characterized by steep topography with elevations ranging from 700 to 1,590 m over short (<2.5 km) distances. At high elevations, the climate is cooler and there is more precipitation than at lower elevations (Swift et al. 1988, Daly et al., 2008, Merker and Chandler 2021, Gaya et al. 2024), providing suitable conditions for many trailing-edge populations that do not occur elsewhere in the southeastern United States (Lewis and Cooper 2019, Merker and Chandler 2020). Because of the strong precipitation gradient at our study site we expected that humidity would also be higher at nesting sites located at higher elevations.

Study Species

In the southern and central Appalachian Mountains, *S. caerulescens* breeding distribution is restricted to elevations greater than ~1,000 m (Cline et al. 2016, Lewis et al. 2022), whereas the congeneric *S. citrina* nests both below and above this elevation. *Setophaga caerulescens* is a Neotropical migrant songbird with a breeding range centered in the northeastern United States and southeastern Canada. A narrow band of the species range extends south through the Appalachian Mountains, where it maintains a trailing-edge population (Figure 1). *Setophaga citrina* is a Neotropical migrant songbird with a breeding range centered in the southeastern United States, such that our study area falls within the core of its range (Figure 1). Both species build open cup nests in the shrub layer, making nests relatively easy to find and monitor. Both species have similar clutch sizes and diets, and only females incubate (Chiver et al. 2020, Holmes et al. 2020).

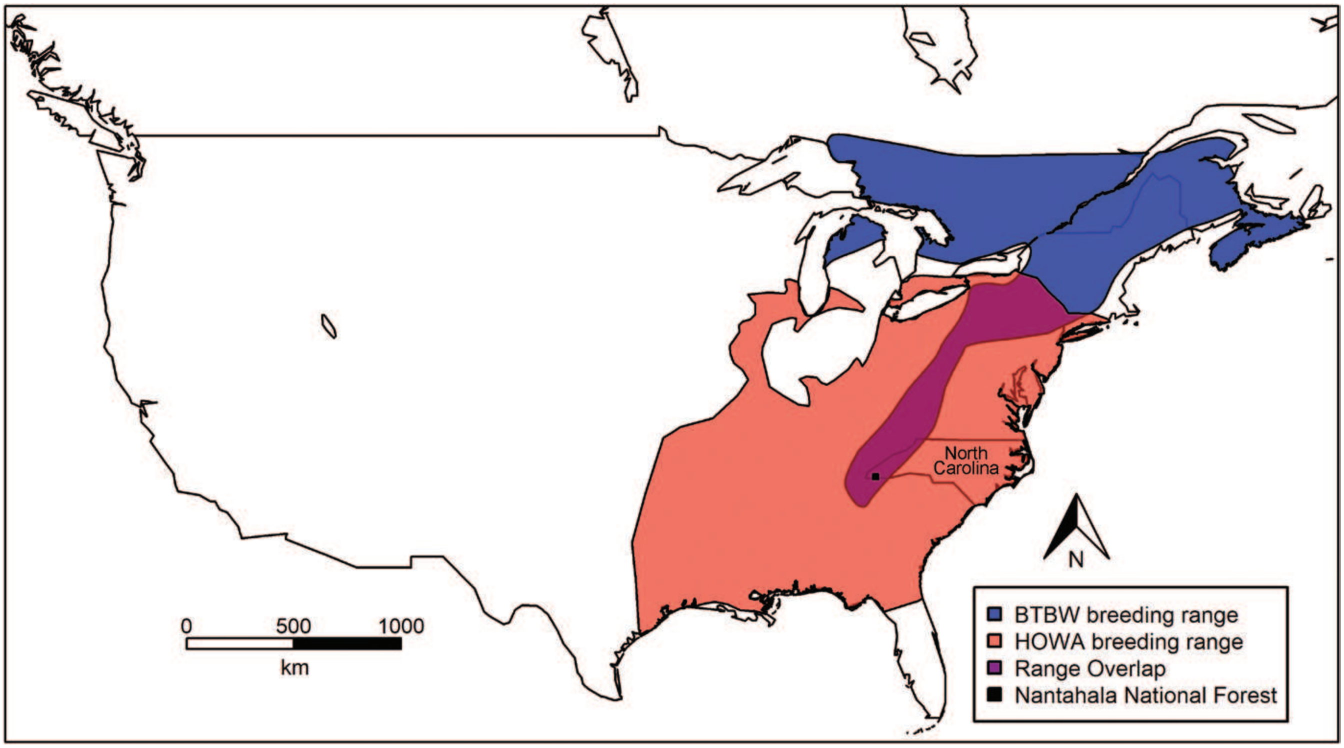

FIGURE 1. Breeding range maps for the trailing-edge species, *Setophaga caerulescens* (Black-throated Blue Warbler), and the core species, *S. citrina* (Hooded Warbler), which were studied in the Nantahala National Forest in western North Carolina, USA.

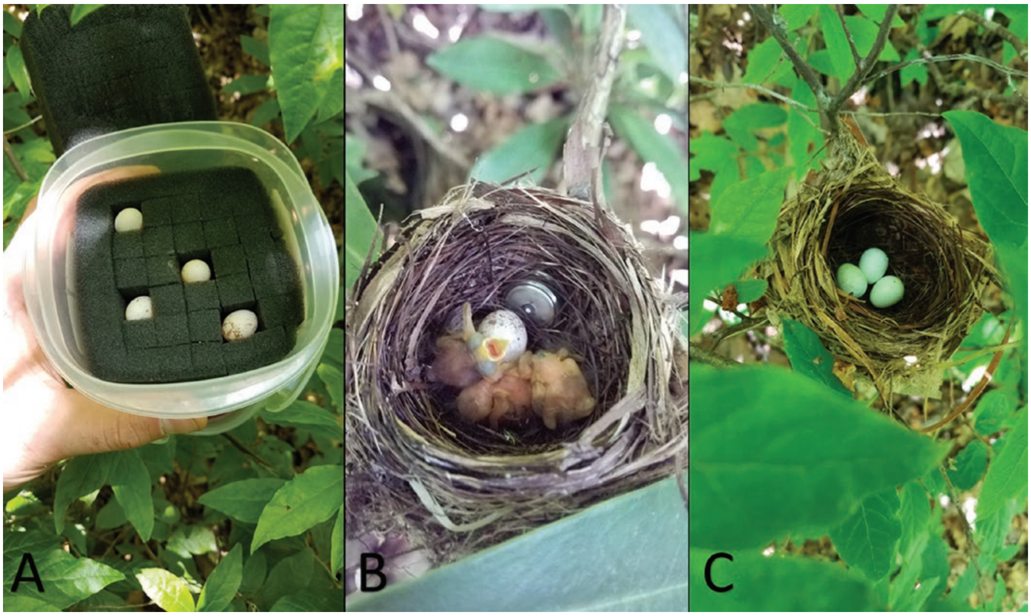

FIGURE 2. *Setophaga caerulescens* eggs (**A**) just after removal from a nest ready to be relocated to a *S. citrina* nest at lower elevation outside the local range boundary of *S. caerulescens*. Example of a hygrochron iButton (**B**) in a nest. Plastic eggs (**C**) used as temporary replacements for real eggs in translocation and control treatment groups.

Reciprocal Egg Translocation Experiment

Nests were located and monitored throughout the 2018–2020 breeding seasons from late April through early-July. We sought to measure and describe nest temperature and relative humidity with hygrochron iButtons (DS1923-F5#; Maxim Integrated Products, San Jose, California, USA). These small (diameter = 1.5 cm, depth = 0.6 cm, temperature accuracy = 0.5°C) sensors were placed in nests (Figure 2B). We also collected ambient temperature and relative humidity data for each nest by hanging a hygrochron iButton within 3 m at approximately nest height. Although the precipitation and temperature gradient at our study site is well documented, relative humidity has not been well described, especially in regards to nesting birds. Temperature and relative humidity were recorded every 4 min during incubation and nestling stages (Smith et al. 2018). Some hygrochron iButtons failed or were lost. At least 2 outer hygrochron iButtons gained the attention of black bears (*Ursus americana*) and are lost forever. Some nests did not receive hygrochron iButtons due to lack of supply. Thus 34 nests lacked internal data and 45 lacked external data and were removed from analyses on hatching success. Observers visited nests every 8 days to replace hygrochron iButtons. The long interval between nest visits reduced observer presence thereby lowering predation risk during incubation (Conway and Martin 2000b, Ibanez-Alamo et al. 2012, Matysiokova and Remes 2018).

Complete clutches of both species were translocated across the local *S. caerulescens* range boundary into nests of the opposite species. Clutches were translocated between low-elevation (warmer, potentially less humid) and high-elevation (cooler, potentially more humid) sites. Eggs were swapped on days 1–4 of incubation to ensure that eggs experienced minimal incubation in their native climate conditions while controlling for egg age at the time of translocation. Clutches were considered eligible for translocation if a nest of each species was found during the building or laying stage so that the clutch completion date (last egg laid) was known, each nest was within 1–2 days of clutch completion, and nests were at substantially different elevations (mean difference: 350 m, range: 247–586 m). Due to sample size restrictions, and our design requirement that nest phenology be closely aligned, we were unable to strictly randomize which clutches were swapped. In the rare event that multiple nests were available from one species to swap with only one of the other species, we randomized which nest was translocated by flipping a coin; the other candidate nest became a control. There was little overlap between elevations of *S. citrina* and *S. caerulescens* nest locations (Supplementary Material Table 1) and only 2 *S. citrina* nests were located within *S. caerulescens* territories.

When 2 eligible nests were found, 2 observers simultaneously collected complete clutches (USFWS Scientific Collection Permit # MB51229D–0) and placed each clutch in a plastic container lined with foam so that each egg was securely surrounded by foam to minimize movement (Figure 2A). Observers placed a hygrochron iButton in the nest, partially within the nest lining to avoid damaging eggs, so that the humidity sensor pointed inward towards the center of the nest (Figure 2B). Observers then placed an equal number of plastic eggs in the nest, recorded the time, and departed (Figure 2C). A combination of walking and driving was used to bring the eggs to the receiving nest of the opposite species. Upon arrival at the receiving nest, the artificial eggs were removed, and the real eggs of the opposite species were placed in the nest. Observers remained within binocular viewing distance (15–20 m) of the nest to confirm that female birds returned to the nest to incubate the eggs of the other species. Nests were checked with binoculars every other day after translocations, and nests were only approached to replace hygrochron iButtons, check for hatching, check for predation, or to measure nestlings.

We used two types of controls. First, eligible nests without an eligible translocation nest of the opposite species were used as positive controls. Positive control ("control" hereafter) clutches were collected and moved using the same protocol as translocated clutches except that they were returned to the same nest. In some cases, due to the remote nature of some nests, eggs were only walked rather than walked and driven. For negative controls ("unmanipulated" hereafter), we used nests found during incubation or nestling stages but not manipulated except for normal monitoring and the addition of hygrochron iButtons. For these unmanipulated nests we assumed that observed hatch rates did not depend on the stage at which the nests were discovered.

Generally, there is a large initial pulse of nest initiation, where most females of each species begin construction on their first nests within a few days of each other. This is a time when it is easiest to find nests because of adult behavior. However, many of these nests fail, often due to predation or weather, thus initiating an asynchronous string of "renests." Because of this asynchronous timing of nest initiation, many renests were eligible for translocation but no reciprocal nest was available or could not be found. Indeed, one major limitation in achieving a larger sample size was the number of nest searchers, which was generally 2. As such, we could not directly account for any phenological peaks in nesting that might have led to differences in variables of interest like temperature or humidity. We tested for a difference in clutch initiation dates between translocated nests and positive control nests using a *t*-test and found no difference ($t = -1.6545$, df = 31.789, $P = 0.1079$). Mean clutch completion date was June 2 for control nests and June 9 for translocated nests.

Experimental translocation was used to assess the effect of manipulating the ambient climate experienced by eggs when they were not being incubated. However, given the constraints of the system, translocation also changed the attendant species incubating eggs. We assumed that the attendant incubating species should have little effect on egg hatch rates because all species of birds attempt to keep eggs within similar microclimate conditions during incubation. Rather, we assumed the translocation effect would manifest through effects experienced when females were off the nests. However, we could not experimentally assess these assumptions. Our field experiment also did not permit disentangling the potential effects of temperature and humidity because they are highly correlated at our study site. However, we attempted to directly measure these variables inside and outside of nests to account for as much variation as possible.

Transportation times did not differ for clutches in the treatment and positive control groups. *Setophaga caerulescens* eggs were out of nests for ~38 min for both translocation and control movements (Supplementary Material Table 2). *Setophaga citrina* eggs were out of nests for slightly longer, with a mean of 47 min for control movements and a mean of 45 min for translocations (Supplementary Material Table 2). The time that eggs were out of nests was not significantly different between species (Supplementary Material Table 2).

We investigated the effects of the translocation experiment on nestling development by measuring nestling tarsal length, wing chord, bill width, bill depth, and mass in experimental and control nests every 2 days. To account for individual variation and asynchronous hatching we marked individuals by coloring their toe-claws and toes with a permanent marker (Slagsvold 1985). Nestlings were then marked with a USGS aluminum leg band 5–7 days after hatching.

We used a binomial generalized linear model (GLM) to test the prediction that translocated eggs of the trailing-edge population of *S. caerulescens* would have lower hatch rates, which we define as the probability of an egg hatching, than eggs in control groups (McCullough and Nelder 1989). Binomial GLMs do not assume a constant variance, and they generalize binary logistic regression by acknowledging that the response variable (number of hatched eggs) is an integer-valued random variable with an upper bound determined by the clutch size (Warton and Hui 2011). Hatch rate was modeled as a function of species and treatment, and we evaluated main effects and the interaction of the two factors. We also used a GLM to test the effects of both mean ambient conditions and internal nest conditions on hatch rates. We also considered the maximum and minimum conditions experienced by eggs. Models were fitted using the *glm* function in R (R Core Team 2023).

We used linear models to evaluate whether temperature and relative humidity inside and outside nests varied with elevation. For inner nest temperature and relative humidity, we included species as a predictor variable. Mean relative humidity was a proportion, and because some values were 1, we subtracted 0.001 from every value before applying a logit transformation to meet the assumption of normally distributed residuals (Warton and Hui 2011). To determine if inner nest conditions differed between species during incubation, we modeled temperature and humidity means during periods of darkness (2100–0500 hours) when females rarely leave the nest (Weathers and Sullivan 1989, Slay et al. 2012). In addition to main effects, we estimated interactions of species and elevation on temperature and humidity inside and outside the nest. Linear models were fit with the *lm* function in R (R Core Team 2023).

We modeled species-specific incubation behavior as a function of ambient conditions using linear mixed effects models (Pinheiro and Bates 2000). We analyzed hygrochron iButton temperature data subset to crepuscular and daylight periods (0530–2100 hours) when females intersperse bouts of foraging or other behaviors and incubation. Using methods similar to Smith et al. (2018), we quantified duration of female off-nest bouts by first taking the difference between temperature measurements inside and outside nests. Periods of continuously decreasing temperature differences followed by either no change or a sudden increase indicated that the female had returned to the nest and resumed incubation. Incubation bout duration was modeled as a function of mean temperature and mean humidity inside and outside the nest during each bout. We included nest identity and day of incubation as random effects to account for unexplained sources of variation not described by the explanatory variables. In addition, we tested for differences in mean temperature and humidity between attending species inside nests during incubation and off-nest bouts using *t*-tests. We used the *lme* function from the *nlme* package in R (R Core Team 2023, Pinheiro et al. 2025).

We used linear models to assess the effects of species, treatment, and brood size on hatchling growth rates. We used the mean change in size of all nestlings within a nest from the first measurement (day 2) to the last measurement (day 6) for each biometric as a response variable. We included brood size as a predictor of nestling growth because nestling development can be affected by the number of nestlings in a brood (Martin 1987). Linear models were fit with the *lm* function in R (R Core Team 2023).

For each analysis, we fit specific single models that represent individual hypothesis and predictions. We based interpretations about the biological reality of statistical patterns based on estimates of uncertainty around statistical parameters and 95% confidence intervals around predicted values. Thus, we present explicit tests of relevant treatment levels representing the biological effect of covariates measured during the study. Results reported below are effect sizes and either standard errors, standard deviations, or 95% confidence intervals. All analyses were conducted with the R statistical software (R Core Team 2023). In figures error bars are 1 standard error (SE) and shaded polygons are 95% confidence intervals.

RESULTS

We found 97 *S. caerulescens* nests and 61 *S. citrina* nests over the 2018–2020 breeding seasons, but only 88 were eligible for translocation, control, or continuous monitoring and not all 88 nests made it to the nestling stage. Some nests were removed from the study because they were abandoned before any eggs were laid. Thirteen reciprocal clutch translocations were performed; 13 clutches were moved as controls; and 49 nests were not manipulated. Eight of 12 *S. caerulescens* clutches translocated to low elevations had at least 1 egg that did not hatch; 1 clutch was depredated. In 2 translocated *S. caerulescens* clutches, only a single egg hatched, and one clutch did not hatch at all. Six of 10 *S. caerulescens* control clutches had at least 1 egg that did not hatch, with 2 unhatched eggs in 2 nests. Seven of 26 unmanipulated *S. caerulescens* nests had 1 unhatched egg. Two of 3 *S. citrina* control clutches had 1 unhatched egg, and 4 of 8 swapped clutches had at least 1 unhatched egg. Five translocated *S. citrina* clutches were depredated before any eggs could hatch. Ten of 23 unmanipulated *S. citrina* clutches had at least 1 unhatched egg, with 1 clutch having 2 unhatched eggs.

Consistent with the abiotic range limitation hypothesis, that hatch rates would be lowest for translocated *S. caerulescens* eggs, the hatch rate for *S. caerulescens* eggs translocated from cooler (but not more humid) conditions to warmer (but not less humid conditions) was 0.60 (SE = 0.07; Figure 3). *Setophaga caerulescens* eggs in control nests hatched at a rate of 0.79 (SE = 0.06) compared to 0.93 (SE = 0.02) in unmanipulated nests (Figure 3). Hatch rates for *S. citrina* eggs translocated from warmer climates to cooler climates was 0.81 (SE = 0.00, Figure 3), similar to the hatch rate (0.80, SE = 0.12) of *S. citrina* eggs in control nests. Unmanipulated *S. citrina* eggs hatched at a rate of 0.88 (SE = 0.03), slightly higher than control or translocated eggs.

Mean temperature and humidity inside nests and adjacent to nests varied with species and elevation. The difference between mean nighttime internal nest temperatures between *S. citrina* and *S. caerulescens* nests was 2.64°C (SE = 4.66) (Figure 4A). Mean nighttime and daytime temperature outside nests decreased with elevation at a rate of 0.004°C m^{-1} (SE = 0.001) elevation (Figure 4C and E). Mean nighttime relative humidity was similar inside both species' nests, even though humidity decreased with elevation inside *S. citrina* nests and increased inside *S. caerulescens* nests with elevation (Figure 4B). Contrary to the prediction that ambient relative humidity be higher at high elevations, mean outer nighttime relative humidity declined at a rate of 0.003% m^{-1} elevation (SE = 0.002) and stayed between 80 and100% (Figure 4D). However, this decline is so small, the resulting difference over 1,000 m elevation is minuscule. Mean outer daytime relative humidity declined at a rate of 0.0005% m^{-1} elevation (SE = 0.0006; Figure 4F). However, the average daytime humidity

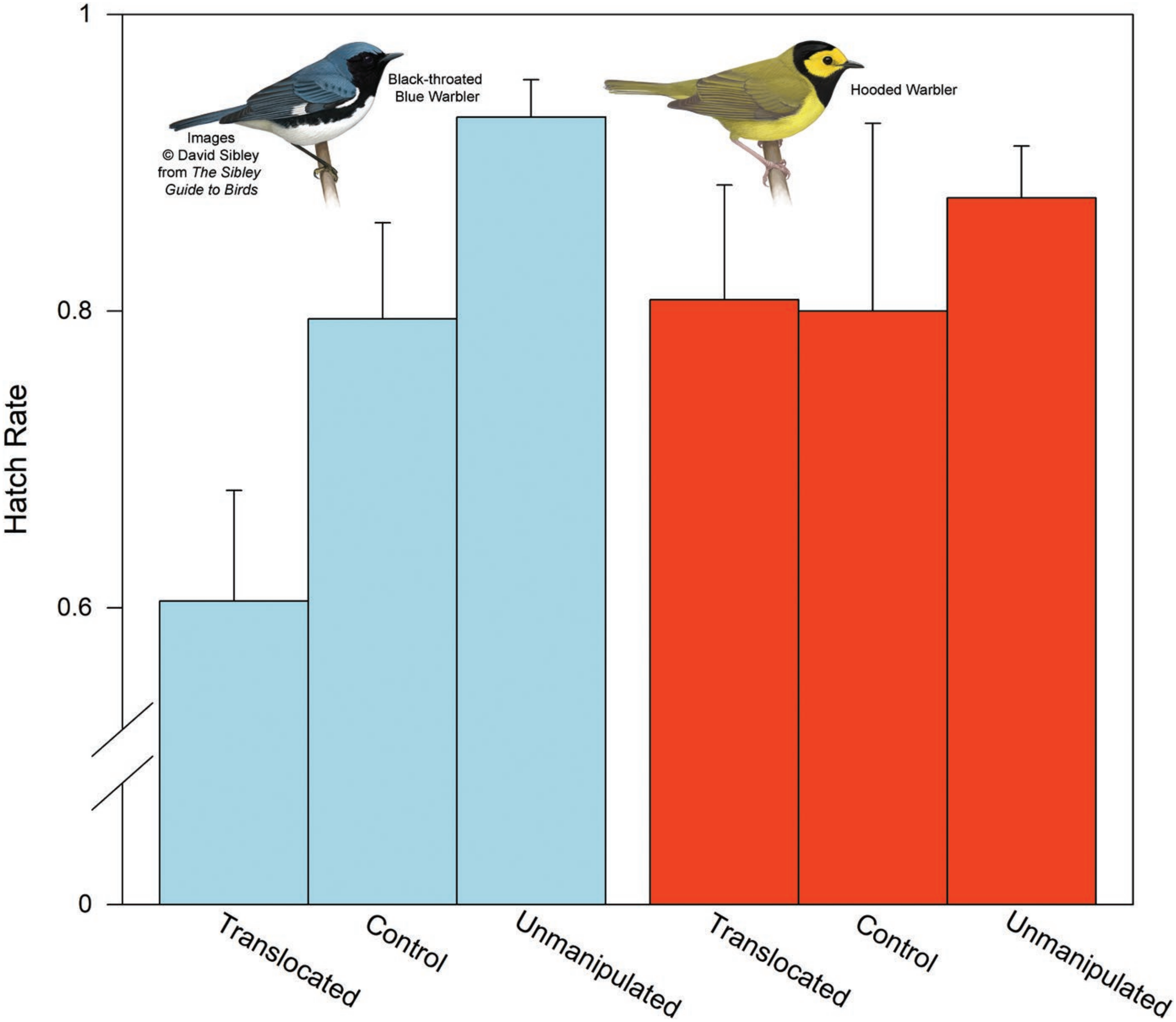

FIGURE 3. Hatch rates of *S. caerulescens* and *S. citrina* eggs in translocated, control, and unmanipulated nests. Thirteen complete clutches were translocated across a climate gradient spanning the local range boundary of the *S. caerulescens* in the Nantahala National Forest, North Carolina, United States. Of the relevant within species pairs, a multiple comparisons test indicated that the only statistically different pair occurred between translocated and unmanipulated *S. caerulescens* nests. All other within species pairs were not statistically different. Error bars are 1 SE. Images of both warbler species reproduced from *The Sibley Guide to Birds* with permission from David Sibley.

outside of species nests varied little overall with *S. citrina* nests having a mean relative humidity of 88.2% (SE = 8.9%) and *S. caerulescens* nests having a mean relative humidity of 90.4% (SE = 6.9%).

Higher mean daytime temperature inside nests during incubation was associated with lower hatch rate of both species, although there was no effect of temperature when females were away from nests (Figure 5). Despite this, the mean daytime internal nest temperature during incubation did not differ significantly by attending species, although *S. citrina* nests were 2.13°C warmer on average (SD = 1.42). Furthermore, mean ambient temperature had no effect on hatch rates for either species (Supplementary Material Figure 1). However, mean ambient daytime temperatures were significantly different between nest locations of each species, with *S. citrina* nest locations being 1.69°C warmer on average (SD = 0.60). Humidity inside and outside nests had no effect on hatch rates (Supplementary Material Figure 1).

Female incubation behavior differed between species. Female *S. caerulescens* incubation bouts lasted a mean of 17.7 min (SD = 11.24), which was 7.21 min shorter than the mean 24.95-min (SD = 18.62) duration of *S. citrina* incubation bouts. The best model describing incubation bout duration for both species included only ambient temperature; however, the effect was only significant for *S. citrina* and incubation bout duration increased 0.19 min °C^{-1} (SE = 0.004) with ambient temperature whereas incubation bout duration stayed relatively stable for *S. caerulescens* 0.011 min °C^{-1} (SE = 0.004; Figure 6A). The effect of ambient humidity on incubation bout duration differed by species and model. *Setophaga caerulescens* incubation bout duration was unaffected by ambient humidity alone (Figure 6C). The effect

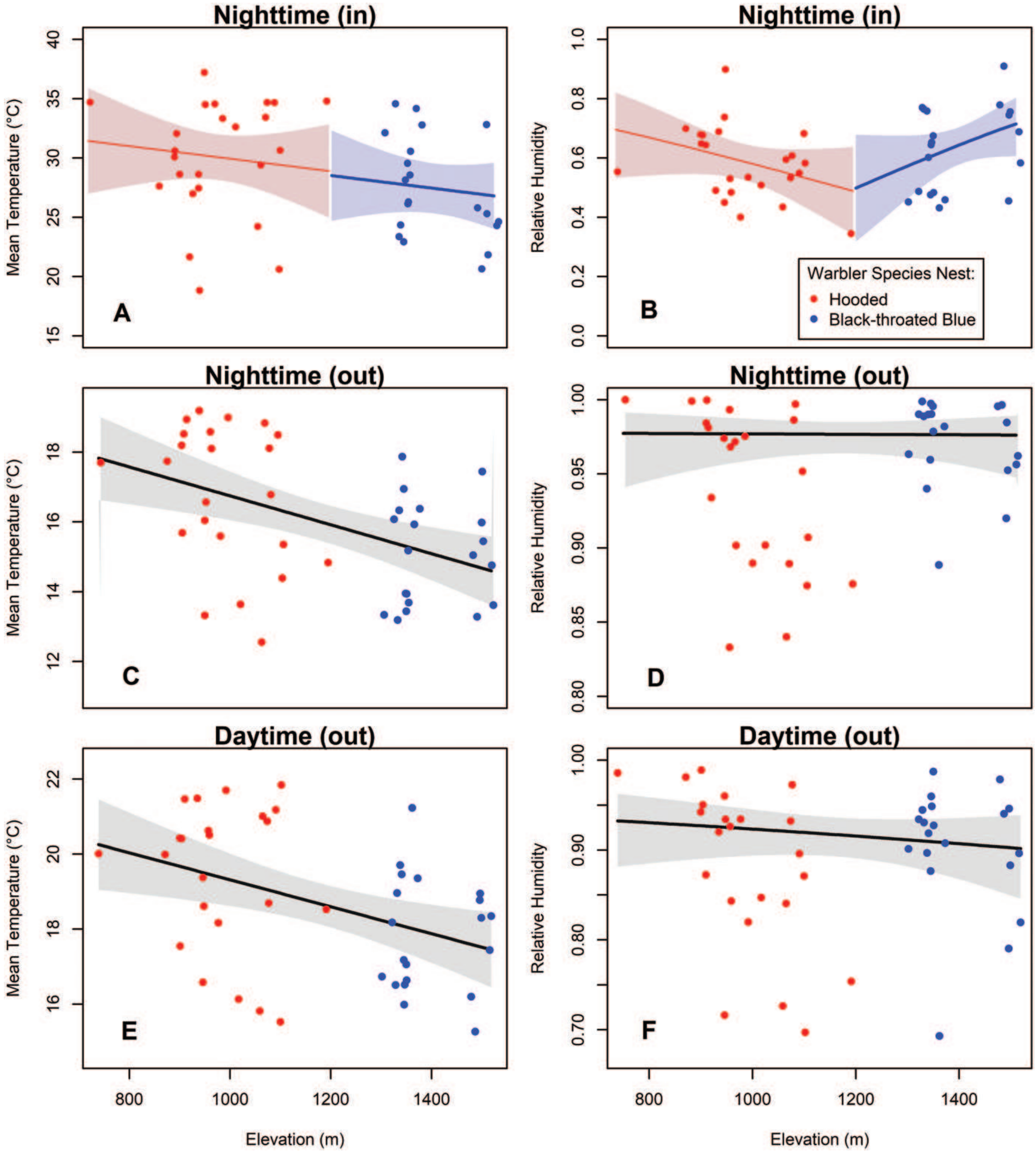

FIGURE 4. Hygrochron iButton measurements of mean temperature and humidity and linear model predictions inside (in) and outside (out) *S. caerulescens* and *S. citrina* nests over an elevation gradient in the Nantahala National Forest, North Carolina, USA. Panels (**A**) and (**B**) represent internal nest temperatures and thus have independent estimates for each species. Panels (**C–F**) represent external conditions and estimates are made across the available conditions. Shaded polygons are 95% confidence intervals.

of ambient humidity on *S. citrina* incubation bout duration was negative, decreasing by 0.05 min % humidity^{-1} (SE = 0.001, Figure 6C). The duration of off-nest bouts by each species was generally unaffected by ambient conditions but *S. caerulescens* spent more time off-nest in warmer conditions (Figure 6B). We detected no effect of ambient humidity on the duration of off-nest bouts for either species (Figure 6D).

Setophaga citrina nestling mass and growth rates were greater than the mass and growth rates of *S. caerulescens* nestlings regardless of brood size or treatment (Supplementary Material Figures 2A and 3A). Tarsal and wing chord growth from day 2 to day 6 varied by species, treatment, and brood size. Growth of these two characters in *S. citrina* nestlings raised in their native nest was greatest in small brood sizes and decreased

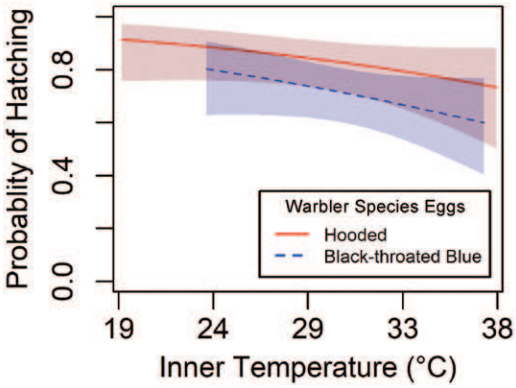

FIGURE 5. Probability of eggs hatching as a function of mean internal nest temperature while females were actively incubating for the trailing-edge *S. caerulescens* eggs and core *S. citrina* eggs in the Nantahala National Forest, North Carolina, USA. Lines are fitted values from generalized linear models including all nests with internal iButton data. Shaded polygons are 95% confidence intervals.

significantly in larger broods, but the opposite trend occurred when *S. citrina* nestlings were raised in *S. caerulescens* nests (Supplementary Material Figures 2B–C and 3B–C). *Setophaga caerulescens* nestlings showed little or no change in tarsal or wing chord growth regardless of which species reared them (Supplementary Material Figures 2B–C and 3B–C). In contrast, growth of nestling bill length (nares to tip) and depth varied by species and brood size but not by treatment. *Setophaga citrina* nestlings had longer and deeper bills than *S. caerulescens* nestlings and growth of both decreased with increasing brood size (Supplementary Material Figures 2D, F and 3D, F). Growth of nestling bill width did not vary by species or treatment but did decrease significantly at larger brood sizes (Supplementary Material Figures 2E and 3E).

DISCUSSION

Our experimental results are consistent with the hypothesis that a trailing-edge population of *S. caerulescens* is limited in part by physiological constraints that determine egg hatch rates. Specifically, we found that translocated *S. caerulescens* eggs hatched at a lower rate than control eggs when placed in nests in warmer conditions. However, for *S. citrina* near the core of its range, hatch rates were similar between eggs in translocated and control groups, indicating lower sensitivity to ambient conditions, as predicted by the abiotic range limitation hypothesis. Reported declines of trailing-edge songbird populations could therefore be partially attributed to a climate-driven reduction in hatch rates (White and Kinney 1974, Stoleson and Beissinger 1999, Conway and Martin 2000a, b, Sekercioglu et al 2008, Stodola et al. 2013, Sauer et al. 2015, Lundblad and Conway 2021, Lewis et al. 2022).

We found an effect of climate on *S. caerulescens* hatch rates, but the mechanism causing this effect remains uncertain. Ambient temperatures did differ between species' nest locations, potentially leading to a mismatch in ideal microclimate conditions (Webb 1987). However, temperatures inside nests were never high enough to result in embryo death (Conway and Martin 2000a, McKechnie and Wolf 2010, Lundblad and Conway 2021) and were not substantially different between nests of *S. caerulescens* and *S. citrina*. Hatch rates of both species were negatively associated with internal nest temperature. Internal nest temperature is determined by both ambient conditions and incubation behavior (Conway and Martin 2000a, Coe et al 2015), suggesting that warmer temperatures at lower elevations directly reduced *S. caerulescens* hatch rates, or warmer temperatures reduced hatch rates indirectly through differences in female incubation behavior at low elevations. Specifically, because *S. citrina* spend more time off the nest, translocated *S. caerulescens* eggs were exposed to warmer conditions for longer than they would have in their natal nests (Figure 6).

An alternative explanation is that reduced hatch rates were caused by translocating eggs to nests of another species. Because *S. caerulescens* is restricted to high elevations at our North Carolina study site, we could not fully control for the effect of the attendant species when translocating eggs to warmer, drier climates at lower elevations. Nonetheless, two lines of evidence suggest that changing attendant species should have little effect on hatch rates. First, the optimal temperature and humidity for eggs are the same for most species (White and Kinney 1974, Webb 1987, Conway and Martin 2000a). The optimal microclimate hypothesis therefore posits that almost any attendant species should provide suitable conditions for eggs *during* incubation. We found no difference between interior nest temperatures of *S. caerulescens* and *S. citrina* when females were incubating, implying that reduction in hatch rates of the trailing-edge eggs was attributable to higher ambient temperatures at lower elevations. Second, *S. citrina* eggs were not negatively affected when translocated to *S. caerulescens* nests. If egg viability depended on the attendant species, then *S. citrina* eggs should have failed at higher rates when moved to *S. caerulescens* nests. In addition, we found that as internal nest temperatures increased, hatch rates decreased for both species, implying that the *S. citrina* eggs would not be negatively affected by the relatively cooler, ambient conditions in *S. caerulescens* nests.

The optimal microclimate hypothesis predicts that all species will adapt behavior to local climate to achieve optimal nest conditions, to the extent possible while meeting the constraints imposed by foraging requirements. Thus, we believe that *S. caerulescens* would have had different incubation behavior if they occurred at lower elevations. We speculate that, in warmer conditions, *S. caerulescens* eggs in *S. citrina* nests may have been unable to cool sufficiently to avoid excessive water loss due to higher temperatures but not a difference in relative humidity. An essential component of incubation behavior is balancing temperature and humidity conditions in the nest to optimize water-loss by altering the duration of incubation and off-nest (primarily foraging) bouts in response to ambient conditions (Rahn et al. 1976, Rahn et al. 1977, Morgan et al. 1978, Rahn et al. 1979, van der Pol et al. 2013, Portugal et al. 2014, Ar and Rahn 2015). Water loss and gas exchange through eggshell pores can affect hatch rates and may explain why eggs of the trailing-edge population of *S. caerulescens* failed to hatch in warmer conditions (Rahn et al. 1976, Rahn et al. 1977, Morgan et al. 1978, Ar and Rahn 2015). Females of each species displayed different incubation behaviors, with *S. citrina* females spending relatively more time incubating eggs. Additionally, only *S. citrina* females increased duration of incubation bouts with warmer ambient temperatures. This finding is consistent with previous studies showing that experimentally heating nests leads some female birds to spend more time incubating their eggs because they are

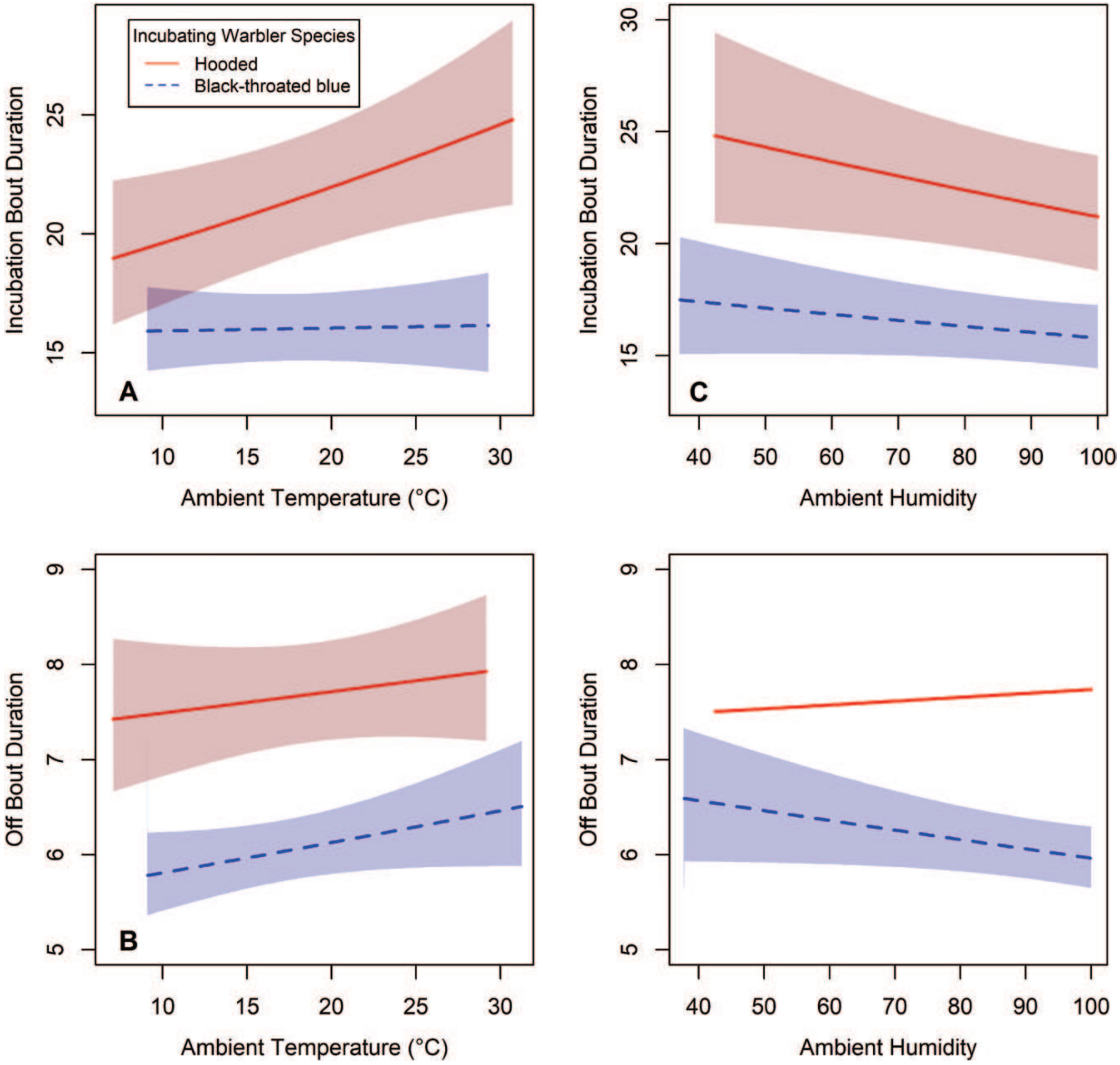

FIGURE 6. Effects of ambient temperature (**A–B**) and humidity (**C–D**) on incubation bout duration (minutes) and off-nest bout duration for *S. citrina* and *S. caerulescens* in the Nantahala National Forest, North Carolina, USA. Shaded polygons are 95% confidence intervals.

less constrained by the energetic cost of keeping eggs warm (Bryan and Bryant 1999, Ardia et al. 2009). *Setophaga caerulescens*, however, did not increase or decrease the duration of their incubation bouts with temperature. These different behavioral responses to ambient conditions may have resulted in a mismatch in water loss and gas exchange rates for eggs laid for different climate conditions. Because incubation behavior is a response to ambient conditions, these same ambient conditions act on the physical properties of the egg when the female is away from the nest.

Nestlings that hatch from swapped eggs had inconsistent but altered growth rates compared with those in their natal nest. Nestlings developing in suboptimal climate conditions often experience altered growth rates (McCarty and Winkler 1999, Dawson et al. 2005, Ospina et al. 2018). Generally, this manifests as a trade-off between development and thermoregulation, with nestlings growing larger in warmer, but not extreme, conditions (Murphy 1985, Larson et al. 2015). In addition, thermoregulation can depend on brood size, with individuals in larger broods generally growing larger faster because of better heat retention (Royama 1966, Seel 1969, Dunn 1976, Clark 1982, Johnson and Best 1982). We predicted that nestlings of the trailing-edge *S. caerulescens* population would grow faster in warmer conditions; however, of the nestling growth measurements, only tarsus and wing lengths of *S. citrina* nestlings changed in response to the translocation treatment. *Setophaga citrina* nestlings had shorter tarsi at larger brood sizes in their native nests and longer tarsi at larger brood sizes in translocated nests. A positive association between tarsus length and brood size has been found in other species, likely because larger broods lose less heat from the nest, making longer tarsi beneficial for thermoregulation

(Ross 1980, Murphy 1985, Rodríguez and Barba 2016). Nestling development depends on many factors including ambient conditions, parental care strategies, food availability, etc. and the response of nestlings to changing ambient conditions deserves more attention given its complexity. Specifically, altered nestling growth rates can affect an individual's future ability to survive, disperse, and successfully reproduce with unknown consequences for trailing-edge populations facing increasing global temperatures (Parmesan and Yohe 2003, Parmesan 2006, William and Blois 2018, Sauve et al. 2021).

Our prediction that relative humidity at nest locations increases with the well described precipitation gradient at our study site was not supported by data collected by hygrochron iButtons (Swift et al. 1988, Daly et al., 2008, Merker and Chandler 2021, Gaya et al. 2024). One explanation for this is the strong association of both *S. caerulescens* and *S. citrina* to nest in the shrub layer (Chiver et al. 2020, Holmes et al. 2020). Both species commonly build nests in Rhododendron (*Rhododendron maximum*), which grows primarily in wetter areas near streams and seeps at our study site across all elevations (Dobbs 1995, Chastain and Townsend 2008). Because of this, relative humidity at nest sites for both species may be higher on average than other locations at similar elevations. However, a better understanding of how relative humidity changes with elevation, topography, and whether southern Appalachian Mountain birds select more humid nesting locations is needed.

In conclusion, we found support for the hypothesis that the southern breeding range limit of a Neotropical migratory songbird is influenced by climate effects on reproductive biology. Our study represents an initial attempt to broadly determine how species at their trailing edge range boundary will respond to encroaching climate conditions immediately outside of the range. We further demonstrate that field egg translocation experiments are a viable approach to investigating this hypothesis. Although we demonstrated that hatch rates declined in a trailing-edge population when eggs were moved to a warmer environment, we were unable to identify the precise mechanism responsible. Because a reduction in hatch rates could have population-level effects, more information on eggshell structure, nest microclimate, and nestling development is needed to predict how trailing-edge populations will respond to changing environmental conditions (Pereyra and Morton 2001, Stein and Badyaev 2011, Higgott et al. 2020, Sauve et al 2021). Nest architecture and the link between nest architecture and nest microclimate are further avenues that merit attention (Rowher and Law 2010, Mainwaring et al. 2014). Future work manipulating temperature and humidity inside the nest while monitoring water loss, gas exchange, and embryo development would also help identify the effects of abiotic factors and climate change on reproductive physiology (Bryan and Bryant 1999, Ardia et al. 2009, van der Pol et al. 2013, Higgott et al. 2020). Regardless of the mechanism, our findings, in conjunction with the anticipated continued increase in global temperatures and extreme weather events, have implications for the fate of trailing-edge populations. If eggs (and nestlings) are adapted to cooler conditions, as suggested by our study, then climate change could lead to population declines and accelerated range shifts by directly reducing the fitness of breeding birds (Parmesan and Yohe 2003, Parmesan 2006, William and Blois 2018, Sauve et al. 2021).

Supplementary material

Supplementary material is available at *Ornithology* online.

Acknowledgments

We would like to thank the many graduate students and field technicians who found and monitored nests in North Carolina. Thanks to Drs. Nicole E. Krauss and Sonia M. Hernandez for comments and thoughts on egg physiology. We would also like to thank the editors and anonymous reviewers for their constructive feedback.

Funding statement

Funding was provided by National Science Foundation grant DEB-1652223, and a USDA McIntire-Stennis grant to the Warnell School of Forestry and Natural Resources. Funding for hygrochron sensors was generously provided by the Georgia Ornithological Society through a Bill Terrell Graduate Research Grant.

Ethics statement

All handling of nestling birds was kept to a minimum and no birds were harmed during the experiment. Our experiment was approved by the University of Georgia Institutional Animal Care & Use Board. Egg collection and capture of adult birds in the field were approved by federal and state permits.

Conflict of interest statement

No conflicts to declare.

Author contributions

R.B.C., S.A.M., and T.S.S. conceptualized the experiment. R.J.C and T.S.S. provided feedback on design and analysis. S.A.M. conducted the experiment, collected the data, performed the analysis, and wrote the first draft of the manuscript; BGF contributed significant edits. All authors contributed to revisions and gave final approval for publication.

Data availability

Analyses reported in this article can be reproduced using the data provided by Merker et al. (2025).

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